DFID R Number: NRE9800 605/522/001A

Caribbean Marine Protected Areas Project: The Role of Marine Protected Areas in Fisheries Management and Biodiversity Conservation in Coral Reef Ecosystems

Final Technical Report
to the
United Kingdom Department for International Development

PEOPLE • SCIENCE • ENVIRONMENT • PARTNERS
ICLARM
THE WORLD FISH CENTER

Executed by:
International Center for Living Aquatic Resources Management
Caribbean/Eastern Pacific Office,
158, Inland Messenger Service,
Road Town, Tortola,
British Virgin Islands.
Tel: (1-284) 495 1291
Fax: (1-284) 495 1389
e-mail: ICLARM-CARIBBEAN@cgiar.org
Project Leader: Dr. John L. Munro
e-mail: j.munro@cgiar.org

Collaborators:
Discovery Bay Marine Laboratory, Centre for Marine Sciences, University of the West Indies, Jamaica
Department of Marine Studies, H.L. Stoutt Community College, Tortola, British Virgin Islands
McLean Marine Science Centre, St. Thomas, U.S. Virgin Islands
Conservation and Fisheries Department, Road Town, Tortola, British Virgin Islands

Start Date: 1 January 1999 **End Date:** 31 December 2001 **Budget:** £600,000

Executive Summary

The purpose of this project has been to address the issue of decreased catch rates and declining income per unit of fishing effort in Jamaica's artisanal fisheries. This is an issue that is not unique to Jamaica. It is faced by fishers in most of the countries surrounding the Caribbean. The absence of any significant fisheries management, combined with excessive population densities and a lack of employment opportunities, has led to increasing fishing effort in Caribbean coastal fisheries, resulting in recruitment and growth overfishing. Decreased catches are shared by ever-increasing numbers of fishers. The goal of the project has been to generate improved and sustainable livelihoods for communities dependent on coral reef fisheries in target areas by devising strategies for improved management of coral reef resource systems, including the use of marine protected areas.

Research activities included comparative socio-economic and biological surveys of commercial fisheries in the British Virgin Islands and in Jamaica, studies of comparative recruitment rates of coral reef fish and systems for small-scale aquaculture based on the capture of pre-settlement reef fish. Rectangular escape gaps were evaluated as a management tool for Antillean trap fisheries. Changes in the stocks of fish in the Discovery Bay Fisheries Reserve in Jamaica were monitored for 62 months following its declaration and ecotrophic models were developed for Discovery Bay and for Hans Creek, a proposed marine protected area in the British Virgin Islands.

It was shown that the adoption of rectangular or diamond-shaped escape gaps, that release slender deep-bodied fish, would significantly reduce the effects of overfishing in Caribbean reefs. Progressive increases in total harvests of about 42% are possible on the north coast of Jamaica, probably accompanied by even larger increases in the value of the trap catch and improvements in harvests of spear and hook-and-line fisheries as a result of improved recruitment rates.

Caribbean reef fisheries are probably largely dependent upon local spawning stocks for their replenishment and recruitment has collapsed in overexploited areas such as Jamaica. Many species are locally extinct. Consequently, the accumulation of a significant spawning stock biomass in newly created fisheries reserves will be a very lengthy process and beneficial effects will be limited in the short term. This might be remedied by restocking reserves with fry of selected species. However, fishery reserves need to be part of an integrated management scheme supported by the fishing community and by other stakeholders.

Inexpensive light traps and aquaculture systems have been developed that might be used for capturing and rearing pre-settlement reef fish or invertebrates, either for restocking fishery reserves or to provide alternative livelihoods.

The ecotrophic models that were developed using Ecopath-with-Ecosim provide a baseline for monitoring changes in the Discovery Bay and Hans Creek ecosystems and can be integrated into ecosystem based management systems for the Discovery Bay fishery.

Background

Reef fisheries are in a state of decline in most parts of the Caribbean, either because of overfishing or because of environmental degradation. Large apex predators, such as groupers and snappers, have become virtually extinct in many fisheries and the composition of the catch has shifted steadily towards larger proportions of herbivorous species. In many countries, increasing numbers of fishers, driven by unemployment to this occupation of last resort, share a smaller and less valuable catch.

In one of the worst cases known, massive algal overgrowth of the coral reefs on the north coast of Jamaica has resulted in severe loss of biodiversity and disruption of the ecosystem. This appears to have been triggered by the Caribbean-wide die-off of the herbivorous long-spined sea urchin (*Diadema antillarum*) in 1984. Because of heavy fishing, the biomasses of herbivorous fishes in Jamaica were too low to control the algae (Hughes 1994). This did not occur elsewhere in the

Caribbean where fisheries were less intense. There is some evidence that stocks of *D. antillarum* are starting to recover at various locations in the Caribbean, including Jamaica. This is leading to a degree of recovery of the coral reefs in Jamaica (Edmunds and Carpenter 2001). However, data collected in Jamaica during the past few years show drastic declines in the biodiversity of the fish community (Klomp et al., in press). This is attributed to the collapse in recruitment of some species and the current unavailability of habitat for others. Without active management, any recovery could take an extremely long time.

ICLARM has undertaken fisheries research on the north coast of Jamaica since mid-1996, in collaboration with the Centre for Marine Sciences of the University of the West Indies (CMS/UWI). CMS/UWI has operated a Fisheries Improvement Project (FIP), based at its Discovery Bay Marine Laboratory, for the past thirteen years at varying levels of effort. This project concentrates on improving the lot of the fishing community and currently has a full-time Education Officer. ICLARM has provided technical inputs to FIP on a continuing basis.

The Discovery Bay Fisheries Reserve was created in November 1996 by the Alloa Fishermen's Co-operative Society, with assistance from FIP (Woodley et al., in press). It is comprised of 27 ha of backreef and seagrass beds, with a few patches of live coral, is mostly less than 2 m deep and serves principally as a nursery habitat for coral reef fish. Despite much effort, the reserve currently has no legal status and remains an assertion of the right of fishers to govern the area in which they fish. Partly in response to the findings of ICLARM research programmes (see below) the fishers in the bay have asked for all of the shallows of Discovery Bay to be proclaimed a fisheries reserve and there are indications that progress is now being made on the legal aspects of this matter.

Between 1996 and 1998 ICLARM made a comparison of catch rates in light traps and small fish traps in Jamaica and in the British Virgin Islands (BVI), where the fishery is relatively lightly exploited (Watson and Munro, in review). This showed that the abundances of commercially-important fish settling from the pelagic zone and of juvenile reef fish was usually two to three orders of magnitude greater in BVI. Some species appear to be virtually extinct in Jamaica. The only species that are common in Jamaica are those that are known to have a specialized post-larval phase that is able to survive extended periods in the pelagic zone or small species, which mature before they are recruited into the wire-mesh fish traps. These findings suggested very strongly that Jamaica is isolated from external sources of recruits to its fisheries and is reliant on the progeny of local breeding stocks. However, mature fish of all of the larger and more valuable species are alarmingly rare in Jamaican waters and it is quite likely that over-fishing with non-selective fish traps is progressively exterminating the most vulnerable species of commercially important reef fish. The findings also suggested that fisheries reserves created in such overfished areas will take many years to accumulate spawning stocks of any significant size and that restocking strategies for important species will be an essential adjunct to the development of fisheries reserves.

The sampling programme in BVI showed that pre-settlement reef fish mostly reach the reefs around new moon and that most fish species, with the exception of groupers, settle in the summer months. Most species use the mangroves, sea grass beds and back reef areas as nursery grounds, but few juveniles of commercially important species are to be seen on the fore-reef. There is great variability between sites and some sites appear to be of major importance as nursery areas.

With a view towards restocking strategies, a technique for rearing post-settlement reef fishes was tested in BVI using several species of snappers, with promising results. The pre-settlement snappers, about 1 cm long, were captured in light traps and reared in floating mesh cages. They were fed by attracting zooplankton into the cages at night using solar powered lights and grew rapidly to 4-5 cm total length. This raised the possibility of using this technique to enhance recruitment rates to newly-created fishery reserves by catching pre-settlement fish and rearing them through the vulnerable early months when, under natural conditions, almost 100% of post-settlement fish are consumed by predators (Watson et al. 2000). Additionally, there is the possibility of using such a system to as a form of small-scale aquaculture (particularly in the aquarium fish industry, where development of sustainable collection techniques is an international concern). If successfully developed, such techniques would have global applicability.

A short study of the social and economic factors underlying the successful creation of the Discovery Bay Fishery Reserve in Jamaica strongly underlined the need for continuing education and information programmes if co-management is to be successful. Although fishers had diverse views on acceptable management strategies there was widespread agreement that juvenile and undersized fish should be protected (Parchment 1998). This undoubtedly accounts for their willingness to ban fishing from all of the shallow areas of Discovery Bay and suggests that a general ban on fishing in shallow back reef areas might be an acceptable strategy.

Changes in the relative abundances of reef fish have been monitored, using 1"-mesh double arrowhead fish traps set in shallow seagrass and back-reef areas, following creation of the Discovery Bay Fishery Reserve in November 1996. Several species have shown significant increases in abundance that may be attributable to the protection afforded by the reserve and may be developing additional spawning stock biomass.

Between December 1996 and May 1998, a total of 6,949 coral reef fish were marked and released within the Discovery Bay Fishery Reserve. Nearly 6,000 recaptures were obtained (including multiple recaptures of the same individuals). Most recaptured fish were caught in the project's traps, fishing within the fishery reserve, measured and re-released. Fishers operating in adjacent areas captured and returned 295 marked fish. This mark-and-recapture program showed that some species remain resident in the reserve for extended periods. Other species move out of the reserve with increasing size and two species of parrotfish moved substantial distances (tens of km) along the narrow northern shelf of Jamaica (Munro 2000). Based on distances moved by marked fish, it was suggested that reserves should ideally cover 10 km of coastline. Given the intensity of exploitation of the shelf, this would be difficult to implement without developing alternative occupations for fishers. Reserves are needed in all areas but it seems likely that reserves at the eastern, up-current, end of the island would be beneficial in distributing larvae to other parts of Jamaica.

Results showed that the Discovery Bay Fishery Reserve is effective in delaying recruitment of some species and in increasing spawning stock biomass of those species that take up residence in the Reserve. The delay in recruitment to the fishery reduces growth overfishing to some degree and increases the average size of fishes in the catch.

Estimates of growth parameters have been obtained for 15 species of reef fish using the mark and recapture data. Most of these parameters were previously unknown. The cumulative length-frequency distributions of 13 species of fish measured in the Discovery Bay Fishery Reserve since its inception have been used, in combination with growth parameters, to derive length-converted catch curves and to estimate rates of mortality and outmigration.

References

Edmunds, P.J. and R.C. Carpenter. 2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proc. Nat. Acad. Sci. 98:5067-5071.

Hughes, T.P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547-1551.

Klomp, K.D., K. Clarke, K. Marks, M. Miller. in press. Condition of reef fish on Jamaica's north coast signals late stages of overexploitation. Proc. Gulf Caribb. Fish. Inst. 54:

Munro, J.L. 2000. Outmigration and movement of tagged coral reef fish in a marine fishery reserve in Jamaica. *Proc. Gulf Caribb. Fish. Inst.* 51: 557-568.

Parchment, P. 1998. 'Co-management' and contradiction: A case study of fishery reserve management in Discovery Bay, Jamaica. Research Paper, submitted in partial fulfillment for the Degree of Master of Science in Development Studies, University of the West Indies, Jamaica.

Watson, M. and J.L. Munro. Comparative settlement and recruitment rates of coral reef fishes in moderately exploited and overexploited Caribbean coral reef ecosystems: their relevance to marine protected area design and management in Jamaica. Submitted to *Bulletin of Marine Science*.

Watson, M., R.M. Power and J.L. Munro. 2000. Use of light-attracted zooplankton for rearing post-settlement coral reef fish. *Proc. Gulf Caribb. Fish. Inst.* 52:340-351.

Woodley, J.D., Z. Sary, P. Gayle, W. Lee, P. Parchment and L. Walling. The Discovery Bay Fisheries Reserve, Jamaica. *Proc. Gulf Caribb. Fish. Inst.* 54:

Project Purpose

The stated goal of the project has been to generate improved and sustainable livelihoods for communities dependent on coral reef fisheries in target areas by devising strategies for improved management of coral reef resource systems, including the use of marine protected areas.

The purpose of this project has been to address the issue of decreased catch rates and declining income per unit of fishing effort in Jamaica's artisanal fisheries. This is an issue that is not unique to Jamaica. It is faced by fishers in most of the countries surrounding the Caribbean. The absence of any significant fisheries management, combined with excessive population densities and a lack of employment opportunities, has led to increasing fishing effort in Caribbean coastal fisheries, resulting in recruitment and growth overfishing. Decreased catches are shared by ever-increasing numbers of fishers.

Research Activities

Socio-economics of the BVI fishing industry and of the Discovery Bay fishery

A study of the economics of the commercial fishery in BVI was undertaken to estimate the value of the fishery, to the fishers and to the BVI economy. The BVI situation is one in which substantial marine resources are shared by a relatively small number of artisanal fishers and stands in marked contrast to the fisheries in Jamaica. The BVI study was based on a programme of structured interviews with fishers. A questionnaire was designed concerning catch rates and fishing grounds and other socio-economic data. With assistance from the BVI Conservation and Fisheries Department 109 fishers were interviewed out of a known total of 174 fishers. A database (MS-Access) was developed for storing and analyzing the data so collected.

A one-year survey of the fishery at Discovery Bay and adjacent areas was executed in collaboration with the Centre for Marine Sciences of the University of the West Indies. A relational database was designed for data compilation and a catch sampling programme launched that lasted a full year, from mid-July 2000. An inventory of fishers, boats and fishing gear was made and updated on a continuous basis. The survey covered five fishing beaches; Rio Bueno in the west, Old Folly and Top Beach in Discovery Bay and Runaway Bay and Salem to the east of Discovery Bay. This represents about 22 km of coastline and 12 km^2 of the shelf exploited by 130 fishers.

Settlement and recruitment of reef fish

Light traps were used to monitor settlement rates of commercially important reef fish from April to September in 1999 and 2000 at three sample stations. Additionally, a comparative study was made of settlement rates around Tortola and in the waters around St. Thomas, U.S. Virgin Islands. This was done in collaboration with colleagues at the MacLean Marine Science Center of the University of the Virgin Islands.

New designs of inexpensive light traps were successfully tested. A light-sensitive switch for the traps was developed that automatically switches on the lights each evening, substantially reducing expenditures on fuel and saving much time.

Crest nets, which filter pre-settlement fish from the flow over reef crests, were tested at several locations in BVI in 1999 and 2000. They were also used in narrow channels between islands.

The programme for monitoring recruitment rates of reef fish, using small 1.2 cm mesh mini-traps, terminated in March 2000, giving a continuous record for 33 months in Tortola and for 42 months in Discovery Bay.

Escape gaps for fishery management

An investigation of the possible use of escape gaps in Antillean fish traps was undertaken during 2000 and 2001, at Discovery Bay in Jamaica and in the more productive waters of BVI. One escape gap size was tested against control traps in Jamaica and three gap sizes were tested against controls in BVI. Morphometric data (length, weight, body depth and body width) were collected for all of the commercially important species.

Aquaculture and stock enhancement

A simple flowing seawater system was designed and installed to maintain three tanks on shore. A light source plankton attractor and an airlift pump were built to supply plankton rich water to floating sea cages or to on-shore tanks.

Plankton samples from the experimental pump were collected at new and full moon periods each month for 18 months to monitor variability in supply.

Pre-settlement reef fish were captured in light traps and crest nets. However, recruitment failures in 1999 and 2000 meant that planned work on rearing snappers could not be undertaken on a large scale and work focused on a variety of ornamental species.

A study was made on mortality rates of newly settled snappers in sea-grass beds.

Monitoring changes in the Discovery Bay Fisheries Reserve

A programme for monitoring stocks in the Discovery Bay Fisheries Reserve, started at the inception of the reserve in November 1996, continued throughout the project, giving a 62-month record of developments. Fish are captured in a set of 15 25 mm (1") mesh double-arrowhead traps that are hauled twice per week. The fish are measured and released. The UWI Fisheries Improvement Programme will continue this work, after the end of this project.

Ecotrophic modelling

Quantitative surveys of the plants, invertebrates and fish in the Hans Creek, BVI and Discovery Bay, Jamaica, ecosystems were undertaken on a quarterly basis over a full calendar year. Aerial photographs were obtained and, with assistance from the GIS unit operated by the BVI Conservation and Fisheries Department, the habitats were mapped.

All data were entered into a custom designed database and simple Ecopath models were developed.

Outputs

According to the Project Logical Framework, the following outputs were expected:

- Assessment of suitability of different targeted coastal areas to act as MPAs (subject to different states of degradation, fishing pressure and possible supply of juvenile recruits).
- Management advice based on knowledge of ecotrophic interaction of reef fish communities in areas affected by different levels of fishing pressure, recruitment and habitat degradation.
- Management advice based on improved fishing gear and practices for the maximization of sustainable yield within and adjacent to MPAs.
- Demonstration of the feasibility for using trapping and grow out methods to sustainably enhance stocks of reef fish.

Socio-economics of the BVI fishing industry and of the Discovery Bay fishery

The value of the BVI fishery in 1998 was estimated at $6.65 million (Pomeroy 1999). The average gross annual income per boat was in excess of $38,000, less operating costs of $7,300 and depreciation of equipment. Depreciation was not estimated in the survey but would probably be around $1,500/year. The average annual income of all fishers and crew members (45% of whom are part-time operators) was $17,780. These figures are illustrative of the value of a fishery that is not greatly overexploited (Table 1).

A year-long survey of the artisanal fishery in the Discovery Bay area was completed in July 2001 (Sary, 2001). The 12 km^2 area of coralline shelf is currently producing a harvest of about 60 metric tons per year and supporting the livelihoods of 130 fishers and an additional 500 dependents (Table 1). The harvest rate of 5 tons per km^2 per year is very high and appears to have declined by 13% in weight and 17% in value (at 2001 prices) since a 1968 survey. However, trap catches in 2000-01 seem to be unchanged relative to surveys in 1996 and 1997 (Sary et al, in press). Fishers with motorized boats averaged a gross income of $5,400 per year, but those without motors earned about US$1,400 per year (Sary et al. in press).

Table 1. Contrasting fisheries: A comparison of catch rates and incomes from fishing in the British Virgin Islands and in the Discovery Bay area on the north coast of Jamaica.

	British Virgin Islands (1998)	Discovery Bay, Jamaica (2000-01)
Number of fishers	374	130
Number of boats in the fishery	174	95
Area of fishing grounds (km^2)	3130	12
Fishers/km^2	0.12	10.8
Boats/km^2	0.06	7.9
Total catch (kg)	819,000	60,800
Total value of catch (US$)	6,650,000	300,000
Catch (kg)/km^2	260	5,070
Value (US$)/km^2	2,125	25,000
Gross $/boat/yr	38,200	3,160
Gross $/fisher/yr	17,800	2,300

We estimated that the compounded loss as a consequence of non-management of the fishery in the vicinity of Discovery Bay over the past 25 years amounts to US$6.4 million for this 12 km^2 area of shelf. If this is estimate is extrapolated to the entire narrow northern, eastern and western shelves the loss is $375 million and if further extrapolated to cover the entire island shelf, the cumulative loss is about $1.3 billion (Sary et al. in press).

Settlement and recruitment of reef fish

The work with light traps demonstrated the extreme variability of recruitment processes on a local and inter-island scale. Two years of heavy settlement of snappers around the eastern end of Tortola in 1998 and 1999 was followed by much diminished recruitment rates in 2000 and 2001(Watson and Munro, in prep.). Further, comparative studies of reef fish settlement around Tortola and St. Thomas, U.S. Virgin Islands, in 2000 and 2001 showed significant differences in the relative abundances of different groups and in the catch compositions in light traps (Watson and Nemeth, in prep.), demonstrating that recruitment events are mediated at a local scale.

The results suggest strongly that attempts to determine preferred locations for fishery reserves or marine protected areas on the basis of the comparative supply of pre-settlement reef fish are based on a false premise. The suitability of a site for supporting a substantial spawning stock biomass should be one of the main criteria. There is a growing body of evidence that inter-island exchange of propagules is the exception rather than the rule and that most recruits will originate from local spawning and that where spawning stocks are seriously depleted, recruitment rates will also be seriously decreased. Under such circumstances the build-up of biomass in newly created fishery reserves will be slow and restocking programmes will be needed to establish spawning stocks within a reasonable timeframe.

Several inexpensive light trap designs were developed and tested (Watson et al. in press). Testing the comparative efficiency of these traps was difficult because of large variation between identical traps set a few hundred meters apart, and because of variation between nights. However, all traps caught fish and the most robust of the new designs caught as many fish as the standard light traps.

Despite successes in the Pacific, crest nets do not appear to be promising tools in the Caribbean region, either for monitoring recruitment or for providing pre-settlement fish for aquaculture or stock enhancement (Watson and Power, 2001).

Escape gaps for fishery management

An investigation of the possible use of escape gaps in Antillean fish traps was undertaken during 2000 and 2001, at Discovery Bay in Jamaica and in the more productive waters of BVI. One rectangular escape gap size was tested against control traps with 25 mm (1") mesh in Jamaica and three rectangular gap sizes were tested against controls in BVI.

Morphometric data (length, weight, body depth and body width) were collected for all of the commercially important species. Over 7000 fish were measured and relationships between body depth and width and fish length were established for 26 species. The theoretical minimum sizes retained by a variety of mesh sizes and escape gap dimensions were determined.

The research showed that undersized fish moved freely out of escape gaps but that the catchability of larger individuals was not reduced. That is, the fishing power of the traps was not reduced. The effect of the introduction of progressively larger escape gaps was calculated for the 21 species that currently comprise 80% of the trap catch in the vicinity of Discovery Bay, Jamaica. It was estimated that the trap catch would be increased by around 42% if 100 mm x 40 mm escape gaps were introduced (Fig. 1) (Munro et al. in press). Escape gaps would also allow many species to reach maturity before recruitment. Consequently, recruitment rates might be expected to improve. The spear and hand line fisheries would also benefit. It was recognized that diamond-shaped escape gaps might give even better results by adding body shape as an additional controlling dimension.

Aquaculture and stock enhancement

A simple flowing seawater system was designed and installed to maintain three tanks on shore and floating sea cages were built for use in rearing pre-settlement fish caught in light traps and crest nets. The sea cages were made by a local sailmaker, using 3.2 mm (1/8th inch) plastic mesh sewn on an industrial machine and were fitted with a large plastic zip. The cages do not need an internal frame, which can sometimes trap fish. They are also easy to open for counting and measuring the fish.

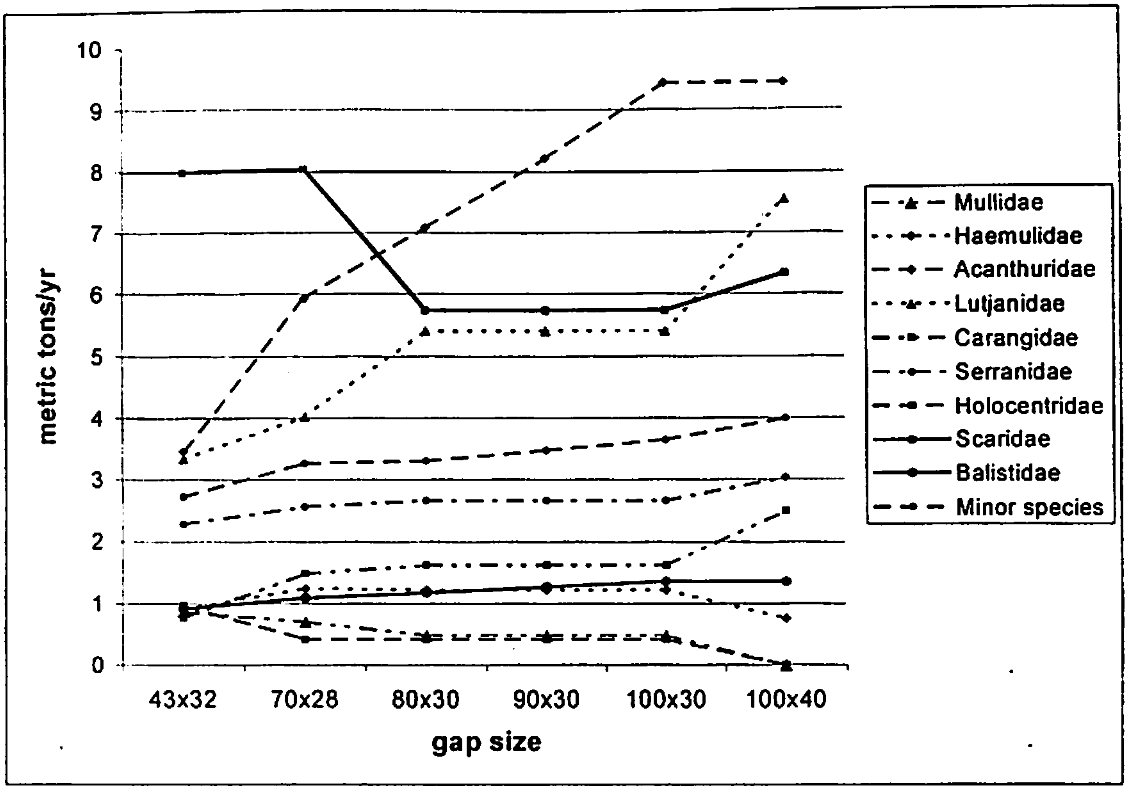


Figure 1. Suggested strategy for the introduction of escape gaps to the Discovery Bay fishery, in which a gap size of 70x28 mm is initially introduced, followed by 80x30 mm. Thereafter, gap width is held at 30 mm while gap heights are progressively increased to 100 mm. Thereafter gap width could be progressively increased to 40 mm. The calculated increase in the trap catch is 42%, accompanied by an even greater increase in value.

Building on previous work in this area, a light source plankton attractor with an 'air lift' pump was designed and constructed. This supplies plankton rich water to floating cages or to on-shore tanks (Power and Watson, in review). The system was successfully used to rear Yellowtail snapper (*Ocyurus chrysurus*), Lane snapper, *Lutjanus synagris,* and a variety of ornamental species (Watson and Power, 2001). Snappers showed good growth rates and mortality in cages was not density dependant over the range investigated. A fairly constant percentage appeared to die initially, possibly due to handling stress, after which mortality rates declined to low levels.

A study of the mortality rates of newly-settled Yellowtail snapper, *Ocyurus chrysurus*, showed very high rates of mortality after settlement that progressively decreased over time. Estimated survival after 30 days varied between 4% and 20%. These values do not include deaths during the process of settlement and show that capturing pre-settlement fish, rearing them for around 30 days and releasing them might be a viable strategy for enhancing recruitment to fishery reserves in over-exploited areas (Watson et al. in review).

Monitoring changes in the Discovery Bay Fisheries Reserve

The programme for monitoring changes in the biomass of fish stocks in the Discovery Bay Fishery Reserve using 2.5 cm mesh traps continued from November 1996 to December 2001, giving a 62 month record since its inception. Present indications are that stock biomasses are increasing very slowly, probably because of recruitment limitation but also because the reserve is essentially a nursery area and many species migrate out of the reserve with increasing age and size Munro and Power, in prep.). The programme might need to be expanded if the proposed expansion of the Reserve to encompass all of Discovery Bay becomes a reality. The data gathered in the monitoring also provide material for measuring recruitment, growth and mortality rates and hence for stock assessments (Munro, in prep 2,3) and the Ecopath modeling programme. The Discovery Bay Marine Laboratory is continuing the monitoring programme.

Ecotrophic modelling

Ecotrophic models were constructed for the Discovery Bay and Hans Creek ecosystems. The accumulated data and models have been compiled on CD-ROMs to provide easily accessible baseline data against which to judge future management efforts. As expected, the models show great differences between the two ecosystems that can be attributed to the heavy fishing at Discovery Bay (Williams and Munro, in prep.).

Educational linkages

The project established a number of linkages with universities and benefited from the active involvement of post-graduate students in aspects of the research. Mr. Peter Parchment, a Jamaican citizen, gained a M.Sc. degree from the University of the West Indies, based in his study of the attitudes of fishers at Discovery Bay to possible management interventions. Ms. Annalie Morris, a permanent resident of BVI and a D.Phil. candidate with the University of York, undertook a preliminary project on the trophic ecology of juvenile snappers. Additionally, the project hosted York University M. Res. candidates, Mr. Stephen Simpson and Ms. Gilda Hassidis, between June and September, 1999. Mr. Simpson worked on alternative light trap designs and Ms. Hassidis on the ecology of juvenile snappers. Ms. Vanessa Bertenshaw, of Plymouth University completed a M.Sc. thesis on the ecology of juvenile Yellowtail snapper, *Ocyurus chrysurus,* and Mr. Robert Power is nearing completion of a M.Sc. thesis for Plymouth University. The title of his thesis is "Coral reef regeneration: an approach based on rearing settlement stage fish". Ms. Gale Persad, a Ph.D. candidate at the University of the West Indies, is currently studying the trophic relations of the pelagic ecosystem of Discovery Bay, Jamaica, which also relates to the work of the Project.

Contribution of Outputs

It is clear from the contrasting reports on the coral reef fisheries in BVI and in Discovery Bay, Jamaica, that Caribbean coral reefs, are capable of producing substantial incomes for individual fishers when lightly exploited and that, even in a degraded state, they are capable of producing harvests in excess of 5 metric tons/ km^2, a point that has not always been accepted. While Jamaica presents a worst-case scenario, the story of overfishing of reef resources is repeated to varying degrees throughout the Caribbean.

There is evidence from Jamaica of a continuing decline in the quality of the catch in terms of size of fish and of value that can only be arrested by active management of the fishery at the community level. Protection of shallow nursery areas appears to be a readily acceptable management approach but gaining acceptance of the idea of protecting entire tracts of coralline shelf, from the shallows to a depth of 200 m is a much more difficult proposition, simply because of the intensive use of the reef in many countries. The introduction of escape gaps in Antillean fish traps has been shown to be one possible solution to the decline in quality and size of catches.

It seems likely that an approach that combined the introduction of escape gaps with the concept of additional management measures, such as fishery reserves, could succeed when undertaken on a consultative basis at the community level. In the countries with the highest degrees of unemployment and the greatest over-use of the reefs, alternative fisheries are possible, including the deployment of fish attraction devices (FADs) for large pelagics, harvests of deep-water shrimp and nephropid lobsters and small-scale aquaculture of marine ornamentals and spiny lobsters based on the collection of pre-settlement post-larvae.

The research has shown that in heavily exploited areas, recruitment rates can be greatly reduced, to the extent that any fishery reserves that are implemented will take a very long time to accumulate a substantial spawning stock biomass and to have any effect on fisheries in the surrounding area. Restocking of such reserves, either with hatchery-reared fry, where the technology is available, or with fry reared from wild-caught pre-settlement larvae, will be essential if such reserves are to show any significant benefits in the medium term.

Publicity to promote the concept of escape gaps in fish traps is needed throughout the Caribbean but the process would be greatly helped by the existence of a successful demonstration site. Likewise, documentary video material about all aspects of tropical fish biology and management receive a ready audience in fishing communities and in schools, but relevant material is scarce.

Annex

Publications

Copies of the following papers are attached:

Published

1. Gell, F.R. and M. Watson. 2000. U.K. Overseas Territories in the northeast Caribbean; Anguilla, British Virgin Islands, Monserrat. p. 615-626 In C. Sheppard (ed.) Seas at the millennium: an environmental evaluation. Elsevier, Oxford.

2. Munro, J.L. 1999. Effects of fishing on coral reef ecosystems. p.143-148 In P.J. Schei, O.T. Sandlund and R. Strand (eds) Proceedings of the Norway/UN Conference on the Ecosystem Approach to Sustainable Use of Biological Diversity. Norwegian Directorate for Nature Management & Norwegian Institute for Nature Research, Trondheim, 1999. 282 p.

3. Munro, J.L. 2000. Outmigration and movement of tagged coral reef fish in a marine fishery reserve in Jamaica. *Proc. Gulf Caribb. Fish. Inst.* 51: 557-568.

4. Watson, M. and R. Power. 2001. Juveniles recruited to sustain aquarium industry. *Reef Encounter* 30:34-37.

5. Watson, M. A fishy tale. 2000. BVI Welcome Magazine, August/September 2000.

6. Watson, M., R.M. Power and J.L. Munro. 2000. Use of light-attracted zooplankton for rearing post-settlement coral reef fish. *Proc. Gulf Caribb. Fish. Inst.* 52:340-351.

In press

1. Munro, J.L. *In press.* Sustainable management of coral reefs in the Caribbean Sea. Proceedings of Caribbean Agriculture, Land and Water Resources Network (CLAWRENET) *Symposium and Annual Technical Meeting, Barbados, October 2000.*

2. Munro, J.L., Z. Sary and F.R. Gell. *In press.* Escape gaps: An option for the management of Caribbean trap fisheries. *Proc. Gulf Caribb. Fish. Inst.* 54:

3. Power, R.M. *In press.* Harvest of settlement stage reef fish for small-scale grow-out or stock enhancement; a feasibility study on the French Grunt, *Haemulon flavolineatum. Proc. Gulf Caribb. Fish. Inst.* 54:

4. Sary, Z., J.L. Munro and J.D. Woodley. *In press.* Status report on a Jamaican reef fishery: Current value and the costs of non-management. *Proc. Gulf Caribb. Fish. Inst.* 54:

5. Sponaugle, S., R.K. Cowen, S.G. Morgan, A. Shanks, J.M. Leis, G. Boehlert, J. Pineda, M.J. Kingsford, C. Grimes, K. Lindeman and J.L. Munro. *In press.* Predicting self-recruitment in marine populations: Biophysical correlates. *Bull. Mar. Sci.*

6. Watson, M, R.M. Power, S. Simpson and J.L. Munro. *In press.* Low cost light traps – designs for coral reef fishery research and sustainable ornamental fisheries. *Naga: The ICLARM Quarterly.*

7. Woodley, J.D., Z. Sary, P. Gayle, W. Lee, P. Parchment and L. Walling. The Discovery Bay Fisheries Reserve, Jamaica. *Proc. Gulf Caribb. Fish. Inst.* 54:

Internal Reports

Copies of all reports, theses and papers under review can be obtained from Dr. J.L. Munro, ICLARM Caribbean/Eastern Pacific Office, 158 Inland Messenger, Road Town, Tortola, British Virgin Islands.

In review

1. Power, R.M and M. Watson. A pump for feeding post-settlement coral reef fish with light attracted zooplankton, with possible applications in the fisheries for marine ornamentals. Submitted to *Journal of the World Aquaculture Society.*

2. Watson, M. and J.L. Munro. Settlement and recruitment of coral reef fishes in moderately exploited and overexploited Caribbean ecosystems: implications for marine protected areas. Submitted to *Bulletin of Marine Science.*

3. Watson, M., J.L. Munro and F.R. Gell. Settlement, movement and early juvenile mortality of the Yellowtail snapper, *Ocyurus chrysurus:* implications for recovery interventions in severely overexploited stocks. Submitted to *Marine Ecology Progress Series*

Technical reports

1. Pomeroy, R.S. 1999. Economic analysis of the British Virgin Islands commercial fishing industry. ICLARM Caribbean/Eastern Pacific Office, Technical Report. 32 p. plus appendices.

2. Sary, Z. 2001. The small-scale fishery on the central north coast of Jamaica in 2000-2001: A biological and socio-economic survey. ICLARM Caribbean/Eastern Pacific Office, Technical Report. 27 p. plus CD-ROM.

Theses

1. Bertenshaw, V.J. 2001. Settlement behaviour and survivorship of *Ocyurus chrysurus* (yellowtail snapper) and other juvenile reef fish species of the British Virgin Islands. M.Sc. (Biological Diversity) thesis, Faculty of Science, University of Plymouth, U.K.

2. Parchment, P. 1998. 'Co-management' and contradiction: A case study of fishery reserve management in Discovery Bay, Jamaica. Research Paper, submitted in partial fulfillment for the Degree of Master of Science in Development Studies, University of the West Indies, Jamaica.

In preparation

1. Munro, J.L. Connectivity and the evolution of self-recruitment mechanisms in marine populations. For submission to *Gulf Caribb. Res.*

2. Munro, J.L. Assessment of the status of exploited fish stocks at Discovery Bay, Jamaica, and of possible management strategies. (Journal not yet chosen)

3. Munro, J.L. Growth and mortality rates of coral reef fish derived from mark-and-recapture and length-frequency data. (Journal not yet chosen)

4. Munro, J.L. and R.M. Power. Seasonality and variability of recruitment and changes in the relative abundance of reef fish following creation of the Discovery Bay Fishery Reserve in Jamaica. (Journal not yet chosen)

5. Power, R.M. Harvest and rearing strategies for post-larval reef fishes: Potentials for alternative reef fisheries and management options. M.Sc thesis. University of Plymouth, UK.

6. Watson, M. and J.L. Munro. Settlement hotspots and recruitment failure - ingredients and rationale for coral reef fisheries management through marine protected areas: an eastern Caribbean example. For submission to *Coral Reefs*.

7. Watson, M. and R.S. Nemeth. Spatial and temporal patterns of coral reef fish supply to neighboring small island states in the eastern Caribbean. For submission to *Env. Biol. Fishes*.

8. Williams, I. and J.L. Munro. Ecopath models of Discovery Bay, Jamaica, and Hans Creek, British Virgin Islands. ICLARM Caribbean/Eastern Pacific Office, Technical Report. 27 p. plus CD-ROM.

Other Dissemination of Results

Seminars describing the outputs of the Project are scheduled or planned for presentation at the Renewable Resources Assessment Group at Imperial College, London (7 January 2002), at the H. Lavity Stoutt Community College in Tortola in March 2002, at the Annual Meeting of the Association of Marine Laboratories of the Caribbean in Mexico in June 2002 and at the Institute for Marine Affairs in Trinidad (date not yet scheduled).

Copies of the entire package of publications produced by the Project will be sent to all Fisheries Departments in the Caribbean Region, to University and Marine Laboratory libraries and to individual scientists and fishery officers working in allied fields.

Socio-economic data and assistance in interpreting the results of the work will be provided directly to the Education Officer of the UWI's Fisheries Improvement Project in Jamaica and to the people responsible for the management of that Project.

Data Sets

Data collected by the Project are currently backed-up on computers at the Discovery Bay Marine Laboratory and the Conservation and Fisheries Department in BVI. Additionally, all data sets will be compiled on CD-ROM and copies provided to all collaborators, to ICLARM's main library in Penang and any other interested persons or organizations.

The data sets include the following:

- A relational database documenting catch rates in light traps and ½" mesh fish traps at various stations around the eastern end of Tortola, BVI, and adjacent islands, including sites designated as proposed marine protected areas, from 1997 to 2000.
- The results of the survey of the BVI fishing industry in 1999.
- A relational database documenting catch rates in light traps and ½" mesh fish traps at stations in and adjacent to the Discovery Bay Fisheries Reserve in Jamaica, from 1996 to 2000 and catch rates in 1"mesh fish traps from 1996 to 2001. Additionally, the database contains mark and recapture data, covering 6949 fish tagged and 5957 fish recovered (including multiple recaptures of the same individuals) in and around the Discovery Bay Fisheries Reserve, from 1996-1999.
- The results of the socio-economic survey of the fishery at Discovery Bay and adjacent areas, July 2000 to July 2001 covering socio-economic data on 130 fishers and their catch rates using traps, nets, spears and hook-and-line.
- A relational database containing morphometric measurements of lengths, weights, body depths, and body widths of over 7,000 fish of 26 species, used for estimating retainable sizes in traps fitted with escape gaps. Additionally, size frequency data for fish captured in traps with escape gaps and in control traps in BVI and in Jamaica in 2000 and 2001.
- Databases of the survey data for Discovery Bay, Jamaica, and Hans Creek, BVI, for Ecopath-with-Ecosim models, together with the models and background documentation.

Future users of the data will include scientists working elsewhere in the Caribbean, researchers at the Discovery Bay Marine Laboratory, marine protected area planners in Jamaica and BVI, Caribbean fisheries departments and environmental agencies.

Appendices

All journal articles and conference presentations, published or in press, and all technical reports, as listed above, are attached.

Effects of fishing on coral reef ecosystems

John L. Munro
Caribbean/Eastern Pacific Office, International Center for Living Aquatic Resources, Management (ICLARM), Tortola, British Virgin Islands

Abstract

Coral reef ecosystems provide a significant proportion of the marine harvests taken by developing countries in the tropics. The harvest includes a wide variety of fish and invertebrates. This contrasts with fisheries in temperate countries in which a relatively limited selection of highly desirable species are marketable. Coral reef organisms are captured by a wide variety of fishing gears but the trawl nets, gill nets and seine nets which characterise industrial-scale temperate water fisheries cannot normally be used in the vicinity of coral reefs. Few of these fishing gears are highly selective for particular species of fishes or invertebrates and often several hundred species are caught by a single method, almost all of which can be sold, bartered or used.

Coral reef fish and invertebrates differ widely in their catchability but the larger, slower-growing, predatory, species are usually vulnerable to a wider array of fishing gears than are smaller, fast-growing, herbivorous species. It thus becomes possible for the most catchable species to become over-fished to the point of local extinction while the overall volume of the catch is not significantly decreased. Over time this leads to changes in the composition of the community in which the organisms at the apex of the food web are progressively eliminated.

Islands which receive a constant influx of larvae from upstream sources are partially buffered against ecosystem changes and local extinctions. Isolated islands are vulnerable to severe structural changes, local extinctions and even the total extinction of some endemic species.

In countries where poverty is combined with open access to aquatic resource systems, over-exploitation of the fisheries can lead to profound changes in the coral reef ecosystems. This can include dramatic increases in the biomasses of some plants and invertebrates as a result of the extinction of their predators and the overgrowth of corals by macro-algae. Invariably there is a concurrent loss of biodiversity.

Introduction

Fisheries generally fall into two categories; pelagic fisheries for species living in the water column or demersal fisheries for species associated with the sea floor. The demersal fisheries can be divided into those on soft, muddy or sandy substrates or those on hard bottoms. In the tropics, solid surfaces usually have a substantial cover of reef-building corals. Coral reefs are almost entirely absent from the eastern margins of tropical oceans and are also absent from areas which are strongly affected by outflows of large rivers that carry heavy sediment loads and reduce salinities. However, almost all countries of the Indian Ocean and the Western and Central Pacific and of the Caribbean have conditions which are favourable for the growth of corals and the development of coral reefs. Where water clarity is high, coral growth can extend to great depths and the emergent crests of reefs are an insignificant fraction of the total area covered by corals.

Coral reef ecosystems take many forms but are generally a combination of ridges or patches of actively growing corals and other sessile organisms and algae, separated by sandy areas. Seagrass beds, often of enormous extent often develop in areas behind the reef crest and in the shoreward parts of lagoons and the shores are often fringed by mangroves. Depending on depth and water clarity the lagoons may be studded with outcrops of coral and patch reefs or have sandy or muddy floors. The high primary and secondary productivity of these linked ecosystems combined with the lagoons of sheltered water that usually form behind reef crests have been positive inducements to human settlement.

Coral reef fisheries

The large trawl and seine nets that characterise temperate water fisheries usually cannot be used where coral reefs occour and coral reef fisheries are characterised by being small-scale, artisanal endeavours. Additionally, the great diversity of species makes marketing and processing difficult for large-scale commercial operations. Typically, in the Indo-West Pacific catches from coral reefs will be comprised of over 1000 species of fish and invertebrates, while in the Caribbean about 180 species can be found in fish markets. However, in most areas about 30 species will normally make up about 90% of the catch (Table 1).

The diversity of species also means that a wide variety of fishing gears are used to provide the catch and the gears may vary seasonally. In the Caribbean, portable fish traps made of wire mesh supported on a framework of mangrove poles are the most widespread gear, but hook and line, bottom longlines and spears are also commonly used. In the Indo-Pacific portable traps are

p. 143-148 In: Schei, P.J., O.T. Sandlund, R. Strand (eds.) Proc. Norway/U.N. Conference on the Ecosystem Approach to Sustainable Use of Biological Biodiversity. Trondheim. 1999.

Table 1. Comparative catch rates of exploited species of reef fishes in light traps and 0.5" fish traps in Tortola, British Virgin Islands and Discovery Bay, Jamaica, over comparable time periods.

Sampling effort	Light traps Tortola 497 catch/100 trapnights	Disc. Bay 240	Fish traps (0.5") Tortola 1349 catch/trap/night	Disc. Bay 978
Serranide				
Epinephelus guttatus	0,8	0,0	0	<0.01
Sphyraenidae				
Sphyraena barracuda	3,0	0,0		
Carangidae				
Caranx bartholomei	9,9	0,4	<0.01	0
Caranx latus	23,7	0,0	<0.01	<0.01
Caranx ruber	66,6	20,5	<0.01	<0.01
Caranx spp.	11,1	0,0		
Scombridae				
Scomberomorus regalis	7,4	0,0		
Lutjanidae				
Lutjanus apodus	18,5	0,0	0,27	0,03
Lutjanus griseus	29,4	0,0	0,01	0
Lutjanus synagris	101,6	0,4	0,08	<0.01
Lutjanus spp.	0,4	0,0		
Ocyurus chrysurus	115,7	0,0	0,81	0,01
Haemulidae				
Haemulon flavolineatum			0 02	0,54
Haemulon plumieri			0,14	0,01
Haemulon sciurus			0,03	<0.01
Mullidae				
Pseudupeneus maculatus	17,7	0,8	0,03	000
Scaridae				
Scarus iserti/taeniopterus			0,28	2,61
Sparisoma aurofrenatum			0,55	0,03
Sparisoma chrysopterum			0,01	0,11
Sparisoma viride			0,01	0,13
Acanthuridae				
Acanthurus bahianus		2,7	0,24	000
Acanthurus chirurgus		32,2	0,09	000
Acanthurus bahianus/chirurgus	12,5			
Acanthurus coeruleus	7,8	6,4	0,17	<0.01
Balistidae				
Balistes vetula	0,0	4,9	0	0

less frequently used and, because of the generally greater tidal range, a variety of fixed traps are used on reef flats. Communal efforts at driving fish into traps or enclosures are common in the Pacific islands. Boats can vary from bamboo rafts to quite sophisticated inboard-powered small craft, depending upon the economic positions of the fishers and the status of the fishery.

A very important factor affecting coral reef fisheries is that apart from the reefs of Florida, Hawaii and Australia, all coral reefs are located within the maritime boundaries of developing countries, including some of the most impoverished countries. In many of these countries (e.g. Philippines, Indonesia, Haiti, Jamaica) the average fisher is not a fish catcher by tradition, he is most often an unemployed, landless, peasant to who the sea is the resource of last resort. Particularly because coral reef lagoons offer relatively sheltered waters for minimalist fishing craft and because shallow sea grass beds and reef flats offer the opportunity to simply gather fish and invertebrates by hand or with a simple spear. In Jamaica, for example, an increasing proportion of the catch is now being taken by young men operating from shore without boats and using home-made spear guns.

Overfishing, catchability and economics

The vulnerability of a species to over-fishing depends on its biological characteristics and its catchability. Generally, small species with high growth rates, high fecundity and early maturity are resilient to exploitation, while large, slow growing species, which mature at a substantial size, are easily over-fished. Species which enter the fishery well before maturity are liable to recruitment over-fishing unless stocks are replenished by larvae originating elsewhere. Additionally, catchability (the fraction of a fish stock that is removed by one unit of fishing effort with a particular fishing gear) is very variable, for a variety of biological, behavioural and physical reasons.

The conventional economic view of single-species fisheries is that as fishing effort increases the total value of the catch of a particular species will rise to a maximum in some form of parabola and then fall as the stock become overexploited. The cost of fishing rises in direct proportion to the effort and at some point the costs exceed the value of the catch and fishing effort is checked by insolvencies (**Figure 1**). The target species is thus saved from being fished to extinction by economic factors. The reality is somewhat more complicated because almost all fishing takes some bycatch and the operators can switch to other target species.

In multi-species coral reef fisheries, in which fishing effort is generalised and all of the species are concurrently taken, the most catchable, large, species face rapid local reductions in biomass and numbers of mature individuals. They become technically over-fished while less catchable, small, species are still being exploited at levels below the maximum possible catch. The composition of catches thus changes progressively. This is illustrated in **Figure 2**, based on Munro and Smith (1984), which shows a hypothetical scenario in which catches of the large predators (1-4) rapidly peak and then decline to negligible levels or to extinction and modest-sized omnivores (5-8) become dominant in the catch. Ultimately, small herbivores (9-11) become the main components of the catch, perhaps increasing in relative abundance because of the absence of predators. The remaining hundreds of species in the catch (aggregated as 12), including relatively rare species, become increasingly rare and some will become extinct, at least at a local level.

Additionally, as shown by the line representing the cost of fishing, the conventional economic constraints on fishing effort do not apply because in most coral reef fisheries the equipment is relatively inexpensive and is often fabricated by the fisher. For persons with no skills and no opportunities for employment the opportunity cost of labour is effectively zero. Even with low costs, some of the most vulnerable species would have been uneconomic to exploit if they alone were targeted.

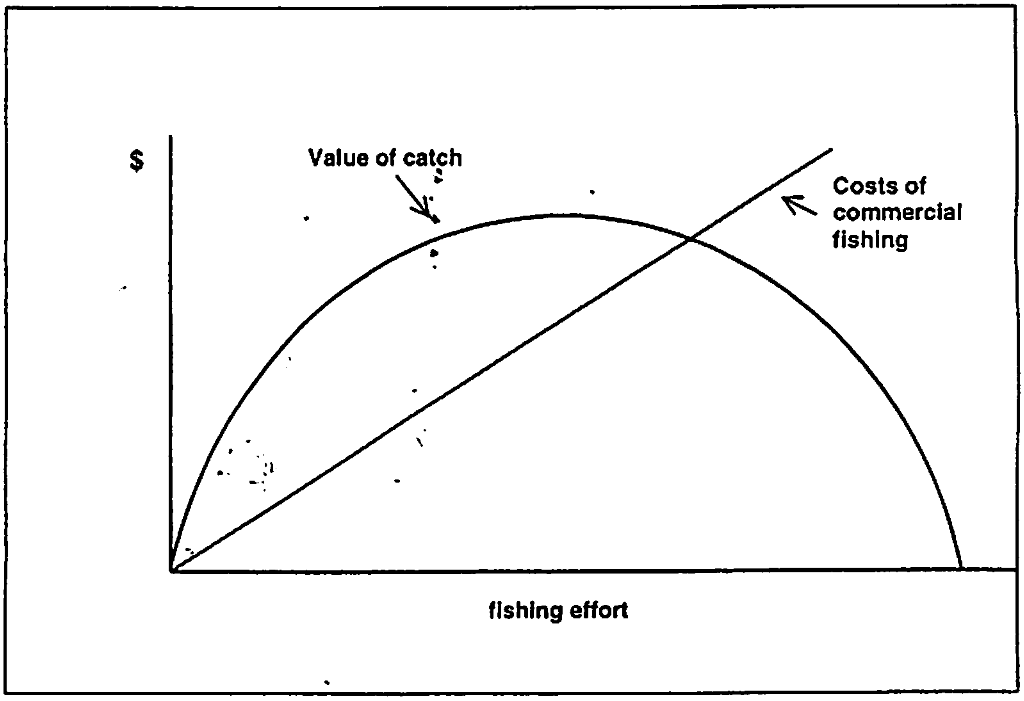


Figure 1. Economics of commercial fisheries showing how commercial fishing effort is constrained when the value of the catch equals the cost of fishing.

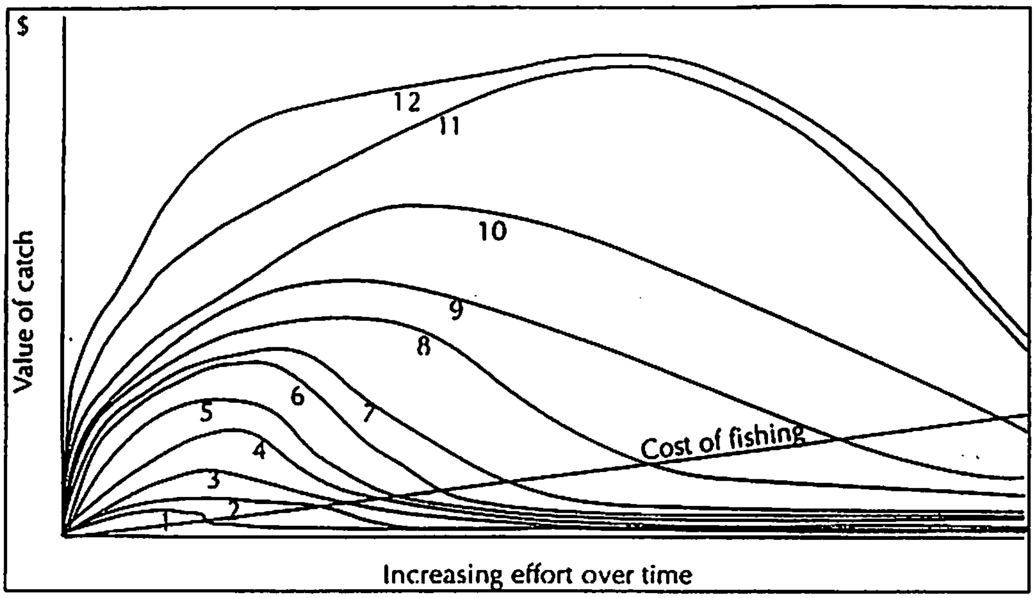


Figure 2. Hypothetical changes in the total value and composition of catches from a coral reef fishery in response to increasing fishing intensity over a period of time and with no restriction on the type of gear or mesh size used. Adapted from Munro and Smith, 1984.

Unfortunately, there is no good time series of catch composition data for any coral reef fishery. However, these effects can be seen in fisheries statistics for Jamaica, where there is a partial record of changes in catch composition over time and with increasing fishing effort at various locations. **Figure 3** shows trap catch rates and composition at various times and locations in Jamaican waters arranged in order of increasing intensity of fishing effort, mostly with Antillean fish traps. The fish families are arranged in rough order of their vulnerability to over-fishing.

Pedro Bank, a large oceanic bank south-west of Jamaica, has three small islands (cays) at its eastern end which are occupied by fishers. However, the south-western part of the bank is outside of the range of most fishing canoes and in 1969-73 it was virtually unexploited. In 1986 it was still very little exploited but groupers has disappeared and grunts and hinds had declined somewhat. Catch rates around the Pedro Cays were modest in 1969-73 but by 1986 had declined to even lower levels than were obtained at Port Royal, near the capital, Kingston, in 1969-73. Even the once-ubiquitous Queen triggerfish (*Balistes vetula*) had virtually disappeared, probably a victim of its high catchability and discoid body shape which ensures that it is caught in small-meshed fish traps long before sexual maturity. Finally, catch rates at Discovery Bay, on the heavily exploited, narrow, northern coast of Jamaica have declined to a few hundred grams of fish per day, principally small parrotfish, surgeonfish and squirrel fish (Sary et al. 1997).

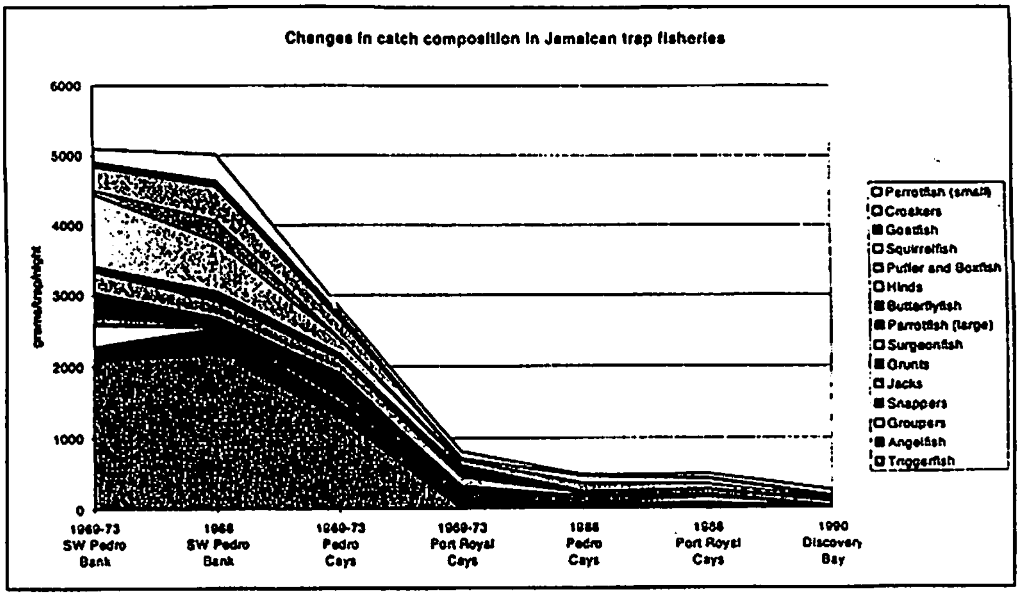
The recruitment problem

Recent work by me and my colleagues has included comparative studies of recruitment rates of reef fish in Jamaica and the British Virgin Islands. As indicators of abundance, we used catch rates of pre-settlement reef fish in light traps and of juvenile reef fish in small-meshed wire fish traps. Table 1 shows that catch rates of most species in Jamaica are two to three orders of magnitude less than in BVI. Juveniles of some species were absent from our catches in Jamaica. Small species of parrotfish and some surgeon fish were the only species which were not significantly reduced in abundance.

Roberts (1997) plotted known current speeds in the Caribbean against the duration of the oceanic pelagic larval life of reef fishes. These generally fall into two categories; those with a larval stage of less than 30 days and those with larvae more specialised for an extended stay in the plankton of up to 60 days. He found that while some islands which are down-current from areas with good fish stocks (e.g. Puerto Rico) can expect larvae to reach their shores with ease, others such as Jamaica are too isolated to receive any substantial inputs of larvae from non-local sources. Our recent work in Jamaica confirmed that with few exceptions the few pre-settlement larvae caught in our light traps in Jamaica were those with specialised oceanic pelagic larval stages, notably surgeonfish and goatfish.

Thus it seems that isolated islands such as Jamaica or the islands of the Eastern Caribbean chain will be very vulnerable to generalised recruitment failures when their fish stocks become depleted. In addition, islands that currently benefit from being downstream from good stocks of mature fish will find that bounty depleted if the upstream stocks are mismanaged.

Figure 3. Changes in the catch rates and composition in Jamaican trap fisheries. Data are presented in order of increasing fishing intensity and fish families in rough order of their vulnerability to overfishing. Data from Munro 1983, Koslow et al 1988 and Sary et al 1997.



Ecosystem effects

It can be expected that that when coral reef fisheries undergo the changes described above, the reduction or elimination of predators will decrease mortality rates of prey species and, to some degree, increase catches of those species. If those intermediate small predators are overfished the herbivores will then respond by increasing in biomass. When they are overfished there will be no control of algal production and biomasses of algae and seagrasses will increase, with most production simply turning to detritus. However, there are few well-documented examples of such effects rippling or cascading through ecosystems.

Currently, reefs on the north coast of Jamaica are almost entirely overgrown by macroalgae and the cover of live coral is extremely low. Although there is not full agreement in this matter it appears that this can be attributed to the long-term effects of overfishing. The island shelf is very narrow (<1 km) and was covered by flourishing coral reefs until 1984. Then several events combined to change the situation. The herbivorous long-spined sea urchin, *Diadema antillarum*, suffered a catastrophic epidemic that spread rapidly through the Caribbean and the north coast of Jamaica took a direct hit from a major hurricane. The reefs were pulverised by heavy seas and massive corals stripped of tissue. Macroalgae colonised all the newly exposed surfaces and in the absence of both sea urchins and herbivorous fish have remained dominant up to the present (Hughes 1994). Other parts of the Caribbean with less heavily exploited fish stocks lost their *D. antillarum* populations and suffered hurricanes, but the reefs were not overgrown by algae. While it cannot be proven that overfishing was the cause of this catastrophe, the evidence certainly points that way. The *D. antillarum* stocks now appear to be rebuilding in Jamaica, and throughout the Caribbean. There are indications of slow recovery of the reefs on the Jamaican north coast. However, reefs covered with spiny sea urchins are also not what the Jamaican fishers or tourists desire.

Work in Kenya has shown changes in reef ecosystems, particularly large increases in sea urchin populations in heavily fished areas caused by the exploitation of their predators (McClanahan 1994, 1997a,b). If these sea urchin stocks were to be decimated by disease (a not uncommon occurrence in echinoderms) Kenyan reefs could face the same problem as Jamaica.

The extinction of a wide variety of species of fish and invertebrates is entirely feasible if they are vulnerable components of multi-species fisheries or if they suffer loss of essential habitat as a result of changes induced by over-fishing, possibly in combination with other anthropogenic effects.

Solutions

It seems that the only solution to the problem of progressive collapse of exploited reef fish communities will be the creation of extensive marine fishery reserves in areas upstream from the major fishing grounds or centres of population. In these areas, substantial spawning stocks of all species could be established and the entire ecosystem restored to something resembling a pristine state (McClanahan 1997b, Russ & Alcala 1998a,b).

This will be very difficult to do and will not suffice alone. Fisheries throughout the world are mismanaged and particularly for small scale fisheries management is extremely difficult for biological, economic and social reasons. However, recent successes in co-management and community-based management seem to point the way forward in which communities take the initiative in establishing management goals and implementing those management measures with the backing of government. For countries with extensive river systems and for high islands, integrated coastal zone management will be an essential adjunct; failing which, uncontrolled pollution and sedimentation will continue to make inroads into coral reef habitats and consequent diminution of fisheries and loss of biodiversity.

References

Hughes,T.P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. - Science 265: 1547-1551.

Koslow, J.A., Hanley F. & Wicklund, R. 1988. Effects of fishing on reef fish communities at Pedro Bank and Port Royal Cays, Jamaica. - Marine Ecology - Progress Series 43: 201-212.

McClanahan, T.R. 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexicity, and sea urchins. - Coral Reefs 13(4): 231-241.

McClanahan, T.R. 1997a. Effects of fishing and reef structure on East African coral reefs. - Proc. 8th Int. Coral Reef Symp. 2: 1533-1538.

McClanahan, T.R. 1997b. Recovery of fish populations from heavy fishing: Does time heal all?. - Proc. 8th Int. Coral Reef Symp. 2: 2033-2038.

Munro, J.L (ed). 1983. Caribbean coral reef fishery resources. - ICLARM Studies and Reviews 7, ICLARM, Manila. 283 p.

Munro, J.L. & Smith, I.R. 1984. Management strategies for multi-species complexes in artisanal fisheries. - Proc. Gulf Caribb. Fish. Inst. 38: 127-141.

Roberts, C.M. 1997. Connectivity and management of Caribbean coral reefs. - Science 278: 1454-1457.

Russ, G.R. & Alcala, A.C. 1998a. Natural fishing experiments in marine reserves 1983-1993: community and trophic responses. - Coral Reefs 17:383-398.

Russ, G.R. & Alcala, A.C. 1998b. Natural fishing experiments in marine reserves 1983-1993: role of life history and fishing intensity in family responses. - Coral Reefs 17: 399-416.

Sary, Z., Oxenford, H.A. & Woodley, J.D. 1997. Effects of an increase in trap mesh size on an overexploited coral reef fishery at Discovery Bay, Jamaica. - Marine Ecology Progress Series 154: 107-120.

ICLARM Contribution # 1550

Escape Gaps: An Option for the Management of Caribbean Trap Fisheries*

JOHN L. MUNRO, ZSOLT SARY AND FIONA R. GELL
ICLARM Caribbean/Eastern Pacific Office,
158 Inland Messenger, Road Town, Tortola,
British Virgin Islands
*ICLARM Contribution # 1644

ABSTRACT

The use of escape gaps set in the corners of Antillean fish traps is suggested as a management mechanism for the intensive trap fisheries of the Caribbean. Escape gaps could be rectangular or diamond-shaped. Rectangular apertures provide two dimensions (width and the diagonal) that can be adjusted to permit the escape of deep-bodied slender fishes while retaining round-bodied fishes and crustaceans. Diamond-shaped escape gaps provide height, width and, to a degree, body shape as controlling dimensions.

Previous investigations have suggested that the effectiveness or fishing power of traps might decrease when mesh size is increased. Preliminary indications from a series of tests with rectangular escape gaps are that appropriately sized escape gaps are effective in releasing undersized fish but do not significantly decrease the catchability of target species.

Yields of deep-bodied fishes such as surgeonfish, triggerfish, hogfish, angelfish, spadefish, porgies and some of the grunts and jacks would be increased, because such fishes are invariably harvested at extremely small sizes by the hexagonal wire meshes commonly used in Caribbean trap fisheries. Morphometric information is presented for twenty-one species to estimate size at first capture with various escape gap sizes, and to calculate potential improvements in yield-per-recruit when using escape gaps.

For severely depleted fisheries, the dimensions of the escape gap would need to be progressively changed as stocks of key fishery species recovered and the composition of the fish communities changed.

KEY WORDS: Fish traps, escape gaps, management, mesh size.

INTRODUCTION

Antillean fish traps or "pots" are the principal fishing gears in most countries in the Caribbean. A wide variety of trap designs are used, ranging from rectangular box traps with a single straight entrance funnel, to more complex designs such as the single-entrance arrowhead trap or the Z or S traps that have two entrances, usually with a down turned entrance funnel (Munro et al 1971). The arrowhead trap is historically important, having been the main trap design used in the past and one still used extensively in Africa and the Middle East. Most modern traps use wire mesh but the original traps were of woven cane.

Some designs of traps might be better than others but they are all exceedingly efficient passive fishing gears. They maintain the catch in good condition until the trap is hauled and do not have to be hauled if the weather is unfavorable. They are relatively inexpensive to construct and, with the advent of plastic coated mesh, quite durable. Almost all species of Caribbean reef fishes will enter traps but catchability (the average fishing mortality caused by one unit of effort) is variable and predatory species tend to be more catchable than herbivores because they often enter traps to prey on the catch (Munro 1999a).

Trap fishing was banned in Bermuda in 1990 (Burnett-Herkes and Barnes 1996) but is largely unregulated elsewhere. Some countries stipulate minimum mesh sizes, ranging from 31 mm to 48 mm and in others a biodegradable panel is mandatory, to ensure that the trap will become inoperable if it is lost. However, there are no limits to the number of traps that can be deployed. This has generally led to a situation in which reef fish stocks suffer from growth and recruitment overfishing in most countries. Deep-bodied species such as surgeonfish, triggerfish, angelfish, hogfish, spadefish, porgies and some species of grunts and jacks are particularly badly affected.

The idea of using escape gaps in traps dates back to the 1950s (Templeman 1958), at which time escape gaps were mandatory in Newfoundland lobster traps. Their use has been investigated in British lobster and crab fisheries (Brown 1982) and in spiny lobster fisheries in Australia (Bowen, 1963), Florida (Lyons and Hunt, 1991) and Hawaii (Polovina et al, 1991). Escape gaps in lobster and crab traps are now required by law in a number of countries. However, it appears that the concept has never been applied to multi-species trap fisheries, such as those of the Caribbean, in which a wide array of fish and invertebrates are concurrently harvested.

Clearly, the ability of a fish or invertebrate to pass through a gap of a given size and shape depends its relative body proportions. With a rigid circular, hexagonal or square mesh, only one dimension, usually body depth, determines whether of not escapement is possible. In contrast, rectangular or diamond-shaped escape gaps offer more possibilities. Rectangular apertures provide two dimensions (width and the diagonal) that can be adjusted to permit the escape of deep-bodied, slender, fishes while retaining round-bodied fishes and crustaceans. Diamond-shaped escape gaps provide height, width and, to a degree, body shape as controlling dimensions.

In the context of Antillean fish traps, several studies (Olsen et al 1978, Stevenson and Stuart-Sharkey 1980, Ward 1988, Rosario and Sadovy 1996, Robichaud et al 1999) have found that increasing mesh sizes appeared to decrease the total catch, including that of fish that should have been retained by the larger mesh. Thus, the catchability of retainable fish appeared to be reduced. This might be attributable to decreased ingress of larger fish as a result of reduced conspecific attraction or because small fishes captured in the trap act as bait for larger fish. Alternatively, it has been suggested that large-meshed traps have a weaker visual impact (Munro 1974), look less like a refuge and therefore attract fewer fish. Bohnsack et al (1989) tested this by covering the sides of traps with a standard small mesh and only varied the mesh size of the upper and lower panels. The weight-frequency distributions of fully retainable fish did not differ markedly in 11 different mesh sizes, suggesting that catchability might not be reduced. Ward (1988) compared the frequency distributions of body depth in the total catches (excluding trunkfish and cowfish) of three different mesh sizes in inshore waters at Bermuda, all fished equal amounts. There was no evidence of reduced catching power for fully retainable fish.

Current evidence therefore suggests that escape gaps would not reduce catchability. That is, the numbers of fish captured in each size group, above the minimum size expected, would not be significantly decreased. However, there is sufficient ambiguity in available reports to warrant further examination of this aspect.

Escape gaps would be ineffective if fish were simply unwilling to pass through the gaps. The effectiveness of escape gaps would also be reduced if undersized fish used the trap as a refuge and were unable to rapidly discern the escape gap and make an exit when the trap was hauled.

METHODS

This study was undertaken at Hans Creek, located on the south coast of Beef Island, adjacent to Tortola, British Virgin Islands (BVI) and in Discovery Bay, on the north coast of Jamaica. We used non-standard double-arrowhead (AA) Antillean fish traps constructed of sticks and 25 mm (1") plastic-coated wire mesh. The wire mesh has a maximum aperture of 33 mm. These AA traps have an outer chamber (sometimes called a parlor) and a second, internal, entrance funnel leading to the inner chamber (Fig. 1). In theory, such a trap should have reduced escapement rates. The traps are 120 cm across, 150 cm along the side and 60 cm high. The horse neck entrance funnel protrudes 50 cm into the trap and terminates in a downward facing pear-shaped aperture 60 cm in circumference and 12 cm wide. The internal funnel is identical. Escape gaps were made of from rectangles of plexiglass (in Jamaica) or galvanized metal (in BVI), with rectangular apertures cut out of them.

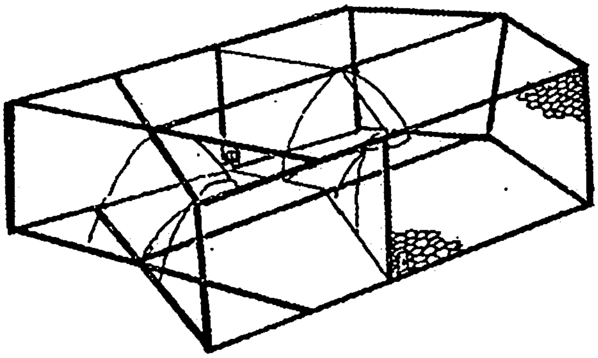


Figure 1. Double arrowhead fish trap fitted with escape gaps. Dimensions are 150 mm along the side, 120 cm wide and 60 cm deep. Plastic-coated hexagonal wire mesh measures 33x25 mm. Wooden poles, fitted externally, support the structure.

As a preliminary experiment, undertaken at Hans Creek, nine traps were fitted with escape gaps between the parlor and the inner chamber but not in the outer walls of the trap. The inner entrance funnel was blocked. If undersized fish passed freely through the gaps, then the average number in each chamber should be equal, provided that no large predator was concurrently trapped in the parlor. The traps were checked by divers and the fishes in each chamber were identified, counted and their sizes estimated.

After that, escape gaps were located in the outer walls of the traps, close to the floor in the acute corners furthest from the apex of the trap. Traps were hauled with a rope attached above the entrance funnel so that any fish in the outer parlor would descend through the inner funnel as the trap was being hauled.

Divers inspected traps fitted with escape gaps to count the numbers of fish in the traps, for comparison with the numbers actually caught. Traps were then hauled and reset, once weekly (in BVI) or twice weekly (in Jamaica). All fish were identified and measured for length (to the end of the middle caudal ray), maximum body depth and body width and then returned to the sea. Traps were set in shallow, 2 m, back reef seagrass and patch reef areas in Jamaica and in 5-8 m at the base of the fore reef at Hans Creek. Traps were unbaited. Catch data were supplemented by diver observations of behavior of fish in the traps. The traps in Hans Creek were frequently attacked and damaged by nurse sharks.

We made one series of observations at each site of the catch rates, catch composition and size frequencies in control traps and traps with escape gaps. These are summarized in Table 1.

Table 1. Summary of locations, dates, depths, soak times and numbers of traps with escape gaps and control traps.

Location	Dates	Depth	Soak	Hauls of control AA traps	Hauls of traps with gaps (mm)
Hans Creek	Mar-Sep 2001	6-9 m	7 d	53 with 33x25 mm mesh	58 with 70x28, 63 with 80x30, 30 with 90x33
Discovery Bay	Feb-May 2000	2-8 m	3-4 d	166 with 33x25 mm mesh	78 with 90x25

The morphometric data gathered during our experiments were compiled in a database, supplemented where necessary by information from the literature andmeasurements made at the BVI Fisheries Complex in Tortola. From these morphometric data we are able to compile a basic analysis of the comparative catch rates of the control traps and of the traps fitted with escape gaps for each of the data sets. This was done by calculating the average catch (numbers and weights of all species) per control trap hauled and, from the size frequency data for the control traps, calculating the proportion of that catch that would have been retained by each of the escape gaps used in that series of observations. This is then repeated for the catch in the trap with the smallest escape gap and then for the next largest. Only one size of escape gap was used at Discovery Bay. If the parts of the catches in the control traps that would have been retained by traps fitted with escape gaps are similar in magnitude to the catches actually taken in the traps with gaps, then the escape gaps can be deemed to not reduce catchability overall.

Twenty-one species make up 78% of the current catch in traps in the Discovery Bay area (Sary 2001). An additional 11.4% of the catch is made up of small catches of spiny lobster (1.2%) and Caribbean king crab (0.8%), various eels (3.5%) and occasional catches of groups of large yellowfin grouper (3.2%), Nassau grouper (1.7%) and red hind (1%) that still survive in the area. However, we have not observed juveniles of the large species of groupers in six years of work in the area and it seems likely that they will eventually become locally extinct. Escape gaps would have little effect on the larger species. A further 10.6% of the catch is made of assorted uncommon fish and invertebrates.

Morphometric data for these 21 most commonly caught species are shown in Table 2. Published values of length at maturity, L_m, are included in Table 2, together with estimates of growth parameters that are required for some of our computations.

In order to assess the effect that escape gaps might have on the harvest of fish from the intensively fished north coast of Jamaica we effected simple yield per recruit analyses for each species. The total landings of each species in traps in the Discovery Bay area, derived from Sary (2001), was weighted by the calculated yield per recruit in the predominant 43x32 mm wire mesh and then recalculated for the three escape gap sizes that we had used in most of our experimental work (70x28 mm, 80x30 mm and 90x33 mm) plus an additional hypothetical size of 100x40 mm. For each of the species considered the length at first capture (l_c) was determined either by body width or depth.

Total mortality rates, Z, prevailing in the Jamaica fishery were calculated from the mean weight of individuals in the catch (Sary 2001) using the formulation of Gulland (1969), which states that

$$W_c = W_\infty \sum_{0}^{3} \frac{U_n Z e^{-nK(tc-to)}}{Z - nK}$$

in which W_c is a function of the asymptotic weight, W_∞, the growth rate, K, the total mortality rate, Z, and the age at entry to the exploited phase, t_c. The theoretical point of origin of the growth curve, to, can be set at zero. U_n is the summation variable in which $U_0 = 1$, $U_1 = -3$, $U_2 = 3$ and $U_3 = -1$.

Natural mortality rates, M, are unknown and in an environment in which predators are extremely scarce, natural mortality rates of adult and sub-adult fish are expected to be very low (Munro 1980). We therefore assumed a exploitation rate, E, of 0.9 and estimated natural mortality as

$$M = Z - EZ$$

RESULTS

Our preliminary observations by divers confirmed that on average nearly equal numbers of undersized fish of all families and genera were found in the inner and outer chambers of the traps that were fitted with internal escape gaps and in which the inner funnel was blocked. This showed that fish would move freely through the escape gaps if they were small enough to do so. There were no

Table 2. Morphometric characteristics of the 21 species of reef fish that yield 78% of the trap catch in the Discovery Bay area in Jamaica. All dimensions are in mm. L = length (either TL = total length or FL = fork length), BD = body depth, BW = body width, L_c = length at first capture in traps with 43x32 mm mesh, L_m = length at maturity, L_∞ = asymptotic length, a and b = values of the length-weight equation ($W = aL^b$), W_∞ = asymptotic weight in g, K = growth coefficient, Z = total mortality rate (calculated from the mean weight of individuals in the catch and the growth parameters). Growth parameters from Munro (1983) and Munro (1999b).

Family	Species		BD:L	BW:L	L_c	L_m	L_∞	a	b	W_∞	K	Z
Acanthuridae	*Acanthurus bahianus*	FL	0.48	0.113	95	155	280	0.0191	3.08	547	0.36	1.1
	A. chirurgus	FL	0.43	0.107	101	210	313	0.0221	3.01	701	0.56	1.3
	A. coeruleus	FL	0.52	0.144	81	130	333	0.0278	3.02	1101	0.24	0.8
Balistidae	*Balistes vetula*	FL	0.47	0.144	92	175	496	0.0516	2.88	3941	0.28	0.4
Carangidae	*Caranx ruber*	FL	0.29	0.113	149	240	540	0.0180	2.99	2724	0.19	0.9
Holocentridae	*Holocentrus ascensionis*	FL	0.30	0.124	145	145	261	0.0198	3.00	352	0.23	0.5
	H. rufus	FL	0.27	0.121	168	135	188	0.0131	3.06	104	0.48	1.0
Haemulidae	*Haemulon flavolineatum*	FL	0.31	0.132	144	155	287	0.0111	3.23	568	0.25	3.1
	H. plumieri	FL	0.33	0.147	130	220	400	0.0238	2.93	1177	0.26	0.8
	H. sciurus	FL	0.31	0.137	137	180	370	0.0200	3.01	1050	0.26	0.4
Lutjanidae	*Lutjanus apodus*	FL	0.31	0.130	138	250	349	0.0089	3.20	770	0.35	0.3
	Ocyurus chrysurus	FL	0.27	0.120	148	300	525	0.0145	3.03	2363	0.18	0.6
Mullidae	*Mulloidichthys martinicus*	FL	0.22	0.132	201	180	250	0.0207	3.00	323	1.07	>10
	Pseudopeneus maculatus	FL	0.22	0.127	199	185	244	0.0229	2.96	293	1.14	>10
Scaridae	*Scarus iserti/taeniopterus*	TL	0.23	0.122	182	155	223	0.0166	3.02	196	0.48	>10
	Sparisoma aurofrenatum	TL	0.29	0.138	155	150	260	0.0129	3.11	324	1.10	6.4
	S. chrysopterum	TL	0.29	0.141	161	240	418	0.0199	3.00	1453	0.78	4.5
	S. rupripinne	TL	0.29	0.146	158	160	465	0.0194	3.00	1951	0.58	1.6
	S. viride	TL	0.33	0.140	140	180	549	0.0370	3.12	9901	0.27	7.8
Serranidae	*Cephalopholis fulva*	TL	0.26	0.142	165	160	325	0.0174	3.00	597	0.30	1.2
	C. cruentata	TL	0.27	0.136	161	160	365	0.0121	3.08	785	0.26	1.2

instances of fish becoming stuck in the escape gap. Secondly, when traps were fitted with escape gaps in the external walls very few undersized fish were observed to be lingering in the trap. The very few that were observed in the traps usually left by the escape gaps when the traps were being hauled.

Tables 3a and b show the results of the comparisons between control traps and traps with escape gaps in Jamaica and BVI. Table 3b shows, for example, that the control traps captured an average of 1214 g of fish and invertebrates, including 382 g that were large enough in body width or depth to be retained in a trap with a 90x33 mm escape gap and, reading vertically, that there is no pattern of decrease in average catch rates in traps with escape gaps.

Table 3a. Average numbers and weight of all species of fish, spiny lobsters, crabs and octopus caught in Discovery Bay, Jamaica, in control traps (33x25 mm mesh) and traps with 90x25 mm escape gaps. The upper row shows (in boldface) the numbers and weight of fish and invertebrates caught in the control traps and the numbers and weights that would have been retained in traps with 90x25 mm escape gaps. The lower row shows the number and weight (in boldface) actually taken in the traps with 90x25 mm escape gaps.

	Numbers/trap		Weight (g)/trap	
	Control	90x25	Control	90x25 mm
Control	**10.2**	1.8	**794**	241
90x25		**4.2**		**336**

Table 3b. Average numbers and weight of all species of fish, spiny lobsters, crabs and octopus caught in Hans Creek, BVI, in control traps (33x25 mm mesh) and in traps with 70x28, 80x30 and 90x33 mm escape gaps. Each row shows the numbers and weight of fish and invertebrates actually caught (in boldface) and the numbers and weights in that catch that would have been retained in traps with successively larger gap sizes.

	Numbers/trap				Weight (g)/trap			
	Control	70x28	80x30	90x33	Control	70x28	80x30	90x33
Control	**10.0**	2.6	1.7	1.0	**1214**	615	507	382
70x28		**2.3**	1.4	0.8		**496**	376	273
80x30			**1.4**	1.0			**647**	598
90x33				**0.7**				**224**

The yield per recruit estimates are shown in Figure 2a-d. All combinations of gap height and width will produce increases in the total harvests, ranging from about 18% with the 70x28 mm gaps, 19% with the 80x30 mm gaps, 22% with the 90x33 mm gaps and 42% with the 100x40 mm gaps. The value of the catch would increase by a somewhat greater amounts owing to the increased catches of snappers and also because larger fish attract better prices, irrespective of species.

In these calculations it has been assumed that the catches of the larger groupers would be unchanged but that is a rather optimistic view in the absence of any significant spawning stock biomass. The crabs and spiny lobsters would be

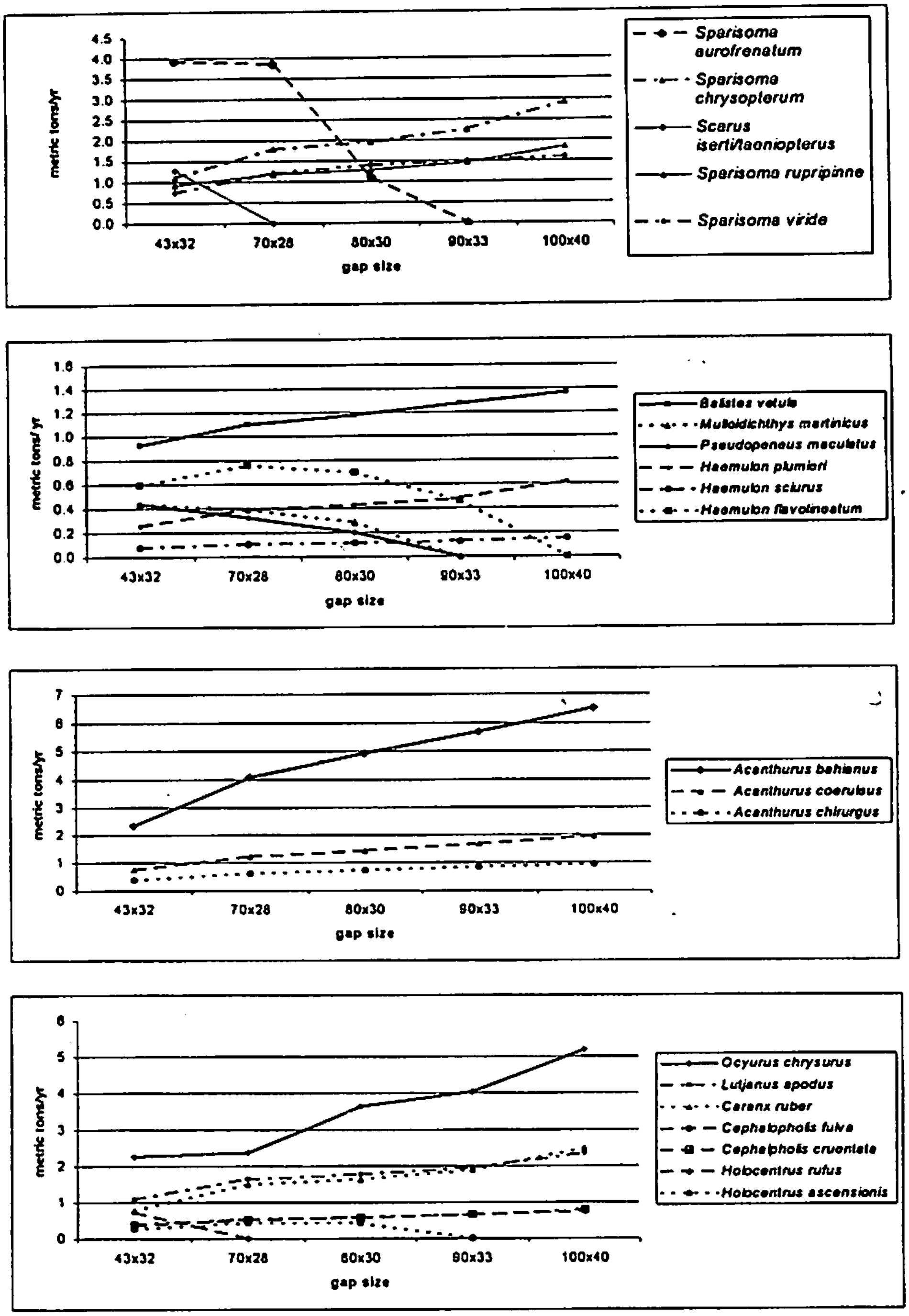


Figure 2. Calculated responses of the 21 species that comprise nearly 80% of the catch in the vicinity of Discovery Bay, Jamaica, to the introduction of escape gaps of various sizes.

unaffected by any gaps as they become catchable in traps when body depths exceed the largest gap sizes considered here. Harvests of eels would be expected to increase by an unknown amount in response to the gaps but as they have no market value they are discounted from the calculations. Note, however, that "trash" fish such as eels, are landed, given away and consumed.

DISCUSSION

The yield per recruit estimates (Fig. 2) showed that all of the tested gap sizes and the hypothetical 100x40 mm gap would produce increases in harvests if they were introduced. The calculated increase would be in the order of 42% if 100x40 mm escape gaps were introduced. However, the immediate effect would be to completely eliminate catches of the small parrotfish (*Scarus iserti/taeniopterus* and *Sparisoma aurofrenatum*), goatfish (*Pseudupeneus maculatus* and *Mulloidichthys martinicus*) and squirrelfish (*Holocentrus asencionus* and *H. rufus*) and a number of minor species, none of which attain a body width much greater than 28 mm. This would be accompanied by an increase in value because larger fish fetch higher prices per unit weight. Additionally, as most deep bodied species other than acanthurids have been virtually exterminated, we can anticipate some recovery of the other deep-bodied species.

However, it would take several years before the current fish stock grew to sizes at which they would be retained in a 100x40 mm gap. The obvious alternative is to progressively increase the gap sizes over a number of years, starting with 70x28 mm and making increases in gap sizes in response to changes in the composition of the catches. Figure 3 shows the likely outcome of a possible conservative strategy in which a gap size of 70x28 mm is initially adopted, then 80 x 30 mm, after which the gap width is held at 30 mm while gap depth is progressively increased. This would enable catches of small parrotfish, goatfish and squirrelfish to be maintained at reasonable levels while catches of surgeonfish trebled. Thereafter, gap width could be progressively increased, particularly with a view to improving harvests of snappers, jacks, larger species of grunts, and the smaller groupers.

The calculations are also based upon the current harvests, which are in turn related to recruitment rates and these have been shown to be massively depleted (Watson and Munro, in review). Table 2 shows the mean sizes at maturity and the sizes at which fish are currently captured in the Jamaican fishery in pots with a mesh size of 43 mm maximum aperture. Most species are captured well before maturity and the spawning stock biomasses of all but the smallest species are extremely small and will remain so unless management measures are adopted throughout the country. Table 2 shows that the surgeonfish, that presently comprise 12.5% of the catch, would reach maturity before recruitment if escape gaps were adopted. This, presumably, would lead to improved recruitment rates and commensurate increases in harvests. However, many of the important jacks, angelfish, porgies, spadefish, and deep-bodied grunts, all of which will be taken by small meshed fish traps well before they reach maturity, have virtually disappeared from the north coast of Jamaica.

Changes in the recruitment rates and community composition would probably have positive effects on the spear, handline and net fisheries (Sary 2001) by making larger fish available to these fishing gears.

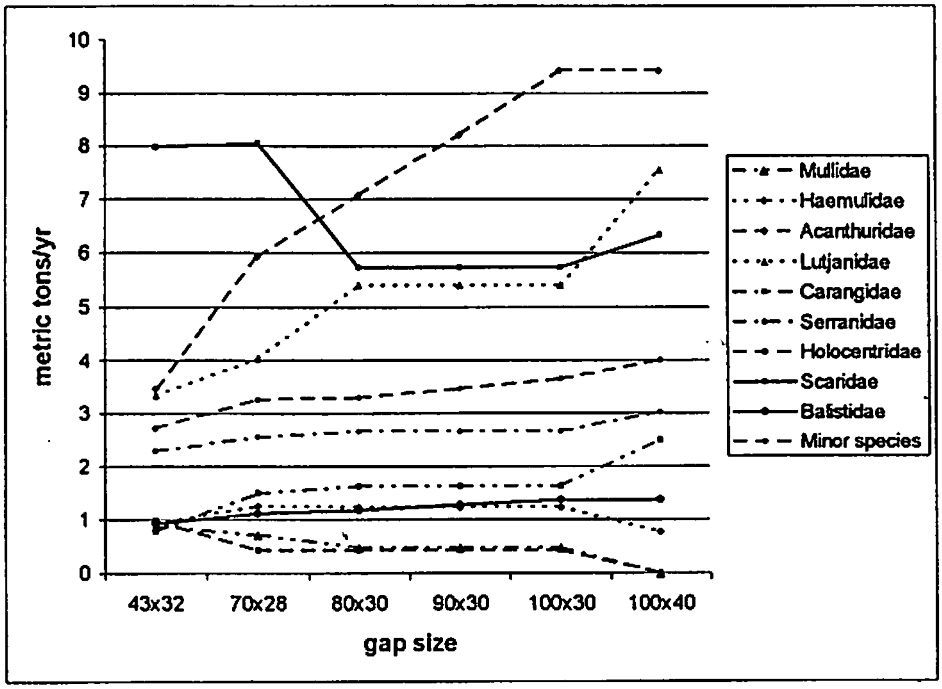


Figure 3. Suggested strategy for the introduction of escape gaps to the Discovery Bay fishery, in which a gap size of 70x28 mm is initially introduced, followed by 80x30 mm. Thereafter, gap width is held at 30 mm while gap heights are progressively increased to 100 mm. Thereafter gap width could be progressively increased to 40 mm.

We believe that the adoption of escape gaps that are progressively increased in size as catch rates improve and catch compositions change offers a partial solution to the management of Caribbean trap fisheries. Such an undertaking would have to be done in close consultation with the fishing community. It would be a difficult task. However, Parchment (1998) recorded a very widespread acceptance of the need to protect juvenile fish and this gives some hope that the fishers might be quite receptive to the idea of escape gaps.

Although we have worked with rectangular escape gaps, because the controlling dimensions are easily measured, we recognize that diamond-shaped gaps might give better results by adding body shape as an additional controlling factor.

ACKNOWLEDGEMENTS

This study was part of the work of the Caribbean Marine Protected Areas Project, funded by the United Kingdom Department for International Development. Robert Power, Ivor Williams, Annalie Morris, Vanessa Bertenshaw, Karen Bech and Patsy Leonard assisted with field work in the BVI and Moana Murray and John Samuels with field work in Jamaica. We thank the

management and staff of the BVI Fisheries Complex in Tortola for permitting us to gather morphometric data at their facility.

REFERENCES

Bohnsack, J.A., D.L. Sutherland, D.E. Harper, D.B. McClellan, M.W. Hulsbeck and C.M. Holt. 1989. The effects of fish trap mesh size on reef fish catch off south-eastern Florida. *Mar. Fish. Rev.* 51:36-46.

Bowen, B.K. 1963. Preliminary report on the effectiveness of escape gaps in crayfish pots. Fisheries Dept. of Western Australia. Report II: 14pp.

Brown, C.G. 1982. The effect of escape gaps on trap selectivity in the United Kingdom crab (*Cancer pajucus* L.) and lobster (*Homarus gammarus* L.). *J. Cons. Int. Explor. Mer.* 40:127-134.

Burnett-Herkes, J. and J. Barnes. 1996. Banning the use of fish pots and other methods introduced in Bermuda to manage declining reef fish stocks. *Proc. Gulf Caribb. Fish. Inst.* 44:239-256.

Gulland, J.A. 1969. *Manual of Methods for Fish Stock Assessment. Part 1: Fish Population Analysis.* FAO Manuals for Fishery Science 4, Rome, Italy.

Lyons, W.B., and J.H. Hunt. 1991. Catch rates of spiny lobsters (*Panulirus argus*) in traps equipped with escape gaps and potential benefits to the South Florida fishery. *Proc. Gulf Caribb. Fish. Inst.* 40:452-470.

Munro, J.L. 1974. The mode of operation of Antillean fish traps and the relationships between ingress, escapement, catch and soak. *J. Cons. Int. Explor. Mer.* 35:337-350.

Munro, J.L. 1980. Stock assessment models: Applicability and utility in tropical small-scale fisheries. p.35-47 *In* S.B. Saila and P.H. Roedel (eds.) *Stock assessment for tropical small-scale fisheries.* Proc. International Workshop, Sept. 1979. Univ. Rhode Island, International Center Marine Resource Development, Kingston, R.I. 198 pp.

Munro, J.L. 1983. *Caribbean Coral Reef Fishery Resources.* ICLARM Studies and Reviews 7, Manila, Philippines.

Munro, J.L. 1999a. Effects of fishing on coral reef ecosystems. p.143-148 in: P.J. Schei, O.T. Sandlund and R. Strand (eds) *Proc. Norway/UN Conference on the Ecosystem Approach to Sustainable Use of Biological Diversity.* Norwegian Directorate for Nature Management and Norwegian Institute for Nature Research, Trondheim, September 1999.

Munro, J.L. 1999b. Marine protected areas and the management of coral reef fisheries. ICLARM Technical Report to Inter-American Development Bank. 41 pp.

Munro, J.L., P.H. Reeson and V.C. Gaut. 1971. Dynamic factors affecting the performance of the Antillean fish trap. *Proc. Gulf. Caribb. Fish. Inst.* 23:184-194.

Olsen, D,A., A.E. Dammann and J.A. LaPlace. 1978. Mesh selectivity of West Indian fish traps. *Mar. Fish. Rev.* 40:15-16.

Parchment, P. 1998. 'Co-management' and contradiction: a case study of fishery reserve management in Discovery Bay, Jamaica. Research Paper for Degree of M.Sc. in Development Studies, University of the West Indies, Kingston. Jamaica.

Polovina, J.J., A.R. Everson and T.K. Kazama. 1991. Evaluation of circular and rectangular escape vents in a multispecies lobster fishery in Hawaii. *Proc. Gulf Caribb. Fish. Inst.* 40:471-481.

Templeman, W. 1958. Lath spacing in lobster traps. Fish. Res. Bd. Canada., Prog. Rep. Atlantic Coast Stations. 69:22-27.

Robichaud, D., W. Hunte & H.A. Oxenford. 1999. Effects of increased mesh size on catch and fishing power of coral reef fish traps. *Fisheries Research* 39: 275-294.

Rosario, A. and Y. Sadovy. 1996. Trap mesh selectivity off the west coast of Puerto Rico. *Proc. Gulf Caribb. Fish Inst.* 44:

Sary, Z. 2001. The small-scale fishery on the central north coast of Jamaica in 2000-01: A biological and socio-economic survey. ICLARM Caribbean/Eastern Pacific Office Technical Report.

Stevenson, D.K. and P. Stuart-Sharkey. 1980. Performance of wire fish traps on the western coast of Puerto Rico. *Proc. Gulf Caribb. Fish. Inst.*32:173-193.

Ward, J. 1988. Mesh size selection in Antillean arrowhead fish traps. Pages 455-467 in: S.C. Venema, J. Muller-Christensen, D. Pauly (eds.) *Contributions to Tropical Fisheries Biology.* FAO Fish. Rep. 389.

Watson. M., and J.L. Munro. Settlement and recruitment of coral reef fishes in moderately exploited and overexploited Caribbean coral reef ecosystems: implications for Marine Protected Area. *Bul. Mar. Sci.* In review.

In Press: Proceedings of the 54th Gulf and Caribbean Fisheries Institute. Providenciales, Turks and Caicos Islands. November 12-17, 2001.

In: Proceedings of the Caribbean Agriculture, Land and Water Resources Network (CLAWRENET)
Symposium and Annual Technical Meeting. Barbados. October 2000.

Sustainable management of coral reefs in the Caribbean Sea

by

John L. Munro[*]

Abstract

Coral reefs are based on a fragile and easily disrupted symbiosis between microalgae, collectively called "zooxanthellae", and coral polyps. The corals, together with macro-algae, form the base of a food web that supports a highly diverse ecosystem. The primary productivity of the system is very high but it is vulnerable to the effects of global warning and environmental degradation caused by physical damage to reefs, by sedimentation and by pollution from plant nutrients, chemical wastes, herbicides, pesticides and oil. Fishing with explosives and various poisons can also threaten the integrity of coral reef ecosystems but over-fishing with conventional fishing gears appears to be the greatest problem. Heavy fishing causes changes in community composition and trophic structure of the ecosystem by selective removal of the most vulnerable species and by eventual reduction in the rates at which juvenile fish are recruited to the stocks. Reduction in the abundance of herbivorous fish, principally by fishing with Antillean fish traps, has probably been a major factor leading to overgrowth of reefs by macroscopic algae in many areas of the Caribbean. Methods for sustainable management of reefs are well understood. However, throughout the Caribbean effective management is constrained by ineffective legislation, lack of community awareness, poverty and unemployment. Resolution of the conflict between immediate human needs and the fragility of coral reef ecosystems is the greatest challenge facing the sustainable management of coral reefs.

1. Distribution of corals and coralline shelves

Coral reefs are distributed throughout shallow tropical and sub-tropical waters, principally on the western margins of the oceans and around oceanic islands. In addition to shallow reef areas and reef crests that emerge on low spring tides, large areas of island and continental shelves have abundant coral patches scattered over sub-tidal areas to depths of up to 100m. These are referred to as "coralline shelves". Shelf edges, particularly those to windward or up-current, often have substantial coral reefs, referred to as sill reefs, which cascade into the depths over the "drop-offs" so favoured by recreational divers.

While some reefs stand alone in the ocean, such reefs are rare. More often, they form an integrated ecosystem with mangrove fringes, stands of seagrasses, sandy lagoon floors, fringing reefs, reef slopes, coralline shelves, sill reefs and drop-offs. The various forms taken by these ecosystems can cover an infinite variety of combinations and permutations, depending upon local topography, geology and climate.

---

[*] ICLARM Caribbean/Eastern Pacific Office, 158 Inland Messenger, Road Town, Tortola, British Virgin Islands.

Fringing reefs surround most Caribbean shores, except adjacent to major inflows of freshwater or sheltered inlets with poor water circulation. Typically, these reefs descend to island or continental shelves, ranging in width from a fraction of a kilometre to over 200 km, before an abrupt drop towards abyssal depths. Oceanic banks, with no or few islands are relatively common in the Caribbean (Pedro Bank, Alice Shoal, Rosalind Bank), while barrier reefs, such as the Belize Barrier Reef and atolls such as Glover Reef are uncommon.

The benefits obtained from coral reefs need little description. In addition to supporting fisheries, the reefs create protected and calm coral lagoons, the fringes of which are so favoured for human settlements and harbours. Hotels cluster around sandy beaches and marinas and boat moorings compete for space in such surroundings. One need only look at tourism brochures for examples of the aesthetic appeal of sparkling coral lagoons. The fringing reefs, invariably backed by narrow lagoons, provide a self-sustaining buffer against storm waves and reduce coastal erosion and damage to shore-side infrastructure.

2. Coral reef ecosystems

Although reef-building or hermatypic corals create the massive framework of the reef, the coral tissue represents a rather small fraction of the biomass of a reef ecosystem. A large part of this tissue is actually composed of the symbiotic algae, zooxanthellae, which play a vital role in the reef ecosystems, both in terms of primary photosynthetic production and in terms of the deposition of the reef framework of calcium carbonate. The other components include a wide variety of algae, diverse invertebrates, fish and a limited array of reptiles, birds and mammals. Seagrass beds, primarily composed of turtle grass (*Thalassia testudinum*) in the Caribbean, also harbour many fish and invertebrates and are grazing areas for manatees in the Caribbean and dugongs in the Indo-Pacific. In particular, seagrass beds serve as nursery areas for a large number of fish species, particularly commercial varieties, which reside on the reefs when adult. Shoreward of the grass beds, many areas support stands of mangroves. In the Caribbean, with its generally low tidal range, the prop roots of the mangrove systems are also nursery grounds for a number of commercial fish species. The prodigious leaf litter of the mangroves finds its way into the wider ecosystem, by way of detrital food chains.

The primary productivity or the rate of carbon fixation by photosynthesis of reef ecosystems is huge, averaging about 7-10 $gC.m^{-2}.d^{-1}$ (Lewis 1977), and equal to or greater than that of major agricultural crops such as rice or sugar cane. Part of this primary production is attributable to the symbiotic zooxanthellae, which are provided with living space, nitrates, phosphates and CO_2 by their hosts and through the photosynthetic process, provide the calcium carbonate that is required for growth of the skeleton of the coral. A wide variety of algae compete with corals for vacant surface area on the reef. Phyto- and zooplankton are filtered from the water brought to the reef by tides and currents by myriads of filter-feeding invertebrates (including corals) and fish. These plankters are the primary sources of the nitrates and phosphates that are essential for primary production. Blue-green algae are able to fix nitrogen, and thus also add to this essential resource.

This primary production, together with the energy derived from filtering zoo- and phytoplankton from the ocean, supports an immensely complicated food web, in which tens of thousands of species of micro-invertebrates, thousands of species of macro-invertebrates and about 300 species of fishes are bound in interdependency (Opitz 1996).

Ecosystems that support large numbers of species are inherently robust and are able to recover from catastrophic natural events. This is particularly so if the component populations are isolated parts or metapopulations of a larger scattered population. Thus reefs damaged by hurricanes or other natural events will be re-colonised by propagules arriving from elsewhere. This process can be quite lengthy and randomised, highly dependent on chance arrivals borne on ocean currents, but ultimately a "typical" reef ecosystem will re-emerge. On the other hand, any process that strikes at the symbiotic relationship of corals and zooxanthellae will undermine the very structure of the reef. Reef erosion results from natural breakage of corals by waves, fragmentation of corals by feeding and boring activities of reef organisms, particularly parrotfish, sponges and molluscs. These convert coral skeletons into sand and make desirable white beaches. However, on a healthy reef this erosion is normally balanced by the rapid growth of coral skeletons. If erosion outpaces accretion, the topography of the reef will be come less diverse, holes will fill with sand and rubble, reef creatures will lose their refuges and the reef will become reduced to a pile of loosely accreted rubble.

3. Climate change

It is clear that, in the absence of anthropogenic impacts, coral reefs will manage very well, as they did a few hundred years ago. One solution is to set aside the most pristine areas that are available and vigorously protect them against all forms of degradation so that at least some examples of undisturbed habitat will survive. The Nature Conservancy has recently purchased the entire Palmyra Atoll in the central Pacific Ocean, for $35 million, for this purpose. Unfortunately, human influence is so all-pervasive that even the remotest islands, the highest mountains, the Antarctic ice shelves and the abyssal depths of the oceans are not immune to environmental change caused by man.

There is mounting evidence that ecosystems are becoming destabilised as a result of global warming. In the case of coral reefs, this has manifested itself particularly through coral bleaching, which is attributed to unusually high surface water temperatures. The process is not well understood, but corals of all species and related organisms such as sea fans, spontaneously expel their zooxanthellae. Alternatively, the symbionts decide to leave because the host is no longer fulfilling its proper role. Without the symbionts, the coral tissue is translucent (bleached), the tissue cannot sustain itself and the coral dies. The thin veneer of tissue rapidly decomposes leaving a white skeleton. This new surface area is promptly colonised by algae or by coral propagules. However, coral spawning is highly seasonal and usually doesn't happen in the hottest months. Consequently, the algae have the opportunity to cover all available surfaces. Reef erosion then exceeds accretion and the reef declines in size and complexity.

If oceans do systematically warm, corals may die off in the tropical regions of the oceans and slowly spread north- and southwards.

An additional complication that has recently been suggested (reference needed 1999), is that increased atmospheric concentrations of CO_2 will interfere with the photosynthesis of zooxanthellae. This is closely inter-related with the deposition of the aragonite skeleton of the corals. The rate of growth of the coral skeleton might be greatly reduced, leading to the progressive decay of reefs. Reefs would be unable to respond to rising sea levels by rapidly growing towards the surface, with terminal consequences for atolls and other low islands.

It seems to be well agreed that sustainable management of any particular resource will not be possible if ecosystems are themselves in a state of change because of global warming. These management solutions are outside of the power of individual states, which can only urge in appropriate fora that necessary action be taken to check and reverse this process.

Hurricanes are a major cause of damage to Caribbean coral reefs, as are their semantic counterparts, cyclones and typhoons in the Indo-Pacific region. Direct hits by hurricanes can reduce reefs to rubble. However, as mentioned above, reef organisms are parts of metapopulations and if all is well elsewhere in the region, devastated reefs will eventually rebuild. If all is not well elsewhere, rebuilding will be a lengthy process and if increased hurricane strikes are a part of global climate change there is little that individual states can do about the situation.

4. Environmental degradation

The effects of human activities on coral reefs were comprehensively reviewed by Salvat (1987). The primary causes of degradation are discussed below.

4.1. *Physical damage to coral reefs*

Reefs are often damaged by reef users. The careless use of boat anchors, often in prime dive locations, is well recognised and increasingly seems to be fairly well taken care of by dive operators, charter yacht companies and others with a financial interest in maintaining the environment that they use. Likewise, careless or inadvertent damage to corals, particularly by inexperienced divers, seems to be on the wane. Tourists have caused serious damage to shallow reefs by tramping over shallow areas and by standing on corals when snorkelling (e.g. Buccoo Reef in Tobago). Ignorance is a major factor and can be counteracted by resort owners and other interested parties providing appropriate information.

Individual fish traps cause little damage. Most fishers aim to set their traps in sandy areas adjacent to corals and when hauling the trap are careful to rapidly get it clear of the reef to avoid damage to the trap. When numerous traps are set attached to a single line, usually on relatively flat shelves, damage to patch reefs is a real possibility, particularly if the line is hauled in heavy seas. Fortunately, destructive techniques such as "muro-ami fishing", which is practised in parts of East Asia, are not prevalent in the Caribbean.

Catastrophic damage to reef crests and adjacent areas that is caused by the grounding of large vessels and by subsequent efforts to recover the vessel is, like hurricane damage, a circumscribed event, with no lasting damage to the reef ecosystem even if the immediate effect is distressing.

The major physical factor impacting on coral reefs is sedimentation. Poor land use, whether for forestry, agriculture, mining or infrastructure development, results in mud, silt and sand flowing into the sea. Heavier particles that settle on corals will simply smother the corals and they will rapidly die if the sediments are not dispersed by strong wave action and currents. Habitat availability is reduced if the interstices of the reef are filled by sediments and biodiversity loss ensues. Turbidity caused by suspended solids reduces photosynthesis and promotes reef erosion. Reefs do not develop adjacent to major rivers for this reason. The damaging sedimentation comes from small streams and ravines passing through vegetated areas. When these areas are logged, the related effects can be catastrophic. The real costs of logging, both to marine and to terrestrial ecosystems, seems likely to be greater that the value of the timber. Progressive clearing of vegetation for small-scale agriculture has effects that are more insidious but the long-tem result is the same. The solution is profoundly difficult if land shortage and lack of alternative employment is the cause of farming on steep slopes.

Sedimentation resulting from infrastructure development seems mostly to arise from ignorance and sometimes merely from greed. Careful engineering and construction can avoid problems but this only happens when relevant authorities take the care to ensure that environmental guidelines are followed and transgressors punished. Some of the worst offenders are resort and marina developers.

Simple application of environment laws can provide remedies if commercial agriculture, mining or infrastructure developments cause sedimentation. As with all commercial developments, if developers are not prosecuted because of their personal standing or political connections, the efforts of conservation agencies become meaningless.

4.2. *Pollution and contamination*

Pollutants fall into four broad categories; plant nutrients, chemical wastes, herbicides and pesticides and oil.

Normally, coralline seas have barely detectable quantities of nitrates and phosphates and those that are released by decomposition are rapidly recycled. When treated or untreated sewage, other organic wastes or agricultural fertilizers run into sea water the growth rates of both phytoplankton and benthic algae are greatly enhanced. Transmission of light through seawater can be greatly reduced and insufficient light reaches the zooxanthellae. The corals consequently die. In shallow reef areas sufficient light may reach the seabed, causing rich growth of macroalgae with the same result; the corals are shaded out and die.

Chemical wastes in industrial and mining effluents and in drilling mud can act and interact in innumerable ways, some chemicals being directly toxic to reef organisms and other acting at subtler levels in disrupting physiological and genetic functions (Brown 1987). Early larval stages are particularly susceptible and aquaculturists are well aware that nothing but the purest seawater will suffice when attempting to rear marine larvae.

Herbicides and pesticides derived from agricultural sources are selectively toxic to many species of marine organisms, as are chemicals traditionally used in anti-fouling paints or coatings. The specific actions of most such chemicals are unknown.

Oil spills can be lethal to all organisms in intertidal zones. Below the tides, the effects on coral do not seem to be very serious, at least in the short term (Loya and Rinkevitch 1987). The vast quantities of oil released in Kuwait waters during the 1991 Gulf War apparently had no visible effects on reef health in adjacent areas (Vogt 1995).

5. Fishing

5.1. *Physical damage*

As mentioned previously, most fishing techniques used on reefs are not seriously destructive, primarily because the fishing gears are usually quite fragile and fishers are eager to avoid loss or damage to their equipment. The exceptions are the massive roller trawls that are designed to roll over or tear through irregular benthic terrain. Such trawls are known to have eliminated coral and associated sponge and seafan communities over large shelf areas of the South China Sea (McManus 1997), the Arufera Sea off Northern Australia and around the Florida Peninsula – to the extent that the roller trawls are no longer needed to fish in these areas. The reefs have been reduced to rubble and sand.

Fishing with explosives is a widespread problem and is regarded as criminal behaviour in even the most tolerant of communities. The reef infrastructure is simply shattered by blasts and most species of organisms are either crushed if they are in the reef framework or die of embolisms if they have swim bladders or lungs.

5.2. *Intoxicants and poisons*

Fish poisons, most often derived from derris root, have been used for fish capture for many centuries. Although high concentrations are usually fatal to small fish, when used in moderation, the effects are usually as an aid to spearing larger fish. The modern derivative, rotenone, is seldom available to artisanal fishers and those wishing to use poisons have easy recourse to inexpensive sodium cyanide or household bleach (Eldredge 1987).

Cyanide has received prominence through its use in the live fish trade in South East Asia. It stupefies the fish and makes them easy to capture. If they are rapidly removed from the tainted water they will recover. This has resulted in the virtual elimination of many of the top predators, mostly groupers and Maori wrasse, from many Indo-Pacific reef systems. Because of the extremely high prices paid for live seafood in Southeast and East Asia, and hence the profitability of the fisheries for these species, the problem has been extremely difficult to overcome (Lau and Parry-Jones 1999). Fortunately, it does not appear to have affected the Caribbean. Cyanide has also been used for the collection of ornamentals for the aquarium trade.

Bleach, with sodium hypochlorite as the active ingredient, is available from any grocery or supermarket. It is fatally toxic to most marine organisms, from bacteria to groupers even in very low concentrations. It has been a serious problem in some countries when used by divers, not only killing the target reef fish in caverns or reef crevices, but most of the reef life in the vicinity. Fortunately, most reef fishers are simply unaware of its possible use in fishing.

5.3. *Changes in community composition and trophic structure caused by selective fishing*

About 180 species of coral reef fish can be found in Caribbean fish markets, of which about 30 species normally make up about 90% of the catch (Munro 1999). Most of this catch is taken in portable fish traps made of wire mesh supported on a framework of mangrove poles. Very few species of reef fish will not enter traps. Hooks are selective for predatory species and spear-fishers will usually shoot at the largest fish they see, regardless of species.

Very few Caribbean reefs are not heavily fished and most are seriously over-fished. The vulnerability of a species to over-fishing depends on its biological characteristics and its catchability. Small species with high growth rates, high fecundity and early maturity are the most resilient to exploitation, while large, slow-growing species, which mature at a substantial size, are easily over-fished. If fishes are taken by fishing gears when they are immature, they are liable to recruitment over-fishing. That is, the numbers of juveniles entering the fishery will decrease because of the scarcity of mature adults. Additionally, catchability (the fraction of a fish stock that is removed by one unit of fishing effort with a particular fishing gear) is very variable, for a variety of biological, behavioural and physical reasons. For example, groupers have high catchability. They will enter fish traps very readily, often to prey on smaller fish already trapped and, once caught, are not very adept at escaping from traps. In contrast, squirrelfish have no particular reason for entering traps and when captured seem to have little difficulty in finding their way back out of an entrance funnel.

As a result of these factors, when all of the coral reef species are concurrently taken, the most catchable, large, species face rapid local reductions in biomass and numbers of mature individuals. They become technically over-fished while less catchable, small, species are still being exploited at levels below the maximum possible catch. The composition of catches thus changes progressively. Catches of the large predators soon reach peak and then decline and modest-sized omnivores then dominate the catch. Eventually, small herbivorous fish become the main components of the catch, and may actually increase in relative abundance for a while because of the absence of predators, before they too become over-fished.

In large-scale fisheries for a limited array of species, serious damage to stocks may be limited and species extinctions are not very likely because, while catch rates decline, the cost of fishing remains the same. Eventually the value of the catch equals these costs and fishing ceases, unless governments unwisely intervene with subsidies. However, in most coral reef fisheries the equipment is relatively inexpensive and it is often fabricated by the fisher. For persons with no other skills and no opportunities for employment, the opportunity cost of labour is effectively zero. Thus fishing can remain a source of income and profits, however marginal, even when stocks have been decimated and the most vulnerable species have become extinct.

This is happening throughout the Caribbean. In Jamaica, which probably has one of the most intensively exploited fisheries in the Caribbean, catch rates have declined to a tiny fraction of those obtained from unexploited stocks. Valuable groupers, snappers and jacks are very seldom caught and small species of low-valued parrotfish and surgeonfish predominate in catches. Deep-bodied fish such as triggerfish and angelfish have virtually disappeared because, owing to their body shape, they become catchable in traps in the first few months of their lives.

5.4. *The recruitment problem*

The view held by fishery scientists for many years was that coral reefs around different islands were closely interlinked by the drift of larvae downstream with prevailing currents. Thus, even overexploited fish stocks could be replenished by larvae derived from less heavily exploited stocks elsewhere (Roberts 1997). In recent years, this sanguine view has changed.

The weight of evidence now is that recruitment is very largely a local affair (Munro and Polunin 1997) and that individual islands or large reef systems are mostly dependent upon having adequate spawning stock biomasses of all of the species in the ecosystem. This is because mortality rates of marine larvae are high (about 20% per day for fish and shrimp) and ocean currents are very erratic and dispersive (Cowen et al. 2000). Consequently, any fish larvae that are transported offshore and actually survive the 20-50 days required to reach metamorphosis have a very great chance of finding themselves in the open ocean, far from any reef system. On the other hand, postlarvae, usually about 2 cm long, derived from eggs and larvae that are trapped in nearshore eddies or gyres, have a good chance of reaching shore because most species have surprisingly great swimming abilities and have no problem swimming many kilometres (up to 25 km.day^{-1}) towards shore (Stobutzki and Bellwood 1994). The stimuli that tell them in which direction to swim are unknown but could include traces of organic reef-related chemicals or reef noises.

Recent comparative studies of recruitment rates of reef fish in Jamaica and the British Virgin Islands (BVI) have shown that catch rates of most species in Jamaica are two to three orders of magnitude less than in BVI. Juveniles of some species were absent from catches in Jamaica. Small species of parrotfish, which mature before entering the trap fishery, and some surgeon fish, which have larvae adapted for an extended life in oceanic waters, were the only species which were not significantly reduced in abundance (Munro and Watson 1999). Jamaica's stocks are not being replenished to any significant degree by fish spawning elsewhere in the Caribbean.

The groupers, which are some of the most valuable components of reef fisheries, are particularly vulnerable to recruitment overfishing because they are protogynous hermaphrodites. All small groupers are female and they change sex around a certain size. As large fish are the first to be eliminated from heavily exploited stocks, insufficient males may be present to ensure successful spawning. There is evidence that this is happening in the Caribbean and the famed Nassau grouper, *Epinephelus striatus*, may become the first species of fish to become extinct in the Caribbean (Sadovy 1993).

5.5. *Ecosystem effects*

If predatory reef fish are over-fished, their prey species can be expected to increase in numbers. If the intermediate small predators are over-fished, the herbivores will then respond by increasing in biomass. When they are over-fished there will be no control of algal production and biomasses of algae and seagrasses will increase, with most production simply turning to detritus.

Currently, reefs on the north coast of Jamaica are almost entirely overgrown by macroalgae and the cover of live coral is extremely low. There is not full agreement on the reasons for this situation, but it appears that this can largely be attributed to the long-term effects of over-fishing (Hughes 1994). The narrow island shelf was covered by flourishing coral reefs until 1984. Then in rapid succession, a catastrophic epidemic swept through the herbivorous long-spined sea urchins, *Diadema antillarum*, throughout the Caribbean and the north coast of Jamaica was hit by Hurricane Allen. The reefs were accordingly reduced to rubble and massive corals stripped of tissue. Macroalgae colonised all the newly exposed surfaces and, in the absence of both sea urchins and herbivorous fish, have remained dominant up to the present. Other parts of the Caribbean with less heavily exploited fish stocks lost their sea urchin populations and suffered hurricanes, but the reefs were not overgrown by algae. Most of the evidence suggests that over-fishing was the cause of this catastrophe. Sea urchin stocks appear to be rebuilding throughout the Caribbean and there are indications of a slow recovery of the reefs on the Jamaican north coast but full recovery is highly unlikely if the herbivorous fish stocks remain drastically depleted.

Changes in the vitality of reefs for any of the reasons mentioned above leads to loss of habitat for many species of fish and invertebrates. Widespread degradation of reefs will lead to extinction of many specialised reef species, reduction in the numbers of linkages in food webs and increasing instability of the component populations of reef ecosystems.

6. Management tools and information

As a result of many decades of research on coral reefs, we have long had sufficient understanding of reef processes to embark on appropriate management strategies. Large numbers of scientific reports and massive compilations of data are available. ICLARM's contributions in this area are particularly important.

ReefBase, a global database on coral reefs and their resources (McManus and Ablan 1997) is available on CD-ROM (Reefbase 2000) and on the Internet. It is close to its objective of covering all of the world's reefs and providing information on reef communities, human and natural stresses, harvests (including mariculture), management and threats. It also provides methods for surveying reefs and for gathering socio-economic data.

A similar concept underlies FishBase, also available on CD-ROM (Froese and Pauly, 2000, FishBase 2000) and on the Internet, and which provides summaries of all available data on almost all fish species in the world. This includes information on nomenclature, distribution, catch statistics, population dynamics parameters, foods and feeding, reproduction, genetics and aquaculture, ichthyoplankton and morphology and physiology. It also enables users to link lists of fish species to biological information and enables country specialists to update country-specific information, including local names of fishes.

In the context of fisheries assessment for management purposes, FishBase allows quick, interactive generation of life-history parameters for species to be assessed, allowing re-calculations using local data if available. Computations include relative yield/recruit, state of exploitation, population resilience indicators, population intrinsic rate of increase and species trophic level. Additionally, use of a spreadsheet routine allows characterisation of the state of exploitation of a species from a length-frequency distribution, calculates lost yield, and provides plots that graphically relate the length frequency profile to length at maturity, biomass and potential biomass. A number of empirical equations are provided that can be used to estimate various life-history parameters such as asymptotic length, length at maturity, life span, age at maturity and length at maximum possible yield per recruit.

A third management tool that is seeing increasing use is the Ecopath software. The original model was applied to French Frigate Shoals in the Hawaiian Islands (Polovina 1984). This was a steady-state model of the reef ecosystem, based on knowledge of biomasses, mortality rates and trophic interrelationships of the main components of the reef communities. Subsequent versions, developed by ICLARM added many levels of sophistication (Christensen and Pauly 1992, 1993). The latest version, called Ecopath-with-Ecosim (EwE), has been developed in collaboration with scientists at the University of British Columbia and it is available on the Internet. It can be used to simulate and thus predict the results of changes in aquatic ecosystems. For example, the effects of the creation of a marine protected area on fish catches in adjacent regions can be predicted, or the effect of increased harvests of fish on the biomass of macroalgae on a reef can be investigated. Such models require much data. A routine in FishBase can be used to obtain parameters for Ecopath models of designated ecosystems. One such area already so defined is the Caribbean Sea and a list of fish species can be generated with parameters needed for Ecopath modelling.

Several Ecopath models have been developed for Caribbean coral reefs (Opitz 1998, Arias-Gonzales et al 1998). Ecopath models are currently under development for the heavily exploited Discovery Bay reef system in Jamaica and the lightly exploited Hans Creek area in BVI, in which the effects of intensive fishing on community structure will be examined (Munro and Watson 1999).

7. Sustainable management

7.1. *Education, legislation and community support*

Databases and models such as Ecopath, FishBase and ReefBase are useful to scientists in understanding management options and for presenting information to administrators, but much more effort must go into public awareness. Without the support of coastal communities, coral reef management is doomed to failure. This is particularly the case where many sectors have interests, often conflicting, in using the coastal zone for income generation, recreation or as a dump for liquid or solid wastes.

Far more effort needs to be put into educating school children about the marine environment, particularly those living in small island states, where the exclusive economic zone is usually vastly larger than the land and where the benefits of sustainable use should accrue to the populace in perpetuity.

It has also been shown that fisheries and conservation legislation is ineffective if the community neither understands nor supports the laws. If impoverished communities perceive that they are disadvantaged by laws, whether or not that is actually true, they will disregard the laws. The police are disinclined to prosecute people who are struggling to make a living. In a recent case in Jamaica, a magistrate treated poaching in a marine reserve as an utterly trivial offence and was clearly unaware that any benefit would accrue to the community from proper management of the reserve.

It has been repeatedly demonstrated that many, if not most, coral reef fisheries are overexploited and consequently yield a smaller and much less valuable harvest than is potentially possible. There are simply too many fishers. Invariably, the underlying reasons are the lack of alternative opportunity and landlessness. In many countries, large proportions of the fishing communities are not fishers by tradition. They are landless people who have moved to the seashore to eke out a living from the only open access resource that is available. Many fishers in Southeast Asia do not eat fish. All that is caught must be sold in order to buy rice. In Jamaica, increasing numbers of young men with no alternative opportunities are taking to spear-fishing, which can provide a small income from a small capital outlay and great personal effort. But, as stated previously, the reefs are already over-fished.

Resolution of the conflict between immediate human needs and the fragility of coral reef ecosystems is the greatest challenge facing the sustainable management of coral reefs.

7.2. *Solutions*

Methods for sustainable management of fisheries are well understood, as are the effects of most sources of environmental change. Harvests in overexploited coral reef fisheries in the Caribbean could be improved by increasing mesh sizes of traps and reducing fishing effort. Catches would be more valuable if desirable species were re-established in the reef ecosystems. Spiny lobsters are an immensely valuable resource and, as they are unaffected by being hauled to the surface in a trap, can easily be released if undersized. Almost inevitably, they will be recaptured when they are larger and much more valuable. This seldom happens and lobsters scarcely larger than prawns are a common sight.

The underlying problem, so well known as "the tragedy of the commons", is that individual fishers are unwilling to restrain their fishing effort, increase mesh sizes and return undersized lobster to the sea, unless they are convinced that their fellow fishers will do likewise. Anyone who breaks the rules will benefit greatly from the restraint shown by the law-abiding fishers. Much the same applies to other users of the reefs, whether they are divers, hoteliers, yachtsmen, industrialists, agriculturists or government agencies.

The only feasible solution so far advanced is "co-management", in which governments work with all stakeholders in the entire watershed, not just the coastal communities, to arrive at equitable solutions to the use of the resource. This requires considerable organisational skills and reasonable funding so that the disadvantaged sectors can actually afford the time to participate.

While various tourism associations, chambers of commerce and agricultural and industrial groups are commonplace, the fishers, who arguably have the greatest impact on coral reefs, are seldom represented by any co-operative and association and cannot speak with a unified voice. But such associations are the only way whereby fishers can be represented in co-management fora. This should also lead the way to community-based management of the resources they exploit.

Community-based management programmes have been reported to have some success in Southeast Asia (Alcala 1998) and are a traditional form of fishery management in parts of the South Pacific. For this to be successful, fishers need to have exclusive access to the fishery resources along a sector of coast where they are active, free from forays mounted by commercial concerns in urban centres. Some success has been reported from several areas in Jamaica, where resourceful organisers with some financial backing have been able to organise coherent groups. A significant development was the recent decision by fishers in Discovery Bay, Jamaica, to set aside all of the shallows of Discovery Bay as a fishery reserve. This decision largely developed as a result of ten years of patient effort by the Fisheries Improvement Project operating from the University of the West Indies' Discovery Bay Marine Laboratory. The necessary proposals have been put forward to the Government. Coming from a representative group in the community, such proposals are readily supported by politicians.

Marine fishery reserves (MFRs) or marine protected areas (MPAs) are widely seen as a major component of efforts to sustainably manage fisheries and coral reefs. They have to be of considerable size in order to rebuild significant spawning stock biomasses that will replenish fisheries in adjacent or down-current areas. Additionally, they have to be founded on a wide degree of community support. Otherwise, as has been amply demonstrated in the Florida Keys, the local community will fight vigorously to prevent the reserve being established in "their" piece of the seascape.

In countries where fishers are some of the poorest members of the citizenry, MPAs or MFRs will displace established fishers. If they are merely forced to regroup in unprotected areas the fishing intensity in the unprotected area will increase, to the detriment of the entire reef resource. Instead, they must be found alternative employment in the MPA, as rangers, dive guides or boatmen, or given a pension equal to earnings foregone on condition that they do not resume fishing.

Direct interventions to re-establish fish stocks or to increase stocks of desirable species by stock enhancement or restocking are rapidly becoming technically and financially feasible, provided sufficient precautions are observed to avoid ecological and genetic pitfalls (Munro and Bell 1997). Various forms of small-scale aquaculture provide alternative income-earning opportunities for fishers in the Indo-Pacific (Bell and Gervis 1999) but none are clearly feasible in the Caribbean at present.

Finally, it must be recognised that all interventions to manage Caribbean coral reefs are very likely to be difficult and expensive. However, we have known how to manage Caribbean reef fisheries for at least thirty years. Can we calculate the compounded loss from non-management of these fisheries? What is the loss sustained as diving tourists progressively move elsewhere in search of reefs that are more attractive? These are very significant and important questions to consider.

8. References

Alcala, AC. 1998. Community-based coastal resource management in the Philippines: A case study. In: Williams MJ (ed.) A roadmap for the future for fisheries and conservation. Manila: International Center for Living Aquatic Resources Management (ICLARM) Conference Proceedings 56, pp. 13-20

Arias-Gonzales, JE. 1998. Trophic models of protected and unprotected coral reef ecosystems in the South of the Mexican Caribbean. Journal of Fish Biology 53 (Supplement): 236-255

Bell, J and Gervis, M. 1999. New species for coastal aquaculture in the tropical Pacific – constraints, prospects and considerations. Aquaculture International 7:207-223.

Brown, BE. 1987. Heavy metals pollution on coral reefs. In: Salvat, B (ed.) Human impacts on coral reefs: facts and recommendations. French Polynesia: Antennae Museum E.P.H.E., pp.119-134

Christensen, V. and Pauly, D. 1992. ECOPATH II - a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling 61:169-185

Christensen, V. and Pauly, D. 1993. On steady-state modelling of ecosystems. In: Christensen, V and Pauly, D (eds) Trophic models of aquatic ecosystems. Manila: International Center for Living Aquatic Resources Management (ICLARM) Conference Proceedings 26. pp. 14-19

Cowen, RK, Lwiza, LMM, Sponaugle, Paris, SCB and Olsen, DB. 2000. Connectivity of marine populations: Open or closed? Science 287: 857-859

Eldredge, LG. 1987. Poisons for fishing on coral reefs. In: Salvat, B (ed.) Human impacts on coral reefs: facts and recommendations. French Polynesia: Antennae Museum E.P.H.E., pp. 61-66

FishBase, 2000. FishBase 2000 CD-ROM. Manila: International Center for Living Aquatic Resources Management (ICLARM).

Froese, R. and Pauly, D (eds). 2000. FishBase 2000: Concepts, design and data sources. Manila: International Center for Living Aquatic Resources Management (ICLARM)

Hughes, TP. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547-1551

Lau, P and Parry-Jones, R. 1999. The Hong Kong trade in live reef fish for food. Hong Kong: TRAFFIC East Asia and World Wide Fund for Nature Hong Kong

Lewis, JB. 1977. Processes of organic production on coral reefs. Biological Reviews 52:305-347

Loya, Y and Rinkevitch, B. 1987. Effects of petroleum hydrocarbons on corals. In: Salvat, B (ed.) Human impacts on coral reefs: facts and recommendations. French Polynesia: Antennae Museum E.P.H.E., pp. 91-102

McManus, JW. 1997. Tropical marine fisheries and the future of coral reefs: A brief review with emphasis on South-east Asia. Proceedings of the Eighth International Coral Reef Symposium 1:129-134

McManus, JW and Ablan, MCA. 1997. ReefBase: a global database on coral reefs and their resources. Manila: International Center for Living Aquatic Resources Management (ICLARM)

Munro, JL. 1999. Effects of fishing on coral reef ecosystems. In: Schei, PJ, Sandlund, OT and Strand, R (eds.) Proceedings of the Norway/UN conference on the ecosystem approach to sustainable use of biological diversity. Trondheim: Norwegian Directorate for Nature Management and Norwegian Institute for Nature Research, pp.143-148

Munro, JL and Bell, JD. 1997. Enhancement of marine fisheries resources. Reviews in Fisheries Science 5:185-222

Munro, JL and Polunin, NVC. 1997. A decade of progress in coral reef fisheries research: 1986-1995. Proceedings of the Eighth International Coral Reef Symposium 2:2003-2008

Munro, JL and Watson, M. 1999. Caribbean Marine Protected Areas Project: The role of marine protected areas in fisheries management and biodiversity conservation in coral reef ecosystems. Phase 1 - 1996-1998. Tortola, BVI: ICLARM Technical Report to the United Kingdom Department for International Development

Opitz, S. 1996. Trophic interactions in Caribbean coral reefs. Manila: International Center for Living Aquatic Resources Management (ICLARM) Technical Report 43:1-341

Polovina, JJ. 1984. Model of a coral reef ecosystem. I. The Ecopath model and its application to French Frigate Shoals. Coral Reefs 3:1-11

ReefBase, 2000. ReefBase: a global database of coral reefs and their resources. Ver. 2000 CD-ROM Philippines: International Center for Living Aquatic Resources Management (ICLARM)

Roberts, CM. 1997. Connectivity and management of Caribbean coral reefs. Science 278:1454-1457

Sadovy, Y. 1993. The Nassau grouper, endangered or just unlucky?. Reef Encounter 13:10-12

Salvat, B. (ed.). 1987. Human impacts on coral reefs: facts and recommendations. French Polynesia: Antenne de Tahiti Museum, E.P.H.E. 253 pp.

Stobutzki, IC and Bellwood, DR. 1994. An analysis of the sustained swimming abilities of pre-settlement and post-settlement coral reef fishes. Journal of Experimental Marine Biology and Ecology, 175:275-286

Vogt, HP. 1995. Coral reefs in Saudi Arabia: 3.5 years after the Gulf War oil spill. Coral Reefs, 14:271-273

Predicting self–recruitment in marine populations: Biophysical correlates and mechanisms

Su Sponaugle[1], Robert K. Cowen[1], Alan Shanks[2], Steven G. Morgan[3], Jeffrey M. Leis[4], Jesús Pineda[5], George W. Boehlert[6], Michael J. Kingsford[7], Kenyon Lindeman[8], Churchill Grimes[9], John L. Munro[10]

[1]Marine Biology and Fisheries, RSMAS, University of Miami, Miami, FL 33149, USA

[2]Oregon Institute of Marine Biology, University of Oregon, 619 Boat Basin Dr., P.O. Box 5389,
Charleston, OR 97420, USA

[3]University of California, Bodega Bay, 2099 Westside Rd., P.O. Box 247, Bodega Bay, CA 94923, USA

[4]Division of Vertebrate Zoology, and Centre for Biodiversity and Conservation Research, The Australian
Museum, 6 College St., Sydney, NSW 2010, AUSTRALIA

[5]Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

[6]National Marine Fisheries Service, Pacific Fisheries Environment Lab, 1352 Lighthouse Ave., Pacific
Grove, CA 93950, USA

[7]School of Biological Sciences, University of Sydney, Sydney, NSW 2006 AUSTRALIA

[8]Environmental Defense, 14630 SW 144 Terrace, Miami, FL 33186, USA

[9]NOAA, NMFS, Santa Cruz Laboratory, 100 Shaffer Rd., Santa Cruz, CA 95064,USA

[10]ICLARM Caribbean/Eastern Pacific Office, Suite 158, Inland Messenger Service, Road Town, Tortola,
British Virgin Islands

07/2001 Draft for submission to *Bulletin of Marine Science Special Publications*

Abstract.

Mounting evidence suggests that some populations of benthic marine organisms may be less demographically "open" than previously thought. The degree to which a population receives recruits from local sources versus other populations has important ecological and management ramifications. For either of these reasons, it is often desirable to estimate the degree to which a population of interest is self-recruiting. Although methods for actual estimation of population self-recruitment are limited and often difficult to employ, the presence of several biological and physical conditions may improve our estimates of self-recruitment for particular populations. Biological traits of benthic adults (relative fecundity, spatial and temporal patterns of spawning and larval release, parental investment), as well as pelagic larvae (stage of development at hatching, pelagic larval duration, vertical migration behavior, horizontal swimming ability, and sensory capabilities) influence where and when larvae are released, where and how they are transported, their ability to actively move in the pelagic realm, and finally, spatial and temporal settlement patterns. Physical variables potentially influencing self-recruitment include site isolation, coastal complexity and flow variability. Within these physical variables we discuss explicit mechanisms by which larvae may be retained in proximity to their natal population. We provide examples from specific locations such as coral reefs, isolated islands and seamounts, and semi-enclosed embayments such as lagoons and estuaries, as well as characteristic oceanographic features such as upwelling systems, fronts, moving convergences, eddies and counter currents.

We evaluate direct and indirect evidence to predict the relationship between these biophysical variables and the degree of self-recruitment in benthic marine organisms. We conclude that physical factors that result in a departure from unidirectional, depth-uniform water flow provide the opportunity for retention of larvae, and therefore of self-recruitment. These physical factors are common in the ocean and vary in intensity among locations and times. Some enable retention of passive larvae (physical retention), whereas others lead to retention only with active behavioral input by the larvae (biophysical retention). Larval behavior that can contribute to or result in retention or return to natal sites ranges from simple vertical orientation that is within the capabilities of the larvae of most taxa to complex sensory abilities and strong swimming that are known to occur in larvae of a few taxa, particularly decapod crustaceans and fishes. For all taxa, both the pelagic larval duration, and the time to behavioral competency will have a strong influence on likelihood of self-recruitment. Understanding the biophysical mechanisms by which larvae are retained near or return to their natal population will be necessary before generalizations can be made. Examples highlight the importance of each variable to processes controlling self-recruitment. For most correlates, further study is clearly warranted. Although certain variables hold promise for predicting self-recruitment, complex, non-linear interactions among these biophysical variables must be considered.

Key phrases and keywords*:* population replenishment; population connectivity; open or closed marine populations; larval retention; larval transport; larval dispersal; larval period; larval behavior; biophysical interactions; oceanography; recruitment

INTRODUCTION

Many benthic marine organisms have life histories that include a pelagic larval phase. Although many taxa exist in local populations (defined here as all the individuals of a species living and reproducing in a particular area naturally delineated by geography or oceanography, or artificially defined by human interest or economics), due to this pelagic larval phase, there has been a strong historical assumption of broad population connectivity via larval dispersal across such species' ranges. A refinement of this paradigm suggests that marine populations range from entirely *closed*, self-sustaining populations (e.g., endemic island species where 100% of recruitment is due to the settlement of offspring produced by that population) to fully *open* populations recruiting only a relatively small proportion of their own offspring back to the population (i.e. receiving a high number of recruits from other populations). This concept can be supported by a few examples from either end of the spectrum, however, there is much more uncertainty between these extremes and many benthic marine populations likely have only a portion of their recruitment "subsidized" (*sensu* Pascual and Caswell, 1991) from external sources. For these recruitment-subsidized populations, the question becomes: relative to a particular area or local population, to what degree is the population self-recruited or subsidized from elsewhere?

Ocean flow fields operating during the pelagic phase theoretically disperse larval propagules (e.g., Fulton, 1989) and enhance population connectivity. However, there have been a number of hypotheses (see Sinclair, 1988) and recently, new evidence (Jones et al., 1999; Swearer et al., 1999; Cowen et al., 2000; reviewed in Swearer et al., this volume) suggesting that, in fact, some populations of benthic marine organisms may be less *open* than previously thought. The interaction of various biophysical mechanisms may fully or partially counter dispersion and enable the retention of larvae near their natal source. Particular species may be more or less likely to exist in open or closed populations depending on their life history traits (both adult and larval) or where their populations are located. For example, species with very short larval periods may be more likely to settle close to their natal source. For species with longer pelagic durations, local populations may be more or less open or closed depending on their immediate physical setting and behavior of the larvae. Not only are multiple variables important in determining relative connectivity, but the complex interactions of these variables likely has contributed to our inability to resolve connectivity patterns in nature.

Of critical importance to any discussion of population connectivity is the need to define appropriate temporal and spatial scales (see Warner and Cowen, this volume). In the ensuing discussion, emphasis is placed on processes contributing to the exchange of individuals (particularly larval stages) over ecologically meaningful scales. Specifically, for the purposes of this paper, self-recruitment refers to *levels of retention that substantially affect the abundance of a local population* (i.e. *populations exhibiting high self-recruitment are those whose numbers are significantly influenced by recruitment of their own offspring).* Even with substantial self-recruitment, rates of exchange among populations are likely much higher than that required to maintain genetic homogeneity of a population. The processes responsible for exchange at ecologically meaningful levels are far more complex, and are likely the processes to which adaptation has occurred, rather than those associated with rare long-distance exchange events (see Strathmann et al., this volume).

Our discussion will focus on *local populations*, the dimensions of which will be defined by the biological traits of the organism and the physical setting as well as the scale of the question (i.e. whether of a management or ecological nature). Our focus is on scales that are smaller than the geographic range of a species (e.g., single component population of a meta-population). For internal consistency, we consider the scale of a local population to be within the range of 1-100 km.

What follows is a short discussion of each of several critical biological and physical variables (defined in Table 1) and how they might contribute to the likelihood of a population exhibiting self-recruitment. Although many of the biological traits and physical processes clearly must interact to either retain propagules near or return propagules to the natal region, for the purposes of our discussion, we first summarize each variable independently and examine it in terms of self-recruitment. The hypothetical relationship between each isolated variable and the proportion of self-recruitment a population experiences is then evaluated based on empirical evidence. Much supporting evidence is drawn from estuarine and coral reef case studies largely because the relationship between retention and biophysical processes may be easier to define in these relatively discrete habitats. However, examples also are drawn from other taxa in other systems such as continental shelves and open ocean gyres. Further, where appropriate, the discussion is broadened to include examples from non-benthic marine populations. In the section on physical processes, we include a brief summary of how different mechanisms may function in particular areas to retain larvae. As will be apparent, many predictions remain largely untested and serve as suggestions for future research.

In this paper, we cite review papers wherever possible to reduce the number of cited papers while at the same time providing the reader with an entry to the literature. Note that the issue of self-recruitment extends over multiple temporal scales from the ecological to evolutionary. These scales clearly overlap, but we have placed most of our emphasis on purely ecological scales. For further detail on how ecological processes discussed herein are translated to an evolutionary scale, see reviews by Bradbury and Snelgrove (2001) and Strathmann et al. (this volume).

A. BIOLOGICAL TRAITS

1. *Adult fecundity*

Adult reproductive characteristics clearly determine population replenishment, but only certain traits may be important to the degree of self-recruitment a population experiences. As a species-level trait, fecundity should not directly influence the likelihood of self-recruitment. If fecundity is similar among all populations of a species, all else being equal, the proportion of self-recruitment for each population should be the same (i.e. for different species, the percent of self-recruitment should be independent of a species' fecundity).

However, where individual fecundity varies among populations of the same species, fecundity may influence local self-recruitment. For example, a population of fishes in a protected area may attain a larger mean body size (e.g., Polunin and Roberts, 1993). Larger fishes typically have a higher reproductive output, thus this protected population would contribute relatively more offspring than other local populations of the species outside the protected area. Assuming complete mixing of propagules from all metapopulations, a higher number of the protected population's offspring should recruit back to the local population. Thus, as a population-level variable, increasing relative individual fecundity should directly enhance the likelihood of local self-recruitment.

2. *Adult mobility and spatial patterns of spawning or larval release*

Adult mobility in marine organisms ranges from zero in sessile adults through animals undertaking basin-scale migration patterns (e.g., tunas). Mobility in general will be tightly coupled to the functional boundaries of a given population, so as such, should not directly influence self-recruitment. However, although adult stages presumably exist in an environment favorable to adult survival, this location may not be conducive to egg or larval survival or subsequent recruitment to the adult population. Some species undergo significant migrations to place their eggs in environments that may maximize offspring survival.

As early as a century ago, it was recognized that spawning locations were spatially more restrictive than the distribution of the population (Damas, 1909). Spawning sites of marine fishes have been hypothesized to maximize larval feeding potential (Lasker, 1975) or minimize predation on propagules by dispersing larvae offshore (Johannes, 1978). In addition, some species may spawn at sites where currents are predictable and geographically stable, allowing for the retention of larval aggregations for several months (e.g., Atlantic herring, Atlantic cod, and haddock: Iles and Sinclair, 1982; O'Boyle et al., 1984; Gagné and O'Boyle, 1984; Smith and Morse, 1985). Currents also may favor the transport of larvae to nursery areas, and the life cycle is completed when juveniles migrate to adult habitats (Harden Jones, 1968). For example, plaice larvae spawned at sites in the North Sea are carried by currents to nursery grounds (Cushing, 1975) and mature fish tend to return to the same spawning site year after year. Due to selection of spawning sites and the subsequent larval drift (Cushing, 1975) or larval retention (reviewed in Sinclair, 1988), North Sea plaice populations may show a substantial degree of self-recruitment. Other examples of spawning migratory behavior include pelagic armorhead (Boehlert and Sasaki, 1988), southern bluefin (Davis et al., 1990), snapper and grouper (reviewed in Domeier and Colin, 1997), and American eels (McCleave and Kleckner, 1987).

Smaller scale migrations are also evident: grunion and capelin enter the intertidal zone to lay their eggs on beaches (Thompson, 1919; Frank and Leggett, 1981); and lingcod spawn in nests close to the topographically complex rocky shoreline so that negatively buoyant larvae hatch into water with reduced alongshore flow (Shaw and Hassler, 1989). However other small-scale migrations may facilitate offshore transport of eggs: spawning at reef promontories is a common behavior for pelagic-spawning reef fishes (Johannes 1978).

Adult invertebrates generally are less vagile than fishes, and long migrations to release offspring are less common. There are notable exceptions, such as the migrations by lobsters (*Panulirus* spp., *Jasus* spp., *Homarus* spp.) on the continental shelves of Australia and the east coast of North America (Rebach, 1983; Campbell, 1986), the onshore spawning migrations by *Cancer* spp. crabs in the North Sea and northeast coast of North America (Nichols et al., 1982; Rebach, 1983), aggregated spawning by the squids *Loligo opalescens* along the coast of California (Cailliet and Vaughan, 1983) and *Illex illecebrosus* along the eastern U.S. coast (Trites, 1983). As with some fish migrations, alongshore adult migrations by adult blue crabs, *Callinectes sapidus*, may compensate for the displacement of larvae by coastal currents and increase the chances of self-recruitment (Oesterling, 1977; Provenzano et al., 1983; McConaugha, 1988; Steele, 1990).

Although these spawning migrations are most often thought to place the larvae in optimal locations for survival it is entirely possible that the locations also enhance retention (e.g., Atlantic herring; Iles and Sinclair, 1982). By enabling more control over where and when offspring are released, increased adult mobility and selection of particular spawning locations could enhance self-recruitment.

3. *Temporal patterns of spawning and larval release*

Physical conditions at the time of larval release or spawning establish the initial conditions for larval dispersal. Thus, when offspring enter the water column at appropriate times, dispersal may be greatly reduced. Offspring release commonly is synchronized to meteorological conditions, short-term environmental cycles (tidal, light-dark) and long-term seasonal cycles. For example, it is hypothesized that coral reef invertebrates and fishes may spawn during months when gyres form, thereby enhancing the probability of larval retention (Johannes, 1978; Lobel, 1978; 1989) and self-recruitment. On shorter time scales, the timing of spawning has been hypothesized to reduce larval transport away from the parental site (Berry, 1986), as well as enhance fertilization (Oliver and Babcock, 1992), or enhance larval survival by swamping local predators or reducing larval encounters with predators (Johannes, 1978; Morgan, 1990).

Lunar and semi-lunar patterns of spawning and larval release are common and may be related to the importance of the tidal amplitude cycle in larval transport. For some reef fishes and corals, spawning coincides with neap tides, when lower rates of offshore flow may enhance initial retention of eggs and larvae near natal reefs (e.g., Babcock et al., 1986; Gladstone and Westoby, 1988; Robertson et al., 1990; Reyns and Sponaugle, 1999). Spawning synchronized to the tidal amplitude cycle also may be related to the frequency of internal waves or bores that may eventually transport larvae and zooplankton shoreward (Shanks 1983, 1988; Barnett et al., 1984; Pineda, 1991; Leichter et al., 1996; 1998).

In a great many other cases, spawning and larval release coincides with spring tides, when strong currents enhance initial transport of eggs and larvae from shorelines (Korringa, 1944; Johannes, 1978; Taylor, 1984; Morgan 1995a). For example, some Indo-Pacific reef fishes and intertidal crabs and fishes worldwide synchronize their ovarian cycles with local tidal cycles and spawn or hatch larvae at times that would promote offshore transport (e.g., Hoffman and Grau, 1989; Taylor, 1984; Colin and Bell, 1991; Morgan, 1995a; Sancho et al., 2000). Eggs and larvae released during strong ebb tides may be rapidly transported away from reefs and shorelines where predators abound to safer open waters (Johannes, 1978; Hovel and Morgan, 1997).

Opposing strategies that favor initial retention or seaward transport are sometimes even evident in closely related species. Although the abalones, *Haliotis rubra* and *H. kamtschatkana*, spawn during periods of little water movement (Breen and Adkins, 1979; Shepherd et al., 1992), resulting in limited larval dispersal and high self-recruitment (*H. rubra*; Shepherd et al., 1992), *H. discus hannai* spawns during typhoons when large waves flush the surf zone and sweep larvae out to sea (Sasaki and Shepherd, 1995), reducing the probability of self-recruitment. In a similar manner, the tubiculous polychaete *Phragmatopoma californica* spawns in response to destructive storms (Barry, 1989), a strategy that would appear to promote dispersal rather than self-recruitment. However, due to the coupling of physical re-circulation systems and larval behaviors, this short-term dispersal away from reefs and shorelines may reduce predation by reef organisms without necessarily leading to widespread transport. For example, some storm events are coupled with downwelling conditions (Winant, 1980), so that larvae swept from the surf zone may be retained nearshore thereby enhancing self-recruitment.

In summary, greater temporal synchrony of spawning suggests greater control over the survivorship and potential fate of larvae, thus greater synchrony generally should contribute to higher self-recruitment. In some cases this is clearly evident in the biophysical retention of animals near the natal source. In other cases, additional constraints such as predation may lead to the initial dispersal of young away from the natal site.

4. Parental investment and larval stage of development at hatching

A classic ecological paradigm states that higher parental investment (larger eggs; longer parental protection) leads to larger, more developed larvae that are able to settle after a short pelagic larval duration (Barlow, 1981; Strathmann, 1985). High parental investment (e.g., reef fishes guarding demersal eggs, Thresher, 1984; external and internal brooding by invertebrates, Levin and Bridges, 1995) should enhance egg, larval and even juvenile survival, as well as enhance self-recruitment by retaining young in the vicinity of the parent for an extended period. Furthermore, if these large, well-developed larvae do not settle in a short time, they often are able to exhibit some form of active swimming behavior (Fisher et al. 2000; Bell and Brown, 1995), which also may enhance retention of larvae near the parental population. In most marine environments, active swimming, either vertically or horizontally, can increase the chances of larval retention near the natal population (e.g., Bousfield, 1955; Wood and Hargis, 1971; Morgan, 1995b; Hill, 1991, Paris and Cowen, in prep.). Support for this contention can be found in the frequently observed nearshore distribution of larvae of reef fish species hatching from benthic eggs (e.g., Marliave, 1986; Kingsford and Choat 1989; Leis, 1991; Boehlert et al., 1992; Brogan, 1994; Cowen and Castro, 1994). Larvae of many species of invertebrates hatch from egg capsules or brood chambers at advanced stages of development. For example, among species with a larval stage, many gastropods hatch as advanced veligers that settle after a brief pelagic period. After being introduced to several islands in the South Pacific, two Southeast Asian gastropods (*Trochus* spp. and *Turbo* spp.) rapidly established viable local populations, suggesting a high degree of self-recruitment (Nash, 1993; Yamaguchi, 1993).

In contrast, the larvae from pelagic-spawned eggs are presumably smaller, less active and less capable of remaining near the source population, as suggested by the prevalence of pelagic-spawned reef fish species well offshore (Leis, 1991; Boehlert et al., 1992; Cowen and Castro, 1994). However, of the two reef fishes for which a high proportion of self-recruitment was measured, one spawns pelagic eggs and the other species spawns benthic eggs (Swearer et al., 1999; Jones et al., 1999), calling into question this paradigm (see also Cowen and Sponaugle, 1997). Thus, high parental investment that produces well-developed hatchlings should increase self-recruitment, but high rates of self-recruitment are still possible for pelagic spawners.

5. Pelagic larval duration

Time spent in the water column (PLD) is perhaps the most often cited biological variable potentially affecting self-recruitment. In simple model predictions of population connectivity, PLD is coupled with mean current flow to predict the degree of population exchange (i.e. Spratly Island fish populations: McManus and Menez, 1997; reef fishes in the Caribbean: Roberts, 1997). Even in more complex models factoring in diffusion and mortality, PLD remains a central variable contributing to the degree to which populations can self-seed (Cowen et al., 2000).

At first glance, the prediction (that population connectivity is inversely related to PLD) seems relatively straightforward and substantiated by both field and modelling studies. Coral planulae, sponge larvae, bryozoans and ascidians have larvae with PLD's of ≤ hours to several days ("anchiplanic" larvae *sensu* R. Scheltema in Levin and Bridges, 1995). Clearly, the probability that a larva will settle within the local population boundaries is greatly increased with a very short pelagic larval duration. At the opposite extreme are organisms with very long larval durations ("teleplanic" larvae with durations between 60 to 365+ d, *sensu* Scheltema, 1971) such as the veligers of several gastropods and bivalves, lobster phylosoma, and anguillid and muraenid (eel) larvae (McCleave and Kleckner, 1987; Hourigan and Reese, 1987; see review by Levin and Bridges, 1995). Given the complexity of the ocean over long time frames and assuming adequate survival over the open ocean, it is intuitive that exchange over long distances is more likely for organisms with long PLD's. This relationship is particularly relevant for organisms with larvae that are comparatively passive for at least a significant portion of their larval period.

A large number of organisms (if not most) exhibit active behavior during some portion of their larval period, and therefore, patterns of population exchange may be more complex than that predicted for relatively passive larvae. In a comparison of dispersal distance for larvae with PLDs of minutes to months, Shanks et al. (in press) found a significant correlation between PLD and dispersal distance. However, a number of organisms dispersed substantially shorter distances than would be expected due to active behavior that limited their dispersal (moving down into the benthic boundary layer). Reef fish larvae with relatively short PLD's (e.g., pomacentrids with PLDs of 24-29d) may remain near source populations (Jones et al., 1999) using simple vertical migration behaviors (Paris and Cowen, in prep.). However, fishes with longer PLD's also may recruit back to source populations (Swearer et al., 1999), suggesting similar interactions with other variables. Active behavior on the part of adults (see above) or larvae can effectively reduce the dispersal of a number of taxa with varying PLDs.

Another mechanism that enables taxa with longer PLDs to recruit successfully to the natal population is plasticity in PLD. For example, a longer, more variable PLD may provide the flexibility to respond actively to favorable environmental cues which are temporally variable (Sponaugle and Cowen, 1994) increasing the chance of return to the natal population. The ability to delay metamorphosis (Victor, 1986a; Cowen 1991) and tolerate slow growth (Pechenik et al., 1996a, b; Searcy and Sponaugle, 2000) also may be beneficial to organisms recruiting to relatively restricted adult habitats. For several endemic fishes (which represent repeated self-recruitment over long time scales), PLD's are particularly long and highly variable (see Bell et al., 1994 for a diadromous Caribbean goby; Randall, 1961 for a Hawaiian surgeonfish; and Cowen and Sponaugle, 1997 for compilation of data from Victor, 1986b and Thresher et al., 1989 on endemic versus non-endemic Hawaiian labrids) lending support to the contention that long PLD's may contribute to, or at least not preclude self-recruitment. A recent study found that endemics were not characterized by any particular PLD (Robertson, 2001). Half of the endemics from seven small, isolated islands had PLDs ≤ 30 days and half had PLDs between 1-3 months long. All endemics clearly experience successful self-recruitment.

In summary, the prediction of an inverse relationship between PLD and self-recruitment may hold for species with larvae that are relatively passive during a portion of their PLD or larvae with very short PLD's. However, there are many exceptions to this relationship and these exceptions are due to active behavior. Active larval behavior may entail rather simple vertical migrations or more robust and directed horizontal swimming (see below). The interaction of behavior with physical processes results in a breakdown of the predicted relationship between PLD and dispersal distance such that the converse is not necessarily true for taxa with active or long-lived larvae.

6. Vertical positioning behavior by larvae

Larval movements need not be extensive or elaborate to enhance self-recruitment. The simplest behavior is vertical movement. The flow field in most coastal water columns is vertically stratified, and consequently, relatively simple vertical positioning by larvae can be an important determinant of larval transport. Even in vertically-mixed water columns, flow in the benthic boundary layer is slower than in the remainder of the water column, and wind stress can establish an Ekman spiral (i.e. frictionally-driven flow with directionality of the flow rotating slowly with depth). Because velocity differs among depths, larvae may position themselves vertically to move horizontally in different directions or speeds.

Classic studies in estuaries have documented three types of vertical migration that mediate horizontal transport of larvae: ontogenetic, diel, and tidal. Strong evidence exists in support of ontogenetic (Bousfield, 1955; Wood and Hargis, 1971; Sandifer, 1975a) and tidal (Weinstein et al., 1980; Cronin and Forward, 1982; Dittel and Epifanio, 1982; Fortier and Leggett, 1983; Laprise and Dodson, 1989; Christy and Morgan, 1998) migrations facilitating self-recruitment. Theoretically, diel vertical migrations also may facilitate retention in estuarine circulations (Hill, 1991; Morgan, 1994; see below).

Beyond strictly estuarine systems, simple upward swimming by larvae may lead to their capture by frontal circulations (Epifanio, 1987; Franks, 1992; Govoni and Grimes, 1992). If the time scales of the fronts approach the larval duration for even relatively passive larvae (or the passive portion of the larval phase for species that become active prior to settlement), such features (see below) may locally retain larvae. Upward movement also has been shown to facilitate onshore transport due to wind (e.g. blue crabs, Epifanio, 1995) and internal waves (Shanks, 1986). Similarly, changes in vertical position with ontogeny have been shown to promote onshore transport of larval fishes and invertebrates by moving larvae into onshore flowing strata (Shanks, 1983,1986; Cowen et al., 1993, 2000; Pineda, 1999; Shanks et al., 2000; Paris and Cowen, in prep.). Such onshore movements might be used as a mechanism to retain larvae near their natal site.

Larvae also may be able to reduce dispersal by remaining in the benthic boundary layer where flow is reduced to very low levels (Nowell and Jumars, 1984; Butman, 1987; Denny, 1988). Among fishes, post-flexion or late-stage larvae of several temperate and tropical families have been found in or near the benthic boundary layer (Barnett et al., 1984; Jahn and Lavenburg, 1986; Leis, 1986; Lindeman, 1986; Steffe, 1990; Breitburg, 1991; Kaufman et al., 1992). For the larvae of several fishes (Barnett et al. 1984; Jahn and Lavenberg, 1986), copepods, barnacles (Barnett and Jahn, 1987) and other larval invertebrates (reviewed by Young and Chia, 1987), this behavior probably decreased offshore dispersal. Shanks et al. (in press) found that for a number of taxa with larvae that remain in the BBL, dispersal distance is less than that predicted based on PLD.

Early attempts to model larval dispersal often had the simplifying assumption that vertical position in the water column makes no difference to horizontal movements of larvae (e.g., Williams et al., 1984; Tegner and Butler, 1985; Roberts, 1997). Recently, more realistic three-dimensional models take vertical position of larvae into account (Black et al., 1991; Werner et al., 1993; Tremblay et al., 1994; Manuel and O'Dor, 1997; Wolanski et al., 1997; Armsworth, 2000), and are, therefore, more likely to predict accurately the dispersal of larvae. Overall, active vertical positioning by larvae enables greater control over horizontal transport and should enhance self-recruitment.

7. Horizontal swimming ability of larvae

Until recently, the literature supported the view that larvae were relatively ineffectual swimmers, with reported values for sustained swimming of less than 3 cm sec^{-1} for invertebrate larvae (Chia et al., 1984) and less than 5 cm sec^{-1} for fish larvae (Blaxter, 1986). However, a growing body of evidence suggests that some late-stage larvae of fishes and decapods are capable of directed onshore swimming. Larvae that can swim faster than surrounding currents (i.e., 'effective' swimmers *sensu* Leis and Stobutzki, 1999), should be better able to control their trajectory during the pelagic period than larvae with little or no swimming ability. Hence, retention could be achieved behaviorally and would not depend entirely on hydrographic 'retention cells'.

Lobster and crab postlarvae may have directed shoreward swimming (Cobb et al., 1989) for 40 – 60 km at velocities reaching 30 cm/s (Phillips and Sastry, 1980). Data supporting this contention include the observation that crab postlarvae orient into flow and swim in straight lines at moderate flow velocities (Mackay, 1943; Luckenbach and Orth, 1990; Fernandez et al., 1994; Shanks, 1995) and toward dissolved chemical cues emanating from estuaries (Wolcott and DeVries, 1994). Late-stage larvae of coral-reef fishes also swim at high speeds (averaging *ca.* 20 cm sec^{-1}; some species up to 65 cm sec^{-1}) that can be maintained for substantial periods (up to 194 hr, covering 94 km; Stobutzki and Bellwood, 1997; Leis and Carson-Ewart, 1997; Leis and Stobutzki, 1999). Such swimming capabilities clearly counter the prevailing view (e.g., Roberts, 1997) that larvae are passive.

Self-recruitment in some reef fishes and crustaceans may be a two-step process. As swimming is not well developed at hatching for many species (Leis and Carson-Ewart, 1997; Fisher et al., 2000), young, poorly developed larval stages are likely retained by depth regulation or entrainment in hydrographic features until they become 'effective' swimmers that can control their trajectories and recruit onshore by directed swimming. This transition from ineffective to effective swimmers can occur within a few days to weeks of hatching in some species (Fisher et al., 2000), but may occur later in others. Such a scenario was proposed for bluefish along the east coast of the U.S. (Hare and Cowen, 1993, 1996). Similarly, Chiswell and Booth (1999) concluded that shoreward swimming of 4-10 cm sec^{-1} by rock lobster post larvae (*Jasus edwardsii*) off New Zealand was required to match observed larval distributions, whereas passive drift best described the distributions of mid-stage larvae. In sum, the capacity for horizontal swimming may enable larvae to exhibit some independence from ocean currents (Armsworth, 2000), reducing (or eliminating) passive dispersal and enhancing self-recruitment.

8. Sensory capabilities of larvae and environmental cue strength

Successful settlement into coastal or isolated environments may depend on the presence and strength of habitat-specific cues to which larvae respond. If larvae have pelagic larval durations of days to months then the probability of returning to a natal area is likely to be low if there is no information on the direction of suitable habitat. Furthermore, the ability of larvae to detect such habitat cues and orient toward those cues should significantly influence their horizontal positioning and the degree to which they can return to a natal site.

Many physical and biological cues could be used by organisms in the marine environment and their concentrations, frequencies and intensities can vary in ways that can be useful for orientation (see reviews by Myrberg and Fuiman, in press and Kingsford et al., this volume). Chemical stimuli, with directional information, may be found in estuarine and reefal plumes (Crossland et al., 1980; Wolanski and Hamner, 1988; Grimes and Kingsford, 1996), from sandy beaches (Kalmun, 1982) and perhaps algae (Walters and DiFiori, 1996). Variation in ambient noise and vibration is considerable and biological (e.g., snapping shrimps, fishes) and physical (waves) sound sources may be relatively predictable in space and time (Rogers and Cox, 1988; Janssen et al., 1990; Cato, 1992). Visual cues including celestial bodies and related polarized light may also provide cues (Waterman, 1989). Local variation in magnetic fields due to magnetic anomalies preserved in volcanic rocks is considerable and is potentially useful for navigation (e.g., salmonids, Quinn and Dittman, 1990), as is the highly predictable magnetic field of the earth itself.

Many invertebrates and fishes can sense variation in water chemistry, sound and vibrations, hydrography, celestial bodies, magnetism, visibility and electrical fields (Phillips and MacMillan, 1987; Blaxter, 1988; Kalman, 1982; Hara, 1994; Kingsford et al., this volume). Salmonid fishes (Quinn and Tolson, 1986), turtles (Grassman et al., 1984) and some invertebrates (Atema and Cowan, 1986) are known to respond to small variations in water chemistry. Tripterygiid fish larvae were recently shown to use sound to navigate (Tolimieri et al., 2000). Larval fishes and invertebrates are influenced by environmental cues close to settlement (Sweatman, 1983, 1985; Seki and Taniguchi, 1996; Welch et al., 1997) and have the necessary sensory morphology for broader scale detection of suitable settlement sites (e.g., Lara, 1999). However, our knowledge of how these senses are used by larval forms for orientation and choice in the pelagic environment is largely speculative. Although much work remains to be done in this area (see Kingsford et al., this volume), the prediction is that the stronger the cues and the better able a larva is to detect and respond to such cues, the greater the likelihood is of self-recruitment.

B. PHYSICAL PROCESSES

1. Geographical site isolation

The more isolated a site is, the more likely it is that the population there is maintained entirely by self-recruitment simply because it is unlikely that an isolated population could be maintained from a distant source. This view is supported by the analysis of Cowen et al. (2000), who show that diffusion and mortality during the pelagic phase should result in extremely low numbers of larvae ever reaching a location from a distant source. For more closely spaced or continuously distributed populations, the exchange of larvae from nearby sources should result in a reduction in the proportion of new recruitment that is locally-derived, and this may occur without a decrease in the absolute number of self-recruits. That is, the recruitment subsidy from nearby locations may increase while the absolute amount of self-recruitment may remain unchanged.

Relevant studies to evaluate these ideas are rare. The case of endemic species is an obvious one, though reflective of longer (evolutionary) time scales. The degree of endemism is greatest (and often the overall diversity is lowest) at the most physically isolated locations (Robertson 2001; see Swearer et al., this volume). At intermediate levels of isolation, some long-distance exchange may maintain gene flow thereby reducing the level of endemism, but the occurrence of such long-distance dispersal events may be too infrequent to be of ecological significance (Schultz and Cowen, 1994).

Examples of isolation are most common for oceanic islands and seamounts, though some estuarine environments are also highly spatially isolated. Depending on the scale of the population (including relative mobility and PLD), a rocky reef in the middle of a long sandy stretch could be considered an isolated habitat. Isolation of neighboring areas also may occur as a result of particular oceanographic conditions (e.g., both sides of major promontories may isolate populations due to topographically-steered currents; see below).

Where sites are largely contiguous, the degree to which self-recruitment is important is largely unknown. Recent studies suggest that levels of self recruitment may be in the range of 30-60%, even where nearby sources are as little as a few km away (Jones et al. 1999) to 100 km (Swearer et al., 1999). However, because neither the actual sources of the exogenous larvae nor the processes leading to such input were identified, the generality of these results remains uncertain.

In summary, isolated sites with large and sometimes endemic faunas demonstrate that self-recruitment mechanisms exist, but this provides no insight as to how important such mechanisms are to typically less isolated populations. Less isolated populations may have similar absolute rates of self-recruitment, although dilution by subsidy from neighboring populations may reduce the overall proportion of self-recruitment. The linkage between site proximity and the relative importance of self-recruitment warrants further study.

2. Coastal complexity

As current flows along a shoreline, it will interact with the topographic relief to generate a complex flow field across a range of length scales characterized by eddies, fronts, upwelling, jets, and convergences (Bakun, 1986; Wolanski and Hamner, 1988; Nittrouer and Wright, 1994). Closely tied to the length scale of these interactions is the time scale of the resulting flow feature. Thus, there is a non-linear interaction between coastal complexity (in terms of both topographic complexity and basin size) and the persistence or residence time of various circulation features. Although clearly due to interactions, each component (topographic complexity, basin size and residence time) is considered separately as potentially convenient correlates of larval retention.

a. Topographic complexity

At a small scale (1 to10 km), topographically influenced circulation has been most actively studied in areas with strong tidal currents. Tidally driven flow variability is evident around topographically complex coral islands (e.g., in the Great Barrier Reef, Wolanski, 1994; Black, 1994) and in the vicinity of headlands (Signell and Geyer, 1991). These conditions serve as mechanisms directly enhancing retention by increasing local water residence time (e.g., short-lived, largely passive larvae of corals and Crown of Thorns starfish, Black et al. 1991; Black, 1994; Sammarco, 1994). For larvae with short pelagic periods or short passive portions of the PLD (i.e. < several days), tidally generated secondary circulation may play an important role in limiting or directing dispersal (Wolanski, 1994). These features are likely less important for organisms with longer larval durations because secondary circulation such as small scale fronts and eddies often break down when the tides reverse (Hamner and Hauri, 1977; Wolanski et al., 1984; Black and Gay, 1987), so. However, these features may create signals that may serve as guideposts for recruiting animals that extend some distances from the island or topographic feature (Kingsford et al., 1991; Reyns and Sponaugle, 1999).

At mesoscales (10 – 100 km), coastal complexity may have a large influence on the degree of self-recruitment. Flow along the western coast of North America provides a clear example of the interaction between coastal complexity and flow (Largier et al., 1993) and its potential influence on recruitment. The coastline is composed of a series of headlands that divert the flow offshore, creating eddies in the lee of the headlands (Ebert and Russell, 1988). These eddies serve as retention favorable areas for a variety of larvae (Wing et al., 1995a, b, 1998). Upwelling "shadows" along a coast (Graham et al., 1992) may play a similar role. In the northwestern Atlantic, cod population structure has been found to occur on mesoscales reflecting the bathymetric complexity of the coast (Bentzen et al., 1996; Ruzzante et al., 1998). This structure is likely the result of local retention due to larval interactions with the resulting oceanography (Ruzzante et al., 1999). Modelling has supported this contention for scallops (Tremblay et al., 1994), cod and haddock (Werner et al., 1993), and similar examples exist for herring populations in the Pacific (O'Connell et al., 1998) and Atlantic (Iles and Sinclair, 1982, Shaw et al., 1999). Topographically-steered flow also may play a role in retaining larvae on isolated islands such as Barbados, West Indies (Cowen and Castro, 1994; see Cowen, in press). Although detailed genetic and/or larval and oceanographic data are rare for many other species and systems, mesoscale circulations associated with coastal bathymetry are likely to be a potent source of larval retention.

At larger scales, great distances between headlands result in relatively large reaches of coastline with potential for uninterrupted flow. Currents along these coastlines potentially can run long distances relatively unimpeded, leading to the potential for greater dispersal of larvae and thereby diminishing the likelihood of self-recruitment. Where a cape or headland protrudes (e.g., Cape Hatteras or Pt. Conception), major currents often meet and large-scale gyres may ensue (Csanady and Hamilton, 1988). Such gyres may serve to close entire populations of organisms, such as the Slope Sea in the western North Atlantic for squid (Trites, 1983) and mesopelagic fishes (Backus et al., 1977, Olson and Backus, 1985), but at scales considerably larger than the local scale of 10's – 100 km.

In summary, topographically-influenced flow likely has a key role in the distribution and retention of larvae, but the greatest effect is probably at intermediate spatial scales. Thus, increasing coastal complexity should contribute to greater opportunities for self-recruitment up to a point, then the effect of increased complexity (i.e. at small scales) will diminish the likelihood of self-recruitment except for the shortest lived larval stages.

b. Embayment or basin size

As noted above, one means of classifying coastal complexity is by the relative size (or scale) of embayments, or basins. The relationship between embayments and self-recruitment depends on the size and openness of the basins. In the case of open basins, the relationship between degree of self-recruitment and basin scale is not linear. Small basins such as small open coves may have a low probability of larval return (i.e. larvae are readily flushed away and the probability of returning to a small point is low), intermediate sized basins may have a high probability of larval return (i.e. larvae do not leave the basin), and very large basins may have little probability of larval return (i.e. larvae are swept far away from the natal source). In the case of enclosed or semi-enclosed basins (e.g., coastal and atoll lagoons and estuaries), larval return to natal sites in small basins would be more likely than in large basins.

Atoll lagoons

Available evidence supports the hypothesis of increased self-recruitment in small semi-enclosed basins. For example, in the atoll lagoons of the western Pacific, a variety of coral-reef fish species are self-recruiting based on distribution and size structure of the larvae (Leis, 1994; Leis et al., 1998) and genetic data (Planes et al., 1998). Likely retention mechanisms are reasonably straightforward: Lagoon circulation consists of inflow through deep channels and across the reef flat by wave pumping and tidal currents balanced by outflow through deep channels or across the leeward reef flat. Water exchange is limited to depths less than the outflow sill depth and vertical stratification may reinforce this limited exchange of water (Andrews et al., 1984), however, because of wind and boundary mixing and a lack of significant freshwater inflow, lagoon waters are frequently well mixed. Wind generated surface currents cause upwelling on the windward side of the lagoon and water is fed into the upwelling zone from a deep counter-current. Strong wave pumping may, however, prevent upwelling or the deep return flow (Leis, 1986). These vertical differences in flow may assist in the retention of larvae, particularly for larvae remaining at depths greater than the outflow sill depth. Lagoon size and the number of fish species completing their pelagic phase in the lagoon are weakly related (Leis et al., submitted). However, even in a large lagoon such as Rangiroa Atoll, Tuamotu Islands (161,000 ha), probably < 10% of the fish species complete their pelagic phase in the lagoon (Leis, unpublished). Despite the seeming advantage of larval development within a lagoon, few fish species complete their larval development there (Leis, 1994; Leis et al., 1998).

Estuaries

Larval transport in estuaries has been well studied. Many estuarine populations of crabs, barnacles, oysters, and fish are largely self-recruiting (Bousfield, 1955; Wood and Hargis, 1971; Cronin, 1982; Weinstein et al., 1980; DiBacco and Levin, 2000), though in these studies no direct measure is made of the spatial scale of the estuary versus the degree of self-recruitment. At least three physical processes may affect the transport of larvae within an estuarine: 1) residual two-layer circulation, 2) tides, and 3) fronts.

Deep estuaries with high river runoff and strong tides often display two-layer circulation; river runoff flows seaward at the surface, seawater flows landward along the bottom, and the residual flow is zero at the interface between these currents. Larvae capable of regulating their depth may exploit these currents to control their dispersal and increase the probability of self-recruitment. For example, during ontogenetic vertical migrations, early larval stages occur in surface currents where they are transported downstream from adult habitats, and older larval stages are transported back upstream by sinking into bottom currents (Carriker, 1951; Bousfield, 1955; Wood and Hargis, 1971). Larvae capitalizing on these flow patterns can complete their development in estuaries (Carriker, 1951; Bousfield, 1955; Wood and Hargis, 1971; Sandifer, 1975a; Fortier and Leggett, 1983; Morgan, 1995b;).

Tidal currents often mix the water column disrupting stratification. Larvae can be retained in a mixed estuary by remaining near the bottom throughout the tidal cycle or migrating higher in the water column during flood than ebb tides. Tidally timed vertical migrations or tidal stream transport has been observed in a number of taxa (e.g., Barber and Lee, 1975; Rothlisberg *et al.*, 1983; Quayle, 1988). For example, post-larvae of the pink shrimp, *Penaeus duorarum* enter nearshore estuarine nursery habitats by ascending into the water column for several hours in response to an increase in salinity and are thus taken shoreward in a series of tidal "hops" with each flood tide (Hughes, 1969).

Larvae of some estuarine dependent organisms develop on the continental shelf and return to estuaries as post-larvae (Sandifer, 1975b; Christy and Stancyk, 1982; Morgan, 1995b). Within an estuary, larval retention and export can occur concurrently indicating that passive physical processes alone are insufficient to explain this differential transport; the larvae must exhibit active behavior. Species that develop on the shelf can recruit as reliably as do species that develop entirely within estuaries (Hovel and Morgan, 1997; Christy and Morgan, 1998) suggesting that reliable biophysical transport mechanisms also exist in the water of the continental shelf. Evidence for self-recruitment of estuarine species that develop in coastal waters, however, remains inferential.

Large basins

There is almost no evidence for the scale of self-recruitment in large basins. Coastal species often are tied to some sort of habitat or circulation feature that may restrict the scale of larval exchange within large basins. For example, many cod and herring populations in the North Atlantic exist at scales much smaller than the scale of the North Atlantic basin (Sinclair, 1988; Ruzzante et al., 1998; Shaw et al., 1999; Pogson et al., 2001). Similarly, the system of eddies in the Gulf of California (Badan-Dangon et al., 1985) may enhance self-recruitment of the Gulf sardine (Hammann et al., 1988) at scales smaller than the basin itself.

The utility of the hypothesis that self-recruitment is related to the size or scale of the basin is compromised by limited evidence and the complex interactions of other factors. Thus, although the prediction is that self-recruitment would peak at intermediate basin sizes, there is no evidence of a clear relationship between basin size and degree of self-recruitment, *sensu stricto*, and more work is needed to refine and test this hypothesis.

c. Water residence time

Residence time of the water is a factor that is related to the size of a basin as well as to other topographic or oceanographic features. However, because the relationship between basin size or topographic feature and water residence time is not necessarily linear, the variables are treated separately. If the likelihood of self-recruitment is inversely related to the rate at which larvae flux away from the natal population, the residence time of the water should play a role in retention. The probability of larval return to their natal sites should decrease in sites where water residence times are short. For example, Gaines and Bertness (1992) explained reduced barnacle settlement in Narragansett estuary in years of lower residence times due to higher freshwater flow rates.

In the open ocean, water residence time can play an important role. Loder et al. (1988) characterized the oceanography at four large banks with anticyclonic gyres. Only Georges Bank had water residence times equal to or greater than the recirculation time of the gyre suggesting that larvae might be consistently passively retained. A similar situation occurs at open ocean seamounts and islands, which interact with currents to create complex flows that may retain larvae (Boehlert and Mundy 1993; Genin et al. 1989; Cowen, in press). At time scales relevant to larval retention (weeks to months), Taylor columns or caps (anticyclonic vortices above topographic obstacles) may be the most likely retention mechanism (Owens and Hogg, 1980; Genin and Boehlert, 1985; Tremblay et al., 1994; Barton et al., 1998). Other flow complexities, including tidal currents and eddies (Hamner and Hauri 1977; Codiga and Eriksen, 1997; Meincke, 1971; Noble and Mullineaux, 1989), upwelling along the flanks of the seamount and associated radial inflow (Freeland, 1994), internal wave reflection (Eriksen, 1982), topographically steered flow (Cowen and Castro 1994), trapped waves (Brink, 1989), and eddies that remain attached to the seamount or island (Bograd et al., 1997) may also contribute to larval retention.

Residence time may vary vertically in the water column (e.g., benthic boundary layer versus surface, wind-driven layer) and spatially along a coast. Black et al. (1990) modeled the likely residence time of neutrally-buoyant material around a coral reef at scales of 100's m, including tidal and frictional forces, and found that water may be resident for days on portions of the reef. Although there are other physical studies of water residence times (particularly in bays and estuaries), these rarely have been directly linked to biological studies. The relative effect of the flow field on larval dispersal will depend on the longevity of the flow relative to the duration of the pelagic larval phase – the greater the longevity of the flow field the greater its role may be in generating self-recruitment. Furthermore, the interaction of biological factors, particularly larval behavior, may upset simple physical relationships by enhancing or decreasing probability of expulsion (Morgan, 1995b; DiBacco and Levin, 2000).

In summary, it is plausible that self-recruitment is positively related to water esidence time, but there is limited direct evidence to test this theory other than those studies stated above. Examining residence time for neutrally-buoyant particles seldom may be relevant because nearly all larvae are capable of vertical movements and other behaviors in the water column. Calculations of residence time with consideration of such behavioral capabilities will likely lend support to this general hypothesis, though scaling issues will continue to confound the relationship.

3. Flow variability (vertical, horizontal) and water column stratification

As a medium of larval transport, water motion can be broken into advective (or flow) and diffusive (or mixing) components. Under strictly non-turbulent conditions, advective properties predominate, and these serve to advect (or carry) larvae away (i.e. unidirectionally). Such flow conditions express limited variability and would result in low larval retention. Under highly turbulent (~ chaotic) conditions, unidirectional advective properties of the flow may be reduced, but the mixing or diffusive properties can be large. Under these conditions, larvae may be highly dispersed, again not favoring retention. However, if the turbulent flow is more coherent and/or convergent, thereby reducing some of the diffusive properties, while reversing some of the advective properties (e.g., tidal reversal, eddies), the resulting transport and dispersal of larvae may be greatly reduced. It is under these conditions of variable flow that larval retention is facilitated.

Flow varies in both horizontal and vertical planes. The processes contributing to this variability also range over wide spatial and temporal scales. The flow environment of most coastal oceans is typified by tidal, wind, seasonal and/or episodic (e.g., storm generated) variability which exists in both horizontal and vertical planes. Such variability provides a variety of mechanisms by which larvae may either be retained within a certain geographical area or to which larvae may actively respond to enhance local retention. However, without the interaction of some sort of behavioral response by the larvae with the flow variability, some highly variable flow conditions might actually enhance diffusion of larvae away from natal sources by mixing. Flow on shelf systems is complex, especially in areas of high topographic complexity like coral reefs. This complexity is often not understood by biologists, and yet it offers many opportunities for both physical and biophysical retention of larvae, leading to self-recruitment.

In addition to variability in the horizontal plane, most flows exhibit vertical flow variability related to factors such as the source of forcing, rotational effects, bottom friction, geostrophic adjustment, and horizontal and vertical gradients in stratification. In conditions where the water column exhibits a two-layer stratification, the upper and bottom layers may move in opposite directions. In these situations, common in coastal oceans, the strongest component of the two-way flow is often in the cross-shore direction (Winant and Olson, 1976). These flows are often associated with the internal tide, and reverse at diurnal, semidiurnal, or double-semidiurnal periods (Baines, 1986). By reducing mixing, such water column stratification should reduce the diffusion of passive propagules, thereby enhancing self-recruitment. If larval behavior is factored in, even greater self-recruitment may be accomplished.

Given the inherent importance of flow variability to larval transport and retention, we follow with a discussion of many of the processes that contribute to variable flow. The intent is to describe the processes and forcing mechanisms in light of examples relating to larval retention (or at least transport). Where behavior interactions can be invoked, the biophysical implications are also discussed. For simplicity, we have categorized by process and not forcing mechanism.

Upwelling/downwelling

Through Ekman transport, winds blowing along a coastline generate upwelling or downwelling (Bakun, 1988). For example, along the West Coast of North America, north winds push the surface waters (depths <~ 50 m) offshore drawing deeper waters to the surface. These denser, upwelled waters converge with the lower density surface waters offshore, creating the upwelling front (Rosenfeld et al., 1994). South winds, in contrast, push the lower density surface waters shoreward causing downwelling flow adjacent to the coast (Winant, 1980; Wing et al., 1995a, b, 1998). With reversals in wind direction, the flow regime quickly changes from one state to the other (Csanady, 1981). During a reversal, the water adjacent to the shore is exchanged with offshore water (Csanady, 1974). The traditional upwelling zones (e.g., Peru-Chile, California, Benguela and Canary Current Systems) have been most actively studied (see Durand et al., 1998) and are the most energetic, with less energetic upwelling occurring along other coasts.

Upwelling and downwelling affect both the cross and along-shore dispersal of larvae. Larvae associated with a water mass will remain adjacent to the shore as long as that water mass remains adjacent to the shore. However, upwelling, downwelling, and the transition between states are characterized by vertical currents. Although few larvae can swim against typical horizontal currents, most can swim more rapidly than vertical currents (Franks, 1992), and have behaviors that could be used to maintain a preferred depth and thus limit their cross-shore dispersal (Peterson, 1998). For example, during upwelling, larvae in surface waters will be swept offshore to the upwelling front. Upwelled waters converge and sink at the front and larvae swimming upward against this sinking water will be trapped at the convergence. When the winds reverse, these larvae may be transported shoreward; the upwelling front becomes a moving convergence (see below) and may "collide" with the shore, resulting in a recruitment pulse for coastal species (Roughgarden et al., 1991; Shanks et al., 2000). Alternatively, near the coast, larvae may be carried away from the surface by downwelling. Larvae swimming upward against this current again will be trapped in a convergence, but in this case, adjacent to shore.

Alongshore flows in upwelling/downwelling systems are typically on the order of 10's of cm sec^{-1}. Larvae spawned into an upwelling event could be transported 10's of km alongshore. However, upon a reversal in the winds and the onset of downwelling, these larvae could be transported back toward the site from which they were spawned. The oscillation from upwelling to downwelling may limit the net alongshore dispersal of larvae and increase the chances that larvae settle back into their natal population.

Evidence for the adaptive exploitation of these currents generated by upwelling and downwelling is sparse. Parrish et al. (1981) suggest that fishes in upwelling regions time their spawning to limit offshore transport. In the Oregon upwelling zone, ontogenetic vertical migrations maintain copepod populations close to shore (Peterson et al., 1979; Wroblewski, 1982). Similarly, adaptive vertical migrations have been suggested for mero- (Shanks, 1986) and holoplankters (Barange and Pillar, 1992; Boucher, 1984). During upwelling, pelagic juvenile rockfish are distributed deeper in the water column, presumably avoiding the offshore flow and retarding their offshore transport (Lenarz et al., 1991).

Fronts

Fronts represent the boundary between water masses and as such, are often characterized by strong horizontal gradients in biological and physical properties as well as strong vertical motions and convergent flow. Larvae or other plankton that are positively buoyant or swim upwards in response to the downwelling at the frontal convergence zone will collect and remain at the front (see review by Le Fèvre, 1986). Therefore, fronts may act as a barrier to the dispersal of larvae, but because they are often ephemeral, their formation and persistence varies with the season, tides and the weather, their effectiveness as a retention mechanism depends on the timing of reproduction and larval duration. To be effective, larvae must be released when a front is present and the front should persist during a major portion of the PLD for passive taxa or of the passive portion of the PLD for active taxa.

Fronts at the mouth of estuaries (estuarine plume fronts) usually form during ebb tides when lower density estuarine water flows out into the ocean; a front forms between these estuarine waters and the higher density seawater (Largier, 1993; O'Donnell, 1993). Because estuarine plume fronts dissipate and reform with the changing tides (e.g., Kingsford and Suthers, 1994), evidence that they act as a barrier to dispersal from estuaries is limited and mixed (Clancy and Epifanio, 1989; Epifanio, 1987; Grimes and Kingsford, 1996). Perhaps the best evidence that estuarine fronts can limit passive dispersal is the finding by Tyler et al. (1982) that the distribution of red-tide dinoflagellates was sharply limited by a frontal boundary that kept them within the estuary during summertime bloom conditions. In addition to serving as a barrier, fronts also may funnel surface-dwelling post-larvae into estuaries from adjacent coastal waters (Kingsford and Suthers, 1994; Eggleston et al., 1998). At the mouth of estuaries during flood tides, axial fronts form parallel to shore. Post-larvae may be advected along these fronts and into the estuaries thereby facilitating recruitment to adult populations.

Shore parallel fronts found over the continental shelf (e.g., shelf break fronts, upwelling fronts, and shallow sea mixing fronts; Bowman and Esaias, 1978) may limit the extent of the offshore dispersal of larvae, but because they do not limit the alongshore dispersal of larvae, these fronts may be relatively unimportant in promoting the self-recruitment of populations. Topographically generated fronts, if they persist long enough, may constrain both the along and cross-shore dispersal of larvae and, hence, may play an important role in self-recruitment. For example, if "upwelling shadow" fronts (fronts that form on the lee side of points in upwelling systems; Graham and Largier, 1997) act as a barrier to larval dispersal, they could trap larvae in the waters immediately adjacent to the lee side of a point.

Moving convergences

Moving convergences can transport larvae shoreward (Pineda, 1999; Shanks, 1983; Shanks, 1988; Shanks et al., 2000). The most ubiquitous type of moving convergence is that caused by tidally generated internal waves. The tide ebbing off the shelf or flowing across a bank or reef generates a lee wave (Maxworthy, 1979). With the reversal in the tide, the lee wave is "released" and propagates shoreward or across the reef as a soliton or non-linear internal wave (Chereskin, 1983; Farmer and

Smith, 1980). As the wave propagates, the original lee wave evolves into a set of solitons. Flow over the top of the waves generates a convergence zone that travels along with the propagating waves (Osborne and Burch, 1980). If the tidal currents are large enough, the leading wave of the set can break forming an internal bore. Internal bores can transport a mass of water shoreward causing a form of upwelling (Pineda, 1991, 1995). Although larvae in near bottom waters may be caught up in the bore and carried shoreward, larval transport by internal bores has received little attention. These large tidally generated internal waves and bores are common in all oceans (e.g., Leichter et al. 1998).

To be transported by a moving convergence an organism must behaviorly remain in the convergence despite the vertical currents present there. A large diversity of organisms are concentrated in moving convergences and transported by them (Kingsford and Choat, 1986; Pineda, 1999; Shanks, 1983, 1988; Zeldis and Jillett, 1982). Most of these organisms are late-stage larvae or post-larvae that can remain in the convergence through buoyancy or by vertical swimming (Le Fèvre, 1986; Larson, 1992; Franks, 1992), and be carried shoreward along with the moving convergence.

Moving convergences alone may have little affect on self-recruitment. However, where hydrography limits alongshore larval dispersal, moving convergences may play an important role in transporting larvae back to the coast where they may recruit into their natal population. Because internal waves are refracted by the bottom topography (Sawyer, 1983), a greater number of larvae may be transported shoreward along stretches of coastline where waves are focused (Shanks and Wright, 1987). Local retention of larvae by the offshore hydrography coupled with differential transport by internal waves may lead to alongshore differences in the amount of shelf-recruitment.

Ocean eddies

Eddies frequently have been proposed to enhance larval retention along continental shelf systems and near islands. Based on extensive physical oceanographic measurements, Lee et al. (1994) and Lee and Williams (1999) hypothesized that the cyclonic circulation of the Tortugas gyre in combination with surface Ekman transports and coastal counter currents promotes retention of locally-spawned larvae along the Florida Keys. Spin-off eddies of the Florida Current may help retain and transport reef fish larvae to inshore settlement (Limouzy-Paris et al., 1997). As with other oceanographic processes, for retention to occur, the temporal scales of the eddy must correspond to the length of larval life or at least it's pre-effective-swimming phase. Larvae must be transported into the eddy, remain there for their larval period, and then be transported back to suitable juvenile habitat by the end of the larval period.

Island wake eddies have received much attention as potential retention mechanisms (Sale, 1970; Lobel and Robinson, 1988; Boehlert et al., 1992; Barton, 1998). Flow in the lee of islands can take the form of an eddy or be broadly unorganized (e.g. Pingree and Maddock, 1980; Heywood et al., 1990; Graham et al., 1992; Wolanski, 1994). Either flow regime may enhance localized retention of larvae (*sensu* Hamner and Hauri, 1981; Wing et al., 1995a, b). Some island wakes clearly have enhanced primary production and abundances of larval fishes, and feeding of the larvae and their condition is enhanced in these areas (e.g., Emery, 1972; Boehlert et al., 1992, Barton et al., 1998; Rissik and Suthers, 2000). This suggests that the wakes are not only sites of larval retention, but also sites of increased growth and survival of larvae, and this should lead to enhanced self-recruitment. However, other eddies contain very few larval fishes (see Lobel and Robinson, 1988). The degree to which eddies truly retain larvae and contribute to self-recruitment is unknown.

Counter currents

Current systems are often bordered by shear-driven counter currents (e.g., the equatorial, McPhaden, 1996; and subtropical counter currents, Uda and Hasunuma, 1969). Nearshore current systems such as the California Current have both nearshore (e.g., the Davidson current) and deep counter currents (Reid, 1962). Such counter currents play a role in maintaining oceanic zooplankton communities (McGowan, 1972), and also may influence larval retention (Parrish et al. 1981). For example, counter currents may retain lobster larvae inshore of both the East Cape Current off New Zealand (Chiswell and Roemmich, 1998) and the Kuroshio Current off Japan (Sekiguchi, 1997).

Although not singularly considered in the literature, without variability in alongshore flow, many larvae would tend to be advected unidirectionally away from the natal source. For example, larvae that make extensive vertical migrations may migrate between counter currents, limiting their alongshore transport. Pelagic juvenile splitnose rockfish, *Sebastes diploproa*, spend up to a year in the California Current, where they are generally transported southward (Boehlert, 1977). Prior to recruitment, they migrate to midwater depths, where they are transported northward and shoreward by the deep undercurrent (Moser and Boehlert, 1991). It is clear that unidirectional flows are not an accurate depiction of ocean circulation. Rather, the inherent flow variability that exists in the ocean may lead to considerable capacity for restricted larval dispersal. At the extreme, however, highly variable flows will be totally chaotic (e.g., storm conditions), sharply increasing the loss of propagules and reducing the likelihood of self-recruitment.

C. SUMMARY: BIOPHYSCIAL LARVAL RETENTION

The degree to which marine populations are "open" is dependent upon a complex blend of biological and physical factors. The interplay between behavior and physics results in larval distributions that are non-random, and often species-specific patterns at varying distances from the source population. The analysis of such larval assemblages (Boehlert and Mundy, 1993; Leis et al., 1998) in light of physical correlates often provides the strongest inferential evidence of retention, because the specific processes creating the assemblages are difficult to observe and have only recently been studied in detail (e.g., Werner et al., 1993; Paris and Cowen, in prep.).

Although many of the above correlates *a priori* (or empirically) predict self-recruitment, some probably are more important than others and none can be considered in isolation. Furthermore, some of the correlates are inter-dependent (e.g., water residence time and basin size; fecundity and parental investment). Adult characteristics that most influence larval position in the water column are temporal and spatial patterns of spawning, both of which likely contribute to self-recruitment. There is little doubt that larval behavior, including vertical positioning and horizontal swimming ability is critical to estimates of self-recruitment. Pelagic larval duration clearly influences larval transport and the chance of retention, but as a correlate, it may be primarily useful for organisms with very short larval durations. Physical processes such as flow variability will significantly influence larval retention, while water residence time is probably only applicable for species with very short larval periods or those living in enclosed basins or estuaries, and site isolation is only useful for highly isolated habitats. Biophysical retention is achieved through the interaction of multiple biological traits with multiple physical processes thus many of these variables will have little predictive value when considered in isolation. The interaction of these variables may be additive or synergistic.

Physical factors that result in departure from unidirectional, depth-uniform water flow provide the opportunity for retention of larvae, and therefore self-recruitment. These physical factors are very common in the ocean and vary in intensity among locations and times. Some enable retention of passive larvae (physical retention), whereas others lead to retention only with active behavioral input by the larvae (biophysical retention). Larval behavior that can contribute to or result in retention or return to natal sites ranges from simple vertical orientation that is within the capabilities of the larvae of most taxa to complex sensory abilities and strong swimming that are know to occur in larvae of relatively few taxa, particularly decapod crustaceans and fishes. For all taxa, both the pelagic larval duration, and the time to behavioral competency will have a strong influence on likelihood of self-recruitment.

Recent work shows that larvae of some taxa have behavioral capabilities that were unexpected a few years ago. Increasing evidence indicates that at least fish and crab larvae are very flexible in their behavior. For example, larvae of coral reef fishes alter their swimming depths in different environments (lagoon versus ocean or on different sides of the same island) and swim faster in open water than adjacent to reef settlement sites, or faster swimming in some directions than in others (see review in Leis and McCormick, in press). Behavior also is flexible across a species' range. The timing of larval release and vertical swimming by crabs changes seasonally and across tidal regimes in response to changes in the phasing of tidal and light-dark cycles (Morgan, 1994, 1996a, b; Schell, 1996; Anastasia, 1999). The ability to adjust behavior to different situations in time and space should greatly enhance survival, retention and self-recruitment.

Until the direct estimates of self-recruitment in marine populations becomes widely feasible (see Thorrold et al., this volume), it often will be necessary to gather indirect evidence of self-recruitment and attempt predictions, such as those described above. On the other hand, estimates alone would not reveal the biophysical mechanisms by which self-recruitment occurs, and without knowledge of these mechanisms, generalizations will be impossible. Further study into the role of these various processes will help to focus our attention on mechanisms that are the most important contributors to controlling the scale of population connectivity in marine populations. The predictions outlined herein are meant to serve as a point of departure -- primarily for gathering data to test such relationships but also for estimating the potential for self-recruitment. Knowledge in this area necessitates both progress in direct estimates of self-recruitment and an understanding of the mechanisms by which it occurs. Understanding the relative importance of self-recruitment to local marine populations is a precursor to addressing fundamental ecological and evolutionary questions (see also Strathmann et al. this volume), as well as issues critical to the successful management and conservation of marine populations.

ACKNOWLEDGEMENTS

This work was conducted as part of the Working Group entitled Open vs. Closed Marine Populations: Synthesis and Analysis of the Evidence, supported by the National Center for Ecological Analysis and Synthesis (NCEAS), a center funded by NSF Grant DEB-94-21535, the University of California, Santa Barbara, the California Resources Agency, and the California Environmental Protection Agency. We thank Bob Warner for organizing the meeting, participating in the discussions leading to this manuscript, and providing editorial comments on several drafts of the manuscript. Several authors (SS, RKC, JP) acknowledge funding through the US National Science Foundation; J. Leis acknowledges Australian Research Council funding through Grants A19530997and A19804335.

LITERATURE CITED

Anastasia, J. R. 1999. Plasticity and the cost of dispersal by estuarine crab larvae. Doctoral dissertation, State University of New York at Stony Brook.

Andrews, J. C., W.C. Dunlap, and N.F. Bellamy. 1984. Stratification in a small lagoon in the Great Barrier Reef. Aust. J. Mar. Freshw. Res. 35: 273-284.

Armsworth, P.R. 2000. Modelling the swimming response of late larval reef fish to different stimuli. Mar. Ecol. Prog. Ser. 195: 231-247.

Atema, J. and D.F. Cowan. 1986. Sex identifying urine and molt signals in the lobster *Homarus americanis*. J. Chem. Ecol. 12: 2065-2080.

Babcock, R.C., G.D. Bull, P.L. Harrison, A.J. Heyward, J.K. Oliver, C.C. Wallace, and B.L. Willis. 1986. Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. Mar. Biol. 90: 379-394.

Backus, R.H., J.E. Craddock, R.L. Haedrich, and B.H. Robison. 1977. Atlantic meso- and bathypelagic zoogeography. Pages 266-287 *in* R.H.Gibbs, Jr., ed. Fishes of the western North Atlantic, Part VII. Sears Foundation for Marine Research, New Haven, CT, USA.

Badan-Dangon, A., C.J. Koblinsky, and T. Baumgartner. 1985. Spring and summer in the Gulf of California: observations of surface thermal patterns, Oceanologica Acta. 8:13-22.

Baines, P.G. 1986. Internal tides, internal waves, and near-inertial motions. Pages 19-31 *in* C.N.K. Mooers, ed. Baroclinic Processes on Continental Shelves, American Geophysical Union, Volume 3, Washington, DC, USA.

Bakun, A. 1986. Local retention of planktonic early life stages in tropical reef bank demersal systems: The role of vertically-structured hydrodynamic processes. Pages 15-32 *in* D. Pauly and A. Yanez-Arancibial, eds. OC/FAO Workshop Report 44 on recruitment in tropical coastal demersal communities. Ciudad del Carmen, Campeche, Mexico: Unesco, Paris.

Bakun, A. 1988. Local retention of planktonic early life stages in tropical demersal reef bank systems: the role of vertically-structured hydrodynamic processes. Pages 15-32 *in* IOC/FAO Workshop on

Recruitment in Tropical Coastal Demersal Communities, Vol. IOC Workshop Report 44, Supplement, Ciudad del Carmen, Campeche, Mexico.

Barange, M. and S.C. Pillar. 1992. Cross-shelf circulation, zonation and maintenance mechanisms of *Nyctiphanes capensis* and *Euphausia hanseni* (Euphausiacea) in the Northern Benguela upwelling system. Cont. Shelf Res. 12: 1027-1042.

Barber, W. E. and C.P. Lee. 1975. Preliminary factors influencing the ingress of planktonic King prawn (*Penaeus plebejus*) post-larvae into Moreton Bay. Pages 45-53 *in* P.C.Young, ed. First Australian National Prawn Seminar. Canberra, Australian Govt. Publishing Service.

Barlow, G. W. 1981. Patterns of parental investment, dispersal and size among coral-reef fishes. Environ. Biol. Fish. 6: 65-85.

Barnett, A. M., A. E. Jahn, P. D. Sertic, and W. Watson. 1984. Distribution of ichthyoplankton off San Onofre, California, and methods for sampling very shallow coastal waters. Fish. Bull. 82: 97-111.

Barnett, A.M. and A.E. Jahn 1987. Pattern and persistence of a nearshore planktonic ecosystem off Southern California. Cont. Shelf. Res. 7:1-25.

Barry, J. P. 1989. Reproductive response of a marine annelid to winter storms: an analog to fire adaptation in plants? Mar. Ecol. Prog. Ser. 54: 99-107.

Barton, E.D., J. Aristegui, P. Tett, M. Canton, J. Garcia-Braun, S. Hernandez-Leon, L. Nykjaer, C. Almeida, J. Almunia, S. Ballesteros, G. Basterretxea, J. Escanez, L. Garcia-Weill, A. Hernandez-Guerra, F. Lopez-Laatzen, R. Molina, M.F. Montero, E. Navarro-Perez, J.M. Rodriguez, K. van Lenning, H. Velez, and K. Wild. 1998. The transition zone of the Canary Current upwelling region. Prog. Oceanogr. 41: 455-504.

Bell, K.N.I. and J.A. Brown. 1995. Active salinity choice and enhanced swimming endurance in 8-day-old larvae of diadromous gobies, including *Sicydium punctatum* (Pisces) in Dominica, West Indies. Mar. Biol. 121: 409-417.

Bell, K.N.I., P. Pepin, and J.A. Brown. 1994. Seasonal, inverse cycling of length-and age-at-recruitment in the diadromous gobies *Sicydium punctatum* and *Sicydium antillarum* in Dominica, West Indies. Can. J. Fish. Aquat. Sci. 52: 1535-45.

Bentzen, P., C.T.Taggart, D.E. Ruzzante, and D. Cook. 1996. Microsatellite polymorphism and the population structure of cod (*Gadus morhua*) in the North West Atlantic. Can. J. Fish. Aquat. Sci. 53: 2706-2721.

Berry, A.J. 1986. Daily, tidal, and two-weekly spawning periodicity and brief pelagic dispersal in the tropical intertidal gastropod *Umbonium vestiarium* (L.) J. Exp. Mar. Biol. Ecol. 95: 211-223.

Black, K.P. 1994. Developments in our knowledge of dispersal on the Great Barrier Reef. Pages 159-192 *in* P.W. Sammarco and M.L. Heron, eds. The bio-physics of marine larval dispersal. American Geophysical Union, Washington DC, USA.

Black, K.P. and S.L. Gay. 1987. Eddy formation in unsteady flows. J. Geophys. Res. 92: 9514-9522.

Black , K.P., S.L. Gay, and J.C. Andrews. 1990. Residence times of neutrally-buoyant matter such as larvae, sewage or nutrients on coral reefs. Coral Reefs 9:105-114.

Black, K.P., P.J. Moran, and L.S. Hammond. 1991. Numerical models show coral reefs can be self-seeding. Mar. Ecol. Prog. Ser. 74:1-11.

Blaxter, J. H. S. 1986. Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. Trans. Amer. Fish. Soc. 115: 98-114.

Blaxter, J.H.S. 1988. Sensory performance, behavior, and ecology of fish. Pages 203-232 *in* J. Atema, R.R. Fay, A.N. Popper and W.N. Tavolga, eds. Sensory biology of aquatic organisms. Springer-Verlag, Berlin.

Boehlert, G. W. 1977. Timing of the surface-to-benthic migration in juvenile rockfish, *Sebastes diploproa*, off southern California. Fish. Bull. 75: 887-890.

Boehlert, G.W. and B.C. Mundy. 1993. Ichthyoplankton assemblages at seamounts and oceanic islands. Bull. Mar. Sci. 53: 336-361.

Boehlert, G.W. and T. Sasaki. 1988. Pelagic biogeography of the armorhead, *Pseudopentaceros wheeleri*, and recruitment to isolated seamounts in the North Pacific Ocean. US Fish. Bull. 86: 453-465.

Boehlert, G.W., W. Watson, and L.C. Sun. 1992. Horizontal and vertical distributions of larval fishes around an isolated oceanic island in the tropical Pacific. Deep-Sea Res. Part A - Oceanographic Research Papers 39: 439-466.

Bograd, S. J., Rabinovich, A. B., LeBlond, P. H. and Shore, J. A. 1997. Observations of seamount-attached eddies in the North Pacific. J. Geophys. Res. 102: 12441-12456.

Boucher, J. (1984). Localization of zooplankton populations in the Ligurian marine front: role of ontogenetic migration. Deep-Sea Res. 31: 469-484.

Bousfield, E. L. 1955. Ecological control of the occurrence of barnacles in the Miramichi estuary. National Museum Canadian Bulletin Biology Series 137: 1-65.

Bowman, M. J. and Esaias, W. E. 1978. Oceanic Fronts in Coastal Processes. Berlin, Heidelberg: Springer-Verlag. 114 p.

Breen, P.A. and B.E. Adkins. 1979. Spawning in a British Columbia population of Northern Abalone, *Haliotis kamtschatkana*. Veliger 23: 178-179.

Bradbury, I.R. and P.V.R. Snelgrove. 2001. Contrasting larval transport in demersal fish and benthic invertebrates: the roles of behaviour and advective processes in determining spatial pattern. Can. J. Fish. Aquatic. Sci. 58: 811-823.

Breitberg, D. 1989. Demersal schooling prior to settlement by larvae of the naked goby. Environ. Biol. Fish. 26: 97-103.

Breitburg, D.L. 1991. Settlement patterns and presettlement behavior of the naked goby, *Gobiosoma bosci*, a temperate oyster reef fish. Mar. Biol. 109: 213-221.

Brink, K.H. 1989. The effect of stratification on seamount-trapped waves. Deep-Sea Res. 36: 825-844.

Brogan, M.W. 1994. Distribution and retention of larval fishes near reefs in the Gulf of California. Mar. Ecol. Prog. Ser.115: 1-13.

Butman, C. A. 1987. Larval settlement of soft-sediment invertebrates: The spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. Oceanogr. Mar. Biol. Ann. Rev. 25:113-165.

Cailliet, G.M. and D.L. Vaughan. 1983. A review of the methods and problems of quantitative assessment of *Loligo opalescens*. Biol: Oceanogr. 2: 379-400.

Campbell, A. 1986. Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, Eastern Canada. Can. J. Fish. Aquat. Sci. 43: 2197-2205.

Carriker, M. R. 1951. Ecological observations on the distribution of oyster larvae in New Jersey estuaries. Ecol. Monogr. 21: 19-38.

Cato, D.H. 1992. The biological contribution to the ambient noise in waters near Australia. Acous. Austr. 20: 76-80.

Chereskin, T. K. 1983. Generation of internal waves in Massachusetts Bay. J. Geophys. Res. 88: 2649-2661.

Chia, F-S, J. Buckland-Nicks, and C.M. Young. 1984. Locomotion of marine invertebrate larvae: a review. Can. J. Zool. 62: 1205-1222.

Chiswell, S.M. and J.D. Booth. 1999. Rock lobster *Jasus edwardsii* larval retention by the Wairarapa Eddy off New Zealand. Mar. Ecol. Prog. Ser. 183: 227-240.

Chiswell, S. and D. Roemmich. 1998. The East Cape Current and two eddies: a mechanism for larval retention? NZ J. Mar. Freshw. Res. 32: 385-397.

Christy, J. and S. Stancyk. 1982. Movement of larvae from North Inlet estuary S.C. with special reference to crab zoeae. Pages 489-510 *in* V. Kennedy, ed. Estuarine comparisons. Academic Press, New York, NY, USA.

Christy, J. H. and S. G.Morgan. 1998. Estuarine immigration by crab postlarvae: mechanisms, reliability and adaptive significance. Mar. Ecol. Prog. Ser. 174: 51-65.

Clancy, M. and C.E. Epifanio. 1989. Distribution of crab larvae in relation to tidal fronts in Delaware Bay, USA. Mar. Ecol. Prog. Ser. 57: 77-82.

Cobb, J. S., D. B. Wang, D. B. Campbell and P. Rooney. 1989. Speed and direction of swimming by postlarvae of the American lobster. Trans. Amer. Fish. Soc.118: 82-86.

Codiga, D. L. and C.C. Eriksen.1997. Observations of low-frequency circulation and amplified subinertial tidal currents at Cobb Seamount. J. Geophys. Res.102: 22993-23007.

Colin, P. L. and L.J. Bell. 1991. Aspects of the spawning of labrid and scarid fishes (Pisces: Labroidei) at Enewetak Atoll, Marshall Islands with notes on other families. Environ. Biol. Fish. 31: 229-260.

Cowen, R.K. 1991. Variation in the planktonic larval duration of the temperate wrasse *Semicossyphus pulcher*. Mar. Ecol. Prog. Ser. 69: 9-15.

Cowen, R.K. In press. Oceanographic influences on larval dispersal and retention and their consequences for population connectivity. Pages *in* P.F. Sale, ed. Ecology of coral reef fishes: recent advances. Academic Press, New York, NY, USA.

Cowen, R.K. and L.R. Castro. 1994. Relation of coral reef fish larval distributions to island scale circulation around Barbados, West Indies. Bull. Mar. Sci. 54: 228-244.

Cowen, R.K., L.A. Chiarella, C.J. Gomez, and M.A. Bell. 1991. Offshore distribution, size, age, and lateral plate variation of late larval/early juvenile sticklebacks (*Gasterosteus*) off the Atlantic coast of New Jersey and New York. Can. J. Fish. Aquat. Sci.s 48: 1679-1684.

Cowen, R.K., J.A. Hare, and M.P. Fahay. 1993. Beyond hydrography: can physical processes explain larval fish assemblages within the Middle Atlantic Bight? Bull. Mar. Sci. 53: 567-587.

Cowen, R.K., K.M.M. Lwiza, S. Sponaugle, C.B. Paris and D.B. Olson. 2000. Connectivity of marine populations: open or closed? Science 287: 857-859.

Cowen, R.K. and S. Sponaugle. 1997. Relationships between early life history traits and recruitment in coral reef fishes. Pages 423-449 *in* R.C. Chambers and E. Trippel, eds. Early life history and recruitment in fish populations. Chapman and Hall, London, UK.

Cronin, T. W. 1982. Estuarine retention of larvae of the crab *Rhithropanopeus harrisii*. Est. Coast. Shelf Sci. 15: 207-220.

Cronin, T.W., and R. B. Forward. 1982. Tidally timed behavior: Effects on larval distributions in estuaries. Pages 505-520 *in* V. Kennedy, editor. Estuarine comparisons. Academic Press, New York, NY, USA.

Crossland, C.J., D.J. Barnes, and M.A. Borowitzka. 1980. Diurnal lipid and mucus production in staghorn coral *Acropora acuminata*. Mar. Biol. 60: 81-90.

Csanady, G. T. 1974. Mass exchange episodes in the coastal boundary layer, associated with current reversals. Rapp. P.-v. Reun, Cons. Int. Explor. Mer 167: 41-45.

Csanady, G. T. 1981. Circulation in the coastal ocean. Adv. Geophys. 23: 101-183.

Csanady, G.T., and P. Hamilton. 1988. Circulation of Slope water. Cont. Shelf Res. 8: 565-624.

Cushing, D. H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge, UK. 278 p.

Damas, D. 1909. Contribution à la biologie des gadids. Rapp. P-v. Réu. Con. Inter. pour l'Explor. Mer 10: 1-277.

Davis, T.L.O., G.P. Jenkins, and J.W. Young. 1990. Patterns of horizontal distribution of the larvae of southern bluefin (*Thunnus maccoyii*) and other tuna in the Indian Ocean. J. Plank. Res. 12: 1295-1314.

Denny, M. W. 1988. Biology and the mechanics of the wave-swept environment. Princeton University Press, Princeton, NJ, USA. 329 p.

DiBacco, C. and L. A. Levin. 2000. Development and application of elemental fingerprinting to track the dispersal of marine invertebrate larvae. Limnol. Oceanogr.. 45: 871-880.

Dittel, A.I., and C.E. Epifanio. 1982. Seasonal abundance and vertical distribution of crab larvae in Delaware Bay. Estuaries 5:197-202.

Domeier, M.L and P.L. Colin. 1997. Tropical reef fish spawning aggregations: defined and reviewed. Bull. Mar. Sci. 60: 698-726.

Durand, M.-H., P. Cury, R. Mendelssohn, C. Roy, A. Bakun. and D. Pauly. 1998. Global versus local changes in upwelling systems. Colloq. Semina. Inst. Fr. Rech. Sci. Dev. Coop., Orstom, Paris, France. 594 p.

Ebert, T. A., and M. P. Russell. 1988. Latitudinal variation in size structure of the west coast purple sea urchin: a correlation with headlands. Limnol. Oceanogr. 33:286-294.

Eggleston, D. B., D. A. Armstrong, W. E. Weis and W. S. Patton. 1998. Estuarine fronts as conduits for larval transport: hydrodynamics and spatial distribution of Dungeness crab postlarvae. Mar. Ecol. Prog. Ser. 164:73-82.

Emery, A. 1972. Eddy formation from an oceanic island: ecological effects. Carib. J. Sci. 12: 121-128.

Epifanio, C. E. 1987. The role of tidal fronts in maintaining patches of brachyuran zoeae in estuarine waters. J. Crust. Biol. 7: 513-517.

Epifanio, C. E. 1995. Transport of blue crab (*Callinectes sapidus*) larvae in the waters off mid-Atlantic states. Bull. Mar. Sci. 57:713-725.

Eriksen, C. C. 1982. Observations of internal wave reflection off sloping bottoms. J. Geophys. Res. 87: 525-538.

Farmer, D. M. and J.D. Smith. 1980. Tidal interaction of stratified flow with a sill in Knight Inlet. Deep-Sea Res. 27: 239-254.

Fernandez, M. O.O. Iribarne, D.A. Armstrong. 1994. Swimming behavior of Dungeness crab, *Cancer magister* Dana, megalopae in still and moving water. Estuaries17: 271-275.

Fisher, R., D. R. Bellwood, and S.D. Job. 2000. The development of swimming abilities in reef fish larvae. Mar. Ecol. Prog. Ser. 202: 163-173.

Fortier, L. and W.C. Leggett. 1983. Vertical migrations and transport of larval fish in a partially mixed estuary. Can. J. Fish. Aquat. Sci. 40: 1543-1555.

Frank, K. T. and W. C. Leggett. 1981. Wind regulation of emergence times and early larval survival in capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 38:215-223.

Franks, P.J.S. 1992. Sink or swim: Accumulation of biomass at fronts. Mar. Ecol. Prog. Ser. 82:1-12.

Freeland, H. 1994. Ocean circulation at and near Cobb Seamount. Deep-Sea Res. 41: 1715-1732.

Fulton, T.W. 1989. The spawning and spawning places of marine food-fishes. Fish. Bd. Scotl. Ann. Rep. 8: 257-282.

Gaines, S.D. and M.D. Bertness. 1992. Dispersal of juveniles and variable recruitment in sessile marine species. Nature 360: 579-580.

Gagné, J.A. and R.N. O'Boyle. 1984. The timing of cod spawning on the Scotian Shelf. The Propagation of Cod *Gadus morhua* L., Flodevigen Rapportser. 1: 501-517.

Genin, A. and G.W. Boehlert. 1985. Dynamics of temperature and chlorophyll structures above a seamount: an oceanic experiment. J. Mar. Res. 28: 907-924.

Genin, A., M. Noble, and P.F. Lonsdale. 1989. Tidal currents and anticyclonic motions on two North Pacific seamounts. Deep-Sea Res. 36: 12 1803-1815.

Gladstone, W. and M. Westoby. 1988. Growth and reproduction in *Canthigaster valentini* (Pisces, Tetradontidae): a comparison of a toxic reef fish with other reef fishes. Environ. Biol. Fishes. 21: 207-221

Govoni, J.J. and C.B. Grimes. 1992. The surface accumulation of larval fishes by hydrodynamic convergence within the Mississippi River plume front. Cont. Shelf Res. 12:1265-1276.

Graham, W.M., J.G. Field, and D.C. Potts.1992. Persistent 'upwelling shadows' and their influence on zooplankton distributions. Mar. Biol. 114: 561-570.

Graham, W. M. and Largier, J. L. 1997. Upwelling shadows as nearshore retention sites: The example of northern Monterey Bay. Cont. Shelf Res. 17: 509-532.

Grassman, M.A., D.W. Owens, J.P. McVey and R. Marquez. 1984. Olfactory-based orientation in artificially imprinted sea turtles. Science 224: 83-84.

Grimes, C.B., and M.J. Kingsford. 1996. How do riverine plumes of different sizes influence fish larvae: do they enhance recruitment? Mar. Freshw. Res. 47: 191-208.

Hammann, M.G., T.R. Baumgartner, and A. Badan-Dangon 1988. Coupling of the Pacific sardine (*Sardinops sagax caeruleus_*) life cycle with the Gulf of California pelagic environment. Calif. Coop. Oceanic Fish. Invest. Rep. 29: 102-109.

Hamner, W.M. and I.R. Hauri. 1977. Fine-scale surface currents in the Whitsunday Islands, Queensland, Australia: effect of tide and topography. Aust. J. Mar. Freshw. Res. 28: 333-359.

Hamner, W.M. and I.R. Hauri. 1981. Effects of isalnd mass:water flow and plankton pattern around a reef in the Great Barrier Reef lagoon, Australia. Limnol. Oceanogr. 26: 1084-1102.

Hara, T.J. 1994. The diversity of chemical stimulation in fish olfaction and gustation. Rev. Fish Biol. Fish. 4:1-35.

Hare, J.A., and R.K. Cowen. 1993. Ecological and evolutionary implications of the larval transport and reproductive strategy of bluefish *Pomatomus saltatrix*. Mar. Ecol. Prog. Ser. 98: 1-16.

Hare, J.A., and R.K. Cowen. 1996. Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Mid-Atlantic Bight nursery habitats. Limnol. Oceanogr. 41: 1264-1280.

Harden Jones, F.R. 1968. Fish migration. Edward Arnold Ltd., London, UK. 325 p.

Heywood, K.J., E.D. Barton, and J.H. Simpson. 1990. The effects of flow disturbance by an oceanic island. J. Mar. Res. 48: 55-73.

Hill, A.E. 1991. Vertical migration in tidal waves. Mar. Ecol. Prog. Ser. 75: 39-54.

Hoffman, K.S. and E.G. Grau. 1989. Daytime changes in oocyte development with relation to the tide for the Hawaiian saddleback wrasse *Thalassoma duperrey*. J. Fish Biol. 34: 529-546.

Hourigan, T.F. and E.S. Reese. 1987. Mid-ocean isolation and evolution of Hawaiian reef fishes. Trends Ecol. Evol. 2: 187-191.

Hovel, K. A., and S. G. Morgan. 1997. Planktivory as a selective force for reproductive synchrony and larval migration. Mar. Ecol. Prog. Ser. 157:79-95.

Hughes, D. 1969. Responses to salinity change as a tidal transport mechanism of pink shrimp, *Penaeus duorarum*. Biol. Bull. 136: 43-53.

Iles, T.D., and M. Sinclair 1982. Atlantic herring: stock discreteness and abundance. Science 215: 627-633.

Jahn, A.E., and R. J. Lavenberg. 1986. Fine-scale distribution of nearshore, suprabenthic fish larvae. Mar. Ecol. Prog. Ser. 31: 223-231.

Janssen, J., S. Coombs, and J. Montgomery. 1990. Comparisons in the use of the lateral line for detecting prey by nototheniods and sculpins. Antarc. J. US. 25: 214-215.

Johannes, R.E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Environ. Biol. Fish. 3: 65-84.

Jones, G. P., M. J. Milicich, M.J. Emslie, and C. Lunow. 1999. Self-recruitment in a coral reef fish population. Nature 402: 802-804.

Kalmun, A.J. 1982. Electric and magnetic field detection in elasmobranch fishes. Science 218: 916-918.

Kaufman, L., J. Ebersole, J. Beets, and C.C. McIvor. 1992. A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition. Environ. Biol. Fish. 34: 109-118.

Kingsford, M. J. and Choat, J. H. 1986. The influence of surface slicks on the distribution and onshore movement of small fish. Mar. Biol. 91: 161-171.

Kingsford M.J. J.H. Choat. 1989. Horizontal distribution patterns of presettlement reef fish: are they influenced by the proximity of reefs? Mar. Biol. 101: 285-297.

Kingsford, M.J., J.M. Leis, A. Shanks, K.C. Lindeman, S.G. Morgan, and J. Pineda. In review. Sensory environments, larval abilities and local self-recruitment. Bull. Mar. Sci. Spec. Pubs. This volume.

Kingsford, M.J. and I. M. Suthers. 1994. Dynamic estuarine plumes and fronts: importance to small fishes and plankton in coastal waters of NSW, Australia. Cont. Shelf Res. 14: 655-672.

Kingsford, M.J., E. Wolanski, and J.H. Choat. 1991. Influence of tidally induced fronts and Langmuir circulations on distribution and movements of presettlement fishes around a coral reef. Mar. Biol. 109: 167-180.

Korringa, P. 1947. Relations between the moon and periodicity in the breeding of marine animals. Ecol. Monogr. 17: 349-381.

Laprise, R., and J.J. Dodson. 1990. The mechanism of retention of pelagic tomcod, *Microgadus* tomcod, larvae and juveniles in the well-mixed part of the St. Lawrence Estuary. Environ. Biol. Fish. 29: 293-302.

Laprise, R., and J.J. Dodson. 1989. Ontogeny and importance of tidal vertical migrations in the retention of larval smelt *Osmersus mordax* in a well-mixed estuary. Mar. Ecol. Prog. Ser. 55: 101-111.

Lara, M. 1999. A comparative study of sensory development in settlement-stage larvae of Caribbean labrids and scarids with implications for ecomorphology and life history strategies. Dissertation. College of William and Mary, Williamsburg, VA, USA.

Largier, J.L., B.A. Magnell, and C.D. Winant. 1993. Subtidal circulation over the northern California shelf. J. Geophys. Res. 98: 18147-18179.

Larson, R.J. 1992. Riding Langmuir Circulations and swimming in circles - a novel form of clustering behavior by the Scyphomedusa *Linuche unguiculata*. Mar. Biol. 112: 229-235.

Largier, J.L. 1993. Estuarine fronts: how important are they? Pages 1-11 *in* J.L. Largier, ed. Estuarine fronts: hydrodynamics, sediment dynamics and ecology. Estuaries 16.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. US Fish. Bull. 73: 453-462.

Lee, T. N., M. E.Clarke, E. Williams, A. F. Szmant, and T. Berger. 1994. Evolution of the Tortugas Gyre and its influence on recruitment in the Florida Keys. Bull. Mar. Sci. 54: 621-646.

Lee, T. and E. Williams. 1999. Mean distribution and seasonal variability of coastal currents and temperature in the Florida Keys with implications for larval recruitment. Bull. Mar. Sci. 64: 35-56.

Le Fèvre, J., 1986. Aspects of the biology of frontal systems. Adv. Mar. Biol. 23: 163-299.

Leichter, J.J., G. Shellenbarger, S.J. Genovese, S. R. Wing. 1998. Breaking internal waves on a Florida (USA) coral reef: a plankton pump at work? Mar. Ecol. Prog. Ser. 166: 83-97.

Leichter, J.J., S.R. Wing, S.L. Miller, and M.W. Denny. 1996. Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal bores. Limnol. Oceanogr. 41: 1490-1501.

Leis, J.M. 1986. Vertical and horizontal distribution of fish larvae near coral reefs at Lizard Island, Great Barrier Reef. Mar. Biol. 90: 505-516.

Leis, J.M. 1991. The pelagic stage of reef fishes: The larval biology of coral reef fishes. Pages 183-230 *in* P.F. Sale, editor. The ecology of fishes on coral reefs. Academic Press, San Diego, CA, USA.

Leis, J. M. 1994. Coral Sea atoll lagoons - closed nurseries for the larvae of a few coral reef fishes. Bull. Mar. Sci. 54: 206-227.

Leis, J. M., and B.M. Carson-Ewart. 1997. *In situ* swimming speeds of the late larvae of some Indo-Pacific coral reef fishes. Mar. Ecol. Prog. Ser. 159: 165-174.

Leis, J. M. and M.I. McCormick. In press. The black box has real fish inside: recent developments in the biology, behaviour and ecology of the pelagic, larval stage of coral-reef fishes. *in* P.F. Sale, ed. Coral Reef Fishes: New insights into their ecology. Academic Press, New York, NY, USA.

Leis, J. M., and I.C. Stobutzki. 1999. Swimming performance of late pelagic larvae of coral-reef fishes: *in situ* and laboratory-based measurements. Pages 575-583 *in* B. Séret and J.-Y. Sire, eds. Proceedings of the 5th Indo-Pacific Fish Conference, Nouméa, 1997, Société Française d'Ichtyologie et Institut de Recherche pour le Développement, Paris, France.

Leis, J.M., T. Trnski, P.J. Doherty, and V. Dufour. 1998. Replenishment of fish populations in the enclosed lagoon of Taiaro Atoll (Tuamotu Archipelago, French Polynesia): evidence from eggs and larvae. Coral Reefs 17: 1-8.

Leis, J.M., T. Trnski, V. Dufour, R. Galzin, M. Harmelin-Vivian and J-P. Renon. Submitted. Local completion of the pelagic larval stage of coastal fishes in coral-reef lagoons of the Society and Tuamotu Islands. Mar. Biol.

Lenarz, W. H., R.J. Larson and S. Ralston. 1991. Depth distributions of late larval and pelagic juveniles of some fishes of the California current. Cal. Coop. Fish. Invest. Rept. 32: 41-46.

Levin, L.A., and T. S. Bridges. 1995. Pattern and diversity in reproduction and development. Pages 1-48 *in* L. McEdward, ed. Ecology of marine invertebrate larvae. CRC Press, Boca Raton, FL, USA.

Limouzy-Paris, C.B., H.C. Graber, D.L. Jones, A.W. Röpke, and W.J. Richards. 1997. Translocation of larval coral reef fishes via sub-mesoscale spin-off eddies form the Florida current. Bull. Mar. Sci. 60: 966-983.

Lindeman, K. C. 1986. Development of larvae of the French grunt, *Haemulon flavolineatum* and comparative development of twelve western Atlantic species of *Haemulon*. Bull. Mar. Sci. 39: 673-716.

Lindeman, K. C., R. Pugliese, G. T. Waugh, and J. S. Ault. 2000. Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. Bull. Mar. Sci. 66: 929-956.

Lindeman, K. C., T. N. Lee, W. D. Wilson, R. Claro, and J. S. Ault. 2001. Transport of larvae originating in southwest Cuba and the Dry Tortugas: evidence for partial retention in grunts and snappers. Proc. Gulf Carib. Fish. Inst. 52:732-747.

Lobel, P.S. 1978. Diel, lunar, and seasonal periodicity in the reproductive behavior of the pomacentrid fish, *Centropyge potteri*, and some other reef fishes in Hawaii. Pacific Sci. 32: 193-207.

Lobel, P.S. 1989. Ocean current variability and the spawning season of Hawaiian reef fishes. Environ. Biol. Fish. 24: 161-171.

Lobel, P. S. and A. R. Robinson. 1988. Larval fishes and zooplankton in a cyclonic eddy in Hawaiian waters. J. Plank. Res. 10: 1209-1223.

Loder, J. W., C.K. Ross and P.C. Smith. 1988. A space- and time-scale characterization of circulation and mixing over submarine banks, with application to the northwestern Atlantic continental shelf. Can. J. Fish. Aquat. Sci. 45: 1860-1885.

Luckenbach, M. W., and R.J. Orth. 1990. Swimming velocities and behavior of blue crab (*Callinectes sapidus* Rathbun) megalopae in still and flowing water. Estuaries 15: 186-192.

MacKay, D.C.G. 1943. The behavior of the Pacific edible crab *Cancer magister* Dana. J. Comp. Psycol. 36: 255-268.

Manuel, J.L., and R.K. O'Dor. 1997. Vertical migration for horizontal transport while avoiding predators: I. A tidal/diel model. J. Plank. Res.19: 1929-1947.

Marliave, J.B. 1986. Lack of planktonic dispersal of rocky intertidal fish larvae. Trans. Amer. Fish. Soc. 115: 149-154.

Maxworthy, T. 1979. A note on the internal solitary waves produced by tidal flow over a three-dimensional ridge. J. Geophys. Res. 84: 338-345.

McCleave, J.D., and R.C. Kleckner. 1987. Distribution of leptocephali of the catadromous *Anguilla* species in the Western Sargasso Sea in relation to water circulation and migration. Bull. Mar. Sci. 41: 789-806.

McConaugha, J.R.1988. Export and reinvasion of larvae as regulators of estuarine decapod populations. Pages 90-103 *in* M. P. Weinstein, ed. Larval fish and shellfish transport through inlets. Amer. Fish. Soc. Symp. 3.

McGowan, J. A. 1972. The nature of oceanic ecosystems. Pages 9-28 *in* C. B. Miller, ed. The biology of the Oceanic Pacific. Oregon State University Press, Corvallis, OR, USA.

McManus, J.W., and L.A.B. Menez. 1997. The proposed International Spratly Island Marine Park: ecological considerations. Proc. 8th Inter. Coral Reef Symp. 2: 1943-8.

McPhaden, M. J. 1996. Monthly period oscillations in the Pacific North Equatorial Countercurrent. J. Geophys. Res. 101 : 6337-6359.

Meincke, J. 1971. Observations of an anticyclonic vortex trapped above a seamount. J. Geophys. Res. 76: 7432-7440.

Morgan, S. G. 1990. Impact of planktivorous fishes on the dispersal, hatching and morphology of estuarine crab larvae. Ecology 71: 1639-1652.

Morgan, S.G. 1994. Influence of tidal regime on the timing of larval release by crabs: Implications for recruitment success. Pages 323-328 *in* K.R. Dyer and R.J. Orth, eds. Changes in fluxes in estuaries: implications from science to management, Olsen and Olsen, Fredensborg, Denmark.

Morgan, S. G. 1995a. The timing of larval release. Pages 157-191 *in* L. McEdward, ed. Ecology of marine invertebrate larvae. CRC Press, Boca Raton, FL, USA.

Morgan, S. G. 1995b. Life and death in the plankton: larval mortality and adaptation. Pages 279-321 *in* L. McEdward, ed. Ecology of marine invertebrate larvae. CRC Press, Boca Raton, FL, USA.

Morgan, S. G. 1996a. Plasticity in reproductive timing by crabs in adjacent tidal regimes. Mar. Ecol. Prog. Ser. 139:105-118.

Morgan, S. G. 1996b. Influence of tidal variation on reproductive timing. J. Exp. Mar. Biol. Ecol. 206: 237-251.

Moser, H.G., and G.W. Boehlert 1991. Ecology of pelagic larvae and juveniles of the genus *Sebastes*. Environ. Biol. Fish. 30: 203-224.

Myrberg, Jr. A.A. and Fuiman, L.A. In press. The sensory world of coral reef fishes. *in* P. Sale, ed. Ecology of coral reef fishes: recent advances. Academic Press, New York, NY, USA.

Nash, W.J. 1993. Trochus. Pages 451-495 *in* A. Wright and L. Hill, eds. Nearshore marine resources of the South Pacific. Institute of Pacific Studies Suva, Forum Fisheries Agency Honiara, International Centre for Ocean Development, Canada.

Nichols, J. H., B. M. Thompson, and M. Cryer. 1982, Producton, drift and mortality of the planktonic larvae of the edible crab (*Cancer pagurus*) off the north-east coast of England. Nether. J. Sea Res. 16:173-184.

Nittrouer, C.N., and L.D. Wright. 1994. Transport of particles across continental shelves. Rev. Geophys. 32: 85-113.

Noble, M. and Mullineaux, L. S. 1989. Internal tidal currents over the summit of Cross Seamount. Deep-Sea Res. 36: 1791-1802.

Norris, K. S. 1963. The function of temperature in the ecology of the percoid fish *Girella nigricans* (Ayres). Ecol. Monogr. 33: 23-62.

Nowell, A.R.M., and P.A. Jumars. 1984. Flow environments of aquatic benthos. Ann. Rev. Ecol. Syst. 15: 303-328.

O'Boyle, R.N., M. Sinclair, R.J. Conover, K.H. Mann, and A.C. Kohler. 1984. Temporal and spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological, and physiographic features. Rapp. P-v Réun., Cons. Inter. l'Explor. Mer 183: 27-40.

O'Connell, M., M.C. Dillon, J.M. Wright, P. Bentzen, S. Merkouris, and J. Seeb. 1998. Genetic structuring among Alaskan Pacific herring populations identified using microsatellite variation. J. Fish Biol. 53: 150-163.

O'Donnell, J. 1993. Surface fronts in estuaries: a review. Estuaries 16: 12-39.

Oliver, J., R. Babcock. 1992. Aspects of the fertilization ecology of broadcast spawning corals-sperm dilution effects and in situ measurements of fertilization. Biol. Bull. 183: 409-417.

Olson, D.B., and R.H. Backus. 1985. The concentrating of organisms at fronts: a cold- water fish and a warm-core Gulf Stream ring. J. Mar. Res. 43: 113-137.

Osborne, A. R. and T. L. Burch. 1980. Internal solitons in the Andaman Sea. Science 208: 451-460.

Osterling, M. J. 1977. Relationship between Florida's blue crab population and Apalachicola Bay. FL Res. Publ. 26: 101-121.

Owens, W. B. and Hogg, N. G. 1980. Oceanic observations of stratified Taylor columns near a bump. Deep-Sea Res. 27: 1029-1045.

Paris, C. and R.K. Cowen. In prep. A retention mechanism for coral reef fish larvae.

Parrish, R. H., C. S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California current. Biol. Oceanogr. 1: 175-203.

Pascual, M. and H. Caswell. 1991. The dynamics of a size-classified benthic population with reproductive subsidy. Theor. Pop. Biol. 39: 129-147.

Pechenik , J.A., M.S. Estrella and K. Hammer. 1996a. Food limitation stimulates metamorphosis of competent larvae and alters postmetamorphic growth rate in the marine prosobranch gastropod *Crepidula fornicata*. Mar. Biol. 127: 267-275.

Pechenik, J.A., K. Hammer, and C. Weise. 1996b. The effect of starvation on acquisition of competence and post-metamorphic performance in the marine prosobranch gastropod *Crepidula fornicata*. J. Exp. Mar. Biol. Ecol. 199: 137-152.

Peterson, W. 1998. Life cycle strategies of copepods in coastal upwelling zones. J. Mar. Sys. 15: 313-326.

Peterson, W. T., C. B. Miller, C. B. and A. Hutchinson. 1979. Zonation and maintenance of copepod populations in the Oregon upwelling zone. Deep-Sea Res. 26: 467-494.

Phillips, B. F., and A. N. Sastry. 1980. Larval ecology. Pages 11-57 *in* J.S. Cobb and B. F. Phillips, eds. The biology and management of lobsters, Volume 2. Academic Press, New York, NY, USA.

Phillips, B.F., and D.L. Macmillan. 1987. Antennal receptors in puerulus and postpuerulus stages of the rock lobster *Panulirus cygnus* (Decapoda: Palinuridae) and their potential role in puerulus navigation. J. Crust. Biol. 7: 122-135.

Pineda, J. 1991. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. Science 253: 548-551.

Pineda, J. 1995. An internal tidal bore regime at nearshore stations along western U.S.A.: Predictable upwelling within the lunar cycle. Cont. Shelf Res. 15: 1023-1041.

Pineda, J. 1999. Circulation and larval distribution in internal tidal bore warm fronts. Limnol. Oceanogr. 44: 1400-1414.

Pingree, R.D. and L. Maddock. 1980. The effects of bottom friction and earth's rotation on an island's wake. J. Mar. Biol. Assoc. U.K. 60: 499-508.

Planes, S., P. Romans, and R. Lecomte-Finiger. 1998. Genetic evidence of closed life cycles for some coral reef fishes within Taiaro Atoll, Tuamotu Archipelago, French Polynesia. Coral Reefs 17: 9-14.

Pogson, G. H., C. T. Taggart, K. A. Mesa and R. G. Boutilier. 2001. Isolation by distance in the Atlantic cod, *Gadus morhua*, at large and small geographic scales. Evolution 55: 131-146.

Polunin, N.V.C. and C.M. Roberts. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Mar. Ecol. Prog. Ser. 100:167-176.

Provenzano, A. J., J. McConaugh, Jr, K.B. Philips, D.F. Johnson, and J. Clark. 1983. Vertical distribution of first stage larvae of the blue crab, *Callinectes sapidus*, at the mouth of Chesapeake Bay. Est. Coast. Shelf Sci. 16: 489-499.

Quayle, D. B. 1988. Pacific oyster culture in British Columbia. Fish. Res. Bd. Canada Bull. 218: 241.

Quinn, T.P., and A.H. Dittman. 1990. Pacific salmon migrations and homing: mechanisms and adaptive significance. Trends Ecol. Evol. 5: 174-177.

Quinn, T.P., and G.M. Tolson. 1986. Evidence of chemically mediated population recognition in coho salmon (*Oncorhychus kisutch*). Can. J. Zool. 64: 84-87.

Randall, J.E. 1961. A contribution to the biology of the convict surgeonfish of the Hawaiian Islands, *Acanthurus triostegus* sandvicensis. Pac. Sci. 15: 215-272.

Rebach, S. 1983. Orientation and migration in Crustacea. Pages 217-264 *in* S. Rebach and D. W. Dunham, eds. Studies in adaptation: the behavior of higher Crustacea. John Wiley and Sons, New York, NY, USA.

Reid, J. L. J. 1962. Measurements of the California counter-current at a depth of 250 meters. J. Mar. Res. 20 : 134-137.

Reyns, N. and S. Sponaugle. 1999. Patterns and processes of brachyuran crab settlement to Caribbean coral reefs. Mar. Ecol. Prog. Ser. 185:155-170.

Rissik, D. and I. M. Suthers. 2000. Enhanced feeding by pelagic juvenile myctophid fishes within a region of island-induced flow disturbance in the Coral Sea. Mar. Ecol. Prog. Ser. 203: 263-273.

Roberts, C. M. 1997. Connectivity and management of Caribbean coral reefs. Science 278: 1454-1456.

Robertson, D.R. 2001. Population maintenance among tropical reef fishes: inferences from small island endemics. Proc. Natl. Acad. Sci. USA. 98: 5667-5670.

Robertson, D.R. , C.W. Petersen and J.D. Brawn. 1990. Lunar reproductive cycles of benthic-brooding reef fishes: reflections of larval biology or adult biology? Ecol. Monogr. 60: 311-329.

Rogers, P.H., and M. Cox. 1988. Underwater sound as a biological stimulus. Pages 131-149 *in* J. Atema, R.R. Fay, A.N. Popper and W.N. Tavolga, eds. Sensory biology of aquatic organisms. Springer-Verlag, Berlin.

Rosenfeld, L. K., F.B. Schwing, N. Garfield and D.E. Tracy. 1994. Bifurcated flow from an upwelling center - a cold water source for Monterey Bay. Cont. Shelf Res. 14: 931-964.

Rothlisberg, P. C., J. A. Cjurch and A.M.G. Forbes. 1983. Modelling the advection of vertically migrating shrimp larvae. J. Mar. Res. 41 : 511-538.

Roughgarden, J., J. T. Pennington, D. Stoner, S. Alexander, and K. Miller. 1991. Collisions of upwelling fronts with the intertidal zone - the cause of recruitment pulses in barnacle populations of central California. Acta Oecologica – Intern. J. Ecol. 12: 35-51.

Ruzzante, D.E., C.T. Taggart, and D. Cook. 1998. A nuclear DNA basis for shelf and bank-scale population structure with microsatellite data: bias and sampling variance. Can. J. Fish. Aquat. Sci. 55: 1-14.

Ruzzante, D.E., C.T. Taggart, and D. Cook. 1999. A review of the evidence for genetic structure of cod (*Gadus morhua*) populations in the Northwest Atlantic and population affinities of larval cod off Newfoundland and the Gulf of St. Lawrence. Fish. Res. 43: 79-97.

Sale, P.J. 1970. Distribution of larval Acanthuridae off Hawaii. Copeia 1970: 765-766.

Sammarco, P.W. 1994. Larval dispersal and recruitment processes in Great Barrier Reef corals: Analysis and synthesis. Pages 35-72 *in* P.W. Sammarco and M.L. Heron, eds. The bio-physics of marine larval dispersal. American Geophysical Union, Washington, DC, USA.

Sancho, G., A.R. Solow, P.S. Lobel. 2000. Environmental influences on the diel timing of spawning in coral reef fishes. Mar. Ecol. Prog. Ser. 206:193-212.

Sandifer, P.A. 1975a. The role of pelagic larvae in recruitment to populations of adult decapod crustaceans in the York River estuary and adjacent lower Chesapeake Bay, Virginia. Est. Coast. Mar. Sci. 3: 269-279.

Sandifer, P. 1975b. Distribution and abundance of decapod crustacean larvae in the York River estuary and adjacent lower Chesapeake Bay, Virginia, 1968-1969. Chesap. Sci. 14: 235-257.

Sasaki, R., and S.A. Shepherd. 1995. Recruitment processes of *Haliotis discus hannai* with special reference to larval distribution and settlement. Pages 325-340 *in* Y. Watanabe, Y. Yamashita and Y. Oozeki, eds. Survival strategies in early life stages of marine resources. A.A. Balkema, Rotterdam, Netherlands.

Sawyer, C. 1983. A satellite study of ocean internal waves: NOAA Tech. Memo. ERL-PMEL-46.

Schell, J. M. 1996. Variation in the timing of vertical swimming by crab larvae and megalopae in a diurnal tidal regime. Masters thesis, State University of New York at Stony Brook, Stony Brook, NY, USA.

Scheltema, R.S. 1971. The dispersal of larvae of shoal-water benthic invertebrate species over long distances by ocean currents. Pages 7-28 *in* D. Crisp, ed. Fourth European Marine Biology Symposium, Cambridge University Press, Cambridge, UK.

Schultz, E.T., and R.K. Cowen.1994. Recruitment of coral-reef fishes to Bermuda: local retention or long-distance transport? Mar. Ecol. Prog. Ser. 109: 15-28.

Searcy, S. and S. Sponaugle. 2000. Variable larval growth in a coral reef fish. Mar. Ecol. Prog. Ser. 206: 213-226.

Seki, T. and K. Tangiguchi. 1996. Factors critical to the survival of herbivorous animals during settlement and metamorphosis. Pages 341-354 *in* Y. Watanabe, Y. Yamashita and Y. Oozeki, eds. Survival strategies in early life stages of marine resources. A.A. Balkema, Rotterdam, Netherlands.

Sekiguchi, H. 1997. Larval recruitment processes of Japanese spiny lobsters: An hypothesis. Bull. Mar. Sci. 61: 43-55.

Shanks, A. L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser. 13: 311-315.

Shanks, A. L. 1986. Vertical migration and cross-shelf dispersal of larval *Cancer spp.* and *Randalia ornata* (Crustacea: Brachyura) off the coast of southern California. Mar. Biol. 92: 189-199.

Shanks, A. L. 1988. Further support for the hypothesis that internal waves can transport larvae of invertebrates and fish onshore. Fish. Bull. 86: 703-714.

Shanks, A. L. 1995. Orientated swimming by megalopae of several eastern north Pacific crab species and its potential role in their onshore migration. J. Exp. Mar. Biol. Ecol. 186:1-16.

Shanks, A.L., B. Grantham, and M. Carr. In press. Propagule dispersal distance and the size and spacing of marine reserves. Ecol. Appl.

Shanks, A. L., J. Largier, L. Brink, J. Brubaker, and R. Hooff. 2000. Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. Limnol. Oceanogr. 45: 230-236.

Shanks, A. L. and W. G. Wright. 1987. Internal-wave-mediated shoreward transport of cyprids, megalopae, and gammarids and correlated longshore differences in the settling rate of intertidal barnacles. J. Exp. Mar. Biol. Ecol. 114: 1-13.

Shaw, P.W., C. Turan, J.M. Wright, M. O'Connell, and G.R. Carvalho. 1999. Microsatellite DNA analysis of population structure in Atlantic herring (*Clupea harengus*), with direct comparison to allozyme and mtDNA RFLP analyses. Heredity 83: 490-499.

Shaw, W.N. and T.J. Hassler. 1989. Life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest): Lingcod. Biol Rep. US Fish and Wild. Serv. 19 p.

Shepherd, S.A., D. Lowe, and D. Partington. 1992. Studies on southern Australian abalone (Genus *Haliotis*) 13. Larval dispersal and recruitment. J. Exp. Mar. Biol. Ecol. 164: 247-260.

Signell, R. P., and W. R. Geyer. 1991. Transient eddy formation around headlands. J. Geophys. Res. 96: 2561-2575.

Sinclair, M. 1988. Marine Populations: an essay on population regulation and speciation. Washington Sea Grant Press, Seattle, WA, USA. 252 p.

Smith, W.G., and W.W. Morse. 1985. Retention of larval haddock *Melanogrammus aeglefinus* in the Georges Bank region, a gyre influenced spawning area. Mar. Ecol. Prog. Ser. 24: 1-13.

Sponaugle, S., and R.K. Cowen. 1994. Larval durations and recruitment patterns of two Caribbean gobies (Gobiidae): Contrasting early life histories in demersal spawners. Mar. Biol. 120: 133-143.

Steele, P. 1990. Migration of the blue-crab, *Callinectes sapidus* Rathburn, in the eastern Gulf of Mexico. Amer. Zool. 30: A137-A137.

Steffe, A.S. 1990. Epibenthic schooling by larvae of the atherinid fish *Leptatherina presbyteroides* - an effective mechanism for position maintenance. Japan. J. Ichthy. 36: 488-491.

Stobutzki, I.C., and D. R. Bellwood. 1997. Sustained swimming abilities of the late pelagic stages of coral reef fishes. Mar. Ecol. Prog. Ser. 149: 35-41.

Strathmann, R. R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. Ann. Rev. Ecol. Syst. 16: 339-361.

Strathmann, R.R., T.P. Hughes. A.M. Kuris, K. Lindeman, S.G. Morgan, J.M. Pandolfi, and R.R. Warner. In review. Evolution of self-recruitment and its consequences for marine populations. Bull. Mar. Sci. Spec. Publ.

Swearer, S. E., J.E. Caselle, D.W. Lea, and R.R. Warner. 1999. Larval retention and recruitment in an island population of a coral reef fish. Nature 402: 799-802.

Swearer, S.E., S.R. Thorrold, J.S. Shima, M.E. Hellberg, G.P. Jones, D.R. Robertson, S.G. Morgan, K.A. Selkoe, G.M. Ruiz, and R.R. Warner. In review. Evidence and life-history correlates of self-recruitment in benthic marine populations. Bull. Mar. Sci. Spec. Publ.

Sweatman, H.P.A. 1983. Influence of conspecifics on choice of settlement sites by larvae of two pomacentrid fishes (*Dascyllus aruanus* and *D. reticulatus*) on coral reefs. Mar. Biol. 75: 225-229.

Sweatman, H.P.A. 1985. The influence of adults of some coral reef fishes on larval recruitment. Ecol. Monogr. 55: 469-485.

Taylor, M. H. 1984. Lunar synchronization of fish reproduction. Trans. Am. Fish. Soc. 113: 484-493.

Tegner, M.J., and R. A. Butler. 1985. Drift-tube study of the dispersal potential of green abalone (*Haliotis fulgens*) larvae in the southern California Bight: implications for recovery of depleted populations. Mar. Ecol. Prog. Ser. 26: 73-84.

Thompson, W. F. 1919. The spawning of the grunion (*Leuestes tenuis*). Calif. Fish. Game Comm. Fish Bull. 3:1-29.

Thorrold, S.R., G.P. Jones, M.E. Hellberg, R.S. Burton, S.E. Swearer, J.E. Neigel, S.G. Morgan, and R.R. Warner. In review. Quantifying larval retention and connectivity in marine populations with artificial and natural markers: can we do it right? Bull. Mar. Sci. Spec. Publ.

Thresher, R.E. 1984. Reproduction in reef fishes. T.F.H. Publications, Inc., Neptune City, New Jersey, USA.

Thresher, R.E., P.L. Colin, and L. Bell. 1989. Planktonic duration, distribution and population structure of western and central Pacific damselfishes (Pomacentridae). Copeia 1989: 420-34.

Tolimieri,N., A. Jeffs, J.C. Montgomery. 2000. Ambient sound as a cue for navigation by the pelagic larvae of reef fishes. Mar. Ecol. Prog. Ser.
207, 219-224.

Tremblay, M.J., J.W. Loder, F.E. Werner, C.E. Naimie, F.H. Page, and M.M. Sinclair. 1994. Drift of sea scallop larvae *Placopecten magellanicus* on Georges Bank: A model study of the roles of mean advection, larval behavior and larval origin. Deep-Sea Res. 41: 7-49.

Trites, R.W. 1983. Physical oceanographic features and processes relevant to *Illex illecebrosus* spawning in the western North Atlantic and subsequent larval distribution. NAFO Sci. Council Stud. 6: 39-55.

Tyler, M.A., D.W. Coats and D.M Anderson. 1982. Encystment in a dynamic environment: deposition of dinoflagellate cysts by a frontal convergence. Mar. Ecol. Prog. Ser. 7: 163-178.

Uda, M. and K .Hasunuma. 1969. The eastward subtropical countercurrent in the western North Pacific Ocean. J. Oceanogr. Soc. Jap. 25 : 201-210.

Victor, B.C. 1986a. Delayed metamorphosis with reduced larval growth in a coral reef fish (*Thalassoma bifasciatum*). Can. J. Fish. Aquat. Sci. 43: 1208-1213.

Victor, B. C. 1986b. Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). Mar. Biol. 90: 317-326.

Walters, L.J. and R.E. DiFiori. 1996. Waterbourne chemical compounds in tropical macroalgae: positive and negative cues for larval settlement. Mar. Biol. 126: 383-394.

Warner, R.R. and R.K. Cowen. This volume. Local retention of production in marine populations: evidence, mechanisms, and consequences. Bull. Mar. Sci. Spec. Publ.

Waterman, T. H., 1989. Animal Navigation. New York: Scientific American Library; p. 243.

Weinstein, M. P., S. L. Weiss, R. G. Hodson, and L. R. Gerry. 1980. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. US Fish. Bull. 78: 419-436.

Welch, J.M., D. Rittschof, T.M. Bullock, and R.B. Forward, Jr. 1997. Effects of chemical cues on settlement behavior of blue crab *Callinectes sapidus* postlarvae. Mar. Ecol. Prog. Ser. 154: 143-153.

Werner, F.E., F.H. Page, D.R. Lynch, J.W. Loder, R.G. Lough, R.I. Perry, D.A. Greenberg, and M.M. Sinclair. 1993. Influences of mean advection and simple behavior on the distribution of cod and haddock early life stages on Georges Bank. Fish. Oceanogr. 22: 43-64.

Williams, D. McB., E. Wolanski, and J.C. Andrews. 1984. Transport mechanisms and the potential movement of planktonic larvae in the central region of the Great Barrier Reef. Coral Reefs 3: 229-236.

Winant, C.D., and J.R. Olson. 1976. The vertical structure of coastal currents, Deep-Sea Res. 23: 925-936.

Winant, C. D., 1980. Downwelling in the Southern California shelf. J. Phys. Oceanogr. 10: 791-799.

Wing, S.R., L.W. Botsford, J.L. Largier, and L.E. Morgan. 1995a. Spatial structure of relaxation events and crab settlement in the northern California upwelling system. Mar. Ecol. Prog. Ser. 128: 199-211.

Wing, S.R., L.W. Botsford, S.V. Ralston, and J.L. Largier. 1998. Meroplanktonic distribution and circulation in a coastal retention zone of the northern California upwelling system. Limnol. Oceanogr. 43: 1710-1721.

Wing, S.R., J.L. Largier, L.W. Botsford and J.F. Quinn. 1995b. Settlement and transport of benthic invertebrates in an intermittent upwelling region. Limnol. Oceanogr. 40: 316-329.

Wolanski, E. 1994. Physical oceanographic processes of the Great Barrier Reef. CRC Press, Boca Raton, Florida, USA. 194 p.

Wolanski, E. and W.M. Hamner. 1988. Topographically controlled fronts in the ocean and their biological influence. Science 241: 177-181.

Wolanski, E., J. Imberger, and M.L. Heron. 1984. Island wakes in shallow coastal waters. J. Geophys. Res. 89: 10553-10569.

Wolanski, E., P. Doherty, and J. Carleton. 1997. Directional swimming of fish larvae determines connectivity of fish populations on the Great Barrier Reef. Naturwissenschaften 84: 262-268.

Wolcott, D. L. and M. C. DeVries. 1994. Offshore megalopae of *Callinectes sapidus*: depth of collection, molt stage and response to estuarine cues. Mar. Ecol. Prog. Ser. 109: 157-163.

Wood, L., and W. J. Hargis, Jr. 1971. Transport of bivalve larvae in a tidal estuary. Pages 29-44 *in* D.J. Crisp, ed. Fourth European Marine Biology Symposium. Cambridge University Press, London, UK.

Wroblewski, J. S. 1982. Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone - a simulation. Deep-Sea Res. 29: 665-686.

Yamaguchi, M. 1993. Green snail. Pages 497-511 *in* A. Wright and L. Hill, eds. Nearshore marine resources of the South Pacific. Institute of Pacific Studies Suva, Forum Fisheries Agency Honiara, International Centre for Ocean Development, Canada.

Young, C.M. and F-S. Chia. 1987. Abundance and distribution of pelagic larvae as influenced by predation, behavior and hydrographic factors. Pages 385-463 *in* A.C. Giese, J.S. Pearse, V.B. Pearse, eds. Reproduction of marine invertebrates. General Aspects: seeking unity in diversity, Vol. IX, Blackwell Scientific Publications, Palo Alto, CA, USA.

Zeldis, J.R. and J.B. Jillett. 1982. Aggregation of pelagic *Munida gregaria* (Fabricius) (Decapoda, Anomura) by coastal fronts and internal waves. J. Plank. Res. 4: 839-857.

Table 1. Definitions of biological and physical variables as correlates of self-recruitment.

	Variable	Definition
A1	Adult fecundity	Number of propagules produced by a mature individual of a particular species; Variation among different local populations has more effect on self-recruitment.
A2	Spatial pattern of spawning/larval release	Directed movements by adults to place propagules in specific location; ranges from asynchronous spawning by sessile animals to highly synchronous spawning migrations.
A3	Temporal pattern of spawning	Timing of propagule release, ranging from asynchronous, random patterns to highly synchronous behaviors.
A4	Parental investment and larval stage of development at hatching	Amount of energy invested in reproduction; stage of development refers to the movement capabilities of the larvae (whether via active swimming or buoyancy control).
A5	Pelagic larval duration	Portion of a species larval development spent free of either parental care and/or contact with the benthos; period during which propagules are susceptible to physical mixing and advection.
A6	Vertical positioning behavior by larvae	Any vertical movement that results from a biological response (swimming and/or buoyancy control) of the organism, including diel, tidal, ontogenetic, and other cue dependent movements.
A7	Horizontal swimming ability of larvae	Active, directed movement by larvae in the horizontal direction.
A8	Sensory capabilities of larvae and environmental cue strength	Ability of larvae to detect and respond to cues of varying strengths emanating from the settlement or natal site.
B1	Geographical site isolation	Degree to which a site (local population) is physically isolated from other sites.
B2	Coastal complexity	Degree to which the coastline is convoluted with respect to bathymetric and topographic features acting to steer the prevailing current. Includes topographic complexity, embayments of several sizes, and water residence time.
B3	Flow variability & water column stratification	Integration of changes in direction of flow and intensity of flow in both horizontal and vertical planes, includes upwelling/downwelling, fronts, convergences, eddies, and counter currents.

Submitted to Bulletin of Marine Science (2001)

Settlement and recruitment of coral reef fishes in moderately exploited and overexploited Caribbean ecosystems: implications for marine protected areas

Maggie Watson and John L. Munro
International Center for Living Aquatic Resources Management,
Caribbean/Eastern Pacific Office,
158 Inland Messenger, Road Town, Tortola, British Virgin Islands

ABSTRACT

Abundances of pre-settlement coral reef fishes were monitored at heavily-exploited Discovery Bay, Jamaica, and at several sites around the moderately-exploited British Virgin Islands (BVI) to investigate the likely rate of population increases in an existing Marine Protected Area (MPA) in Jamaica and a proposed MPA in BVI. Light traps set concurrently at Discovery Bay and at three fringing reefs in BVI caught many species of pre-settlement reef fishes, except grunts and parrotfish and one BVI site (Hans Creek) may be an area of particularly high settlement. In contrast, heavily exploited fish stocks at Discovery Bay had greatly reduced settlement rates compared with all three sites in BVI. Settlement rates of unexploited species were more similar in Discovery Bay and BVI. Abundances of juvenile fish caught in wire-mesh traps were monitored over several years in Discovery Bay and at three sites in BVI. Consistently low numbers of exploited species were taken at Discovery Bay compared to the BVI sites, indicating that settlement and recruitment rates have been low in recent years. Exploited fish populations in the small MPA at Discovery Bay are expected to increase very slowly as a result of settlement and recruitment limitation, while the proposed MPA at Hans Creek (BVI) could be effective in enhancing adjacent fisheries.

INTRODUCTION

It has been clearly established that increases in average individual size, stock abundances and diversity of marine organisms occur as a result of the creation of Marine Protected Areas (MPAs) (Bohnsack 1996 provides a brief review). Such areas are therefore a source of increased production of eggs and larvae. However, there is a general lack of knowledge about the sources of juvenile fishes that survive and grow within MPA's to create the increased supply of eggs and larvae, i.e. are these fish products of local spawning or do they arrive from distant areas? Also, we know little about the rates at which fish (particularly commercially important species) settle from the plankton, and their subsequent rates of survival in nursery areas. Thus the mere declaration of MPA's is no guarantee that increases in productivity will occur. For example, if an MPA is in an area that receives few new settlers, the build-up of biomass in the MPA might be extremely slow. Additionally, if the eggs and larvae from the protected populations are swept offshore, the MPA might be ineffective in enhancing recruitment to stocks in adjacent exploited areas.

In this study, we explored the range of settlement rates over one season and recruitment rates over several years at both the Discovery Bay Marine Reserve (Jamaica) and at several sites around Tortola (British Virgin Islands) including a proposed Marine Protected Area at Hans Creek. As described below, these two locations were considered likely to represent opposite extremes of the expected range of settlement abundances for coral reef fish in the Caribbean. We assessed the likely ecological outcomes of variation in settlement and recruitment to the existing and proposed MPAs. We define settlement, following Keough and Downes (1982), as the point at which an individual settles from the pelagic to the benthic environment, and recruitment as the number of individuals surviving an arbitrary period after settlement (Connell 1985); in this case until they become vulnerable to small mesh fish traps.

The Discovery Bay Fishery Reserve was established in Jamaica in November 1996, covering 27 ha of backreef shallows and seagrass beds. Fishing pressure is extreme in the surrounding waters (Hughes 1994, Sary et al 1997). Overfishing combined with other factors suggest recovery of fish in the reserve may be slow. There is little live coral within the reserve because the entire reef system suffered complete algal overgrowth in the 1980s and coral cover has not recovered since that time. Also, as the north coast of Jamaica is relatively straight and has few embayments, conditions for retaining locally spawned eggs and larvae are not favourable. Further, based upon known surface currents and assuming passive behaviour, Roberts (1997) suggested that fish stocks at Discovery Bay in Jamaica are unlikely to receive settlers from other countries if the species have pelagic phases lasting less than one month. However, species with an extended pelagic phase (> two months) could come from areas to the east of Jamaica, such as Haiti and the northern Dominican Republic, the eastern end of Cuba and the Turks and Caicos Islands. More recent work suggests that larval mortality and dilution effects, combined with active behaviour, may drastically limit successful long-distance transport of fish larvae (Cowen *et al.* 2000). If correct, relatively isolated islands such as Jamaica may be even more reliant on their own stocks than previously thought.

In contrast, reefs of the British Virgin Islands (BVI) complex in the northeastern Caribbean are not heavily fished (Pomeroy 1999). A number of MPAs are proposed, including one of our study sites, Hans Creek. The shelf surrounding the islands supports relatively high spawning stock biomasses and local geography might be conducive to local retention of eggs and larvae in topographically induced gyres or eddies. Additionally, reefs may also receive settlers from islands and banks to the east.

Our study cannot not distinguish between local retention of fish larvae on individual reefs, and supply from nearby islands within healthy reef systems such as BVI and it's neighbours. Rather, it assesses whether remote, heavily over fished islands (such as Jamaica) continue to receive larvae from upstream sources even when local populations (such as at Discovery Bay) suffer recruitment over-fishing so that local recruitment is negligible. By inference, if recruitment consistently fails in such heavily exploited areas, local retention must previously have been an important process for replenishment.

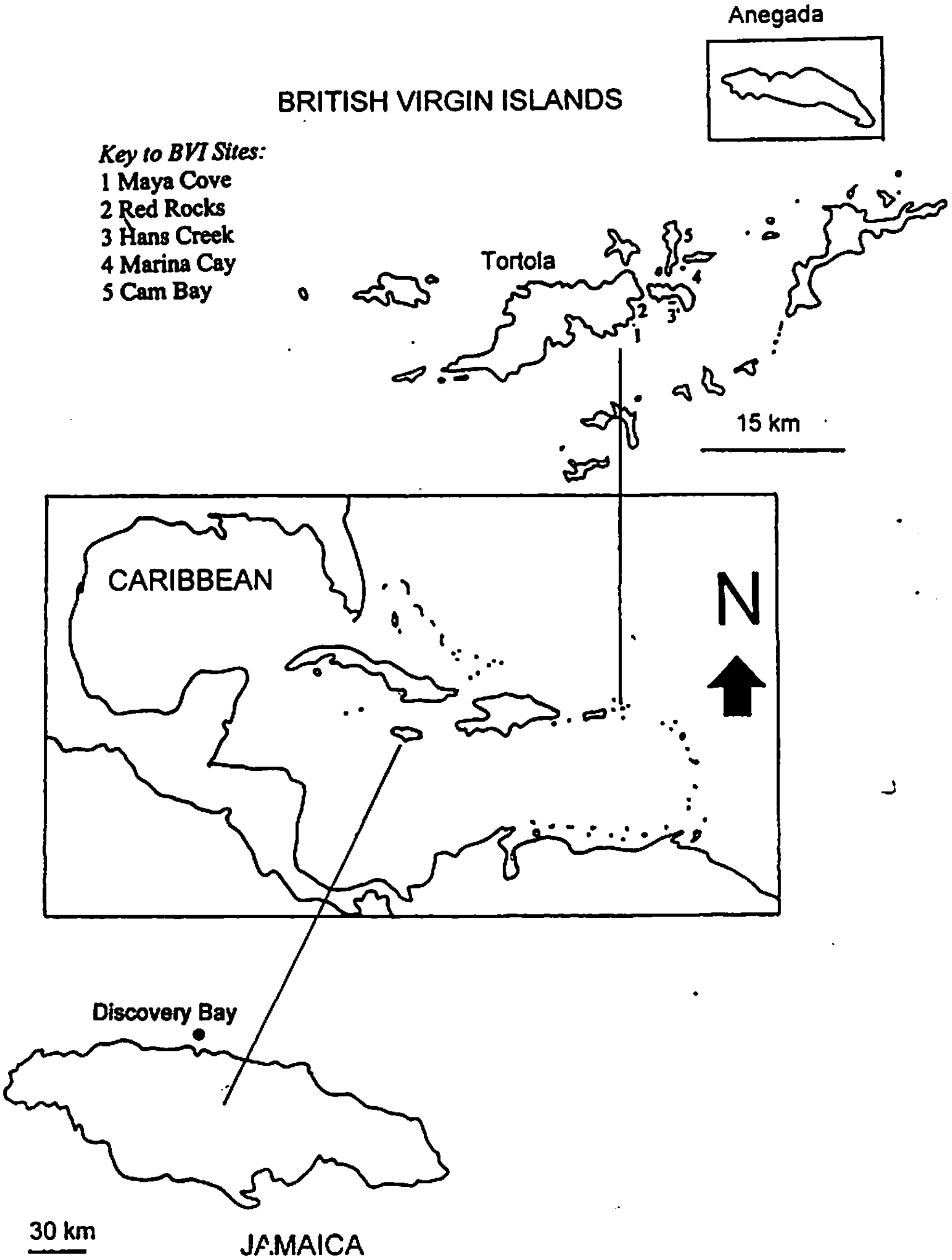


Figure 1. Map of the study sites in the British Virgin Islands (five sites) and at Discovery Bay, Jamaica.

METHODS

Light traps designed to catch fish settling from the plankton (modified after Stobutzki and Bellwood 1997 and described further in Watson *et al.* in press) were set about 100m seaward of the fore-reef at Discovery Bay, on the north coast of Jamaica, and seaward of well-defined fringing reefs near the eastern end of Tortola, BVI. The traps were suspended 2 m below the surface over depths of 15-25 m. We chose to set the traps in this depth of water to ensure that only late pelagic stage fish were attracted to the light, rather than individuals that had already settled on shallow reefs. Traps were spaced at least 80 m apart, lit before dusk and checked as early as possible the following morning. All samples were sorted and released at the trap site. Where fish were too immature to recognise, they were reared in aquaria until their juvenile colouration developed (usually for one or two days) and they could be identified.

Comparisons of catch rates were made between light traps deployed between November 1997 and August 1998 in both BVI and Discovery Bay. In BVI, four traps were set at one site (Hans Creek) between 16th November and 13th December 1997. From 16th February, four traps were set two or three times a week at Hans Creek until trapping was extended to a second site in March (Marina Cay) and to a third site in April (Cam Bay). In view of emerging lunar periodicity (see Results) sampling was then adjusted to include five or six days before the new moon (day zero) setting three traps at each of the three sites (Hans Creek, Marina Cay and Cam Bay - see Fig. 1. for locations). In Discovery Bay, four traps were set every night from 16th November to 19th December 1997 and five traps two or three times a week from March to April. Subsequently, 4 to 6 traps were set two or three days a week and more frequently leading up to new moons until 24th August 1998. Sampling was occasionally interrupted by bad weather or equipment problems. Where equipment failed, the data were discarded. Thus the actual number of samples collected varied (Fig. 2.).

Five groups of three double arrowhead 0.5 inch wire mesh traps (described by Munro 1999) were set in backreef/seagrass (mainly *Thalassia testudinum*) habitat near the west back reef in Discovery Bay between October 1996 and March 2000. Between July 1997 and July 1999, identical traps were set in each of three back-reef/seagrass areas at Tortola chosen for their ecological similarity to the shallow backreef habitat at Discovery Bay. The sites were at Hans Creek, Maya Cove and Red Rocks (Fig. 1) and each had shallow seagrass-dominated lagoon or backreef areas within a short distance of reefs. Eight traps were set altogether at Tortola, two in each of two backreef and seagrass areas at Hans Creek, and two traps at Maya Cove and Red Rocks (mixed seagrass and backreef habitat). Sampling at Maya Cove and Red Rocks ended in July 1999, but sampling was expanded to 12-16 traps at Hans Creek and continued until March 2000. In BVI and Jamaica, the fish caught by each trap were recorded by snorkelers every three or four days, and then released.

The abundance of each species in each wire mesh trap was divided by soak time, and the average monthly catch rate was calculated for each site. These values were then averaged to provide the mean species abundance for each site over the entire sampling period. In presenting these data our objective was to set the catches of settling fish from one season of light trapping within a longer temporal perspective on juvenile recruitment, rather than to statistically test the scale of spatial variation or its causes. We wanted to examine whether the reduced settlement at Discovery Bay was simply a temporal 'blip' or reflected a long-term trend. Thus data from wire mesh traps were pooled in ways that precluded the use of techniques such as analysis of variance but which maximized the time scales examined.

RESULTS

Light traps

Fish in the families Atherinidae, Engraulidae and Clupeidae were caught frequently, numbering thousands. Because of their pelagic life cycle, these fish were excluded from all further analyses. Abundance of late pelagic stage reef fish taken at Discovery Bay and three British Virgin Islands sites are compared for exploited and non-exploited families in Fig. 2. Exploited families were Acanthuridae, Balistidae, Carangidae, Lutjanidae, Mullidae, Scombridae, Serranidae and Sphyraenidae. Note, however, that the light traps were not effective in catching grunts (Haemulidae) or parrotfish (Scaridae). All other families were considered to be unexploited.

Data from the most complete BVI time series (Hans Creek) indicated that both exploited and unexploited families had a summer settlement season, which in 1998 began in April and peaked in August (Fig. 2.). On a finer temporal scale Fig. 2. reveals a peak in settlement preceding the new moon.

The number of traps set at each site was too low to estimate variation in catches precisely because the numbers of fish varied substantially among traps. For example, on 19th August 1998 we caught 407 *Ocyurus chyrusurus* in one trap at Hans Creek while neighbouring traps caught 55 and 14. The middle trap of the array caught the most fish, ruling out sequential depletion of larvae in a current. However overall, approximately 2.3 - 2.8 times as many exploited fish were caught at Hans Creek than at Marina Cay and Cam Bay in BVI, demonstrating substantial variation in settlement over a few kilometers (Fig. 2). Notwithstanding this variation, settlement of exploited species to Discovery Bay was severely reduced compared to sites in BVI (13.2 times less than Hans Creek and 5.5 and 4.6 less than Marina Cay and Cam Bay). By contrast, settlement of unexploited fish was relatively similar.

The commonest demersal reef associated species in light traps in BVI (in descending order) were *O. chrysurus*, *Lutjanus synagris*, *Caranx ruber*, *L. griseus* and *C. latus*. In Discovery Bay, the most abundant species were *Acanthurus chirurgus*, *C. ruber*, *A. bahianus*, *A. coeruleus* and *Balistes vetula*, and many of the exploited species were virtually absent from the catch (Table 1). Only two snappers (*L. synagris*) were caught during the entire sampling period at Discovery Bay. Settlement in Discovery Bay peaked on one night in March with a catch of 182 fish. Of these, 82 were *Ophioblennius atlanticus* and 35 were *Monocanthus tuckeri*.

Wire Mesh Traps

Inter-annual variation in settlement and recruitment rates is common for many fish, and peaks of settlement are not necessarily expected to be synchronous for widely separated locations. Catch rates from monitoring with half inch mesh traps over several years provide a longer temporal context for light trapping data. Catches from the half inch mesh traps at Discovery Bay were dominated by herbivorous species (Fig. 3). The catch rates of surgeonfish and parrotfish were generally similar or greater

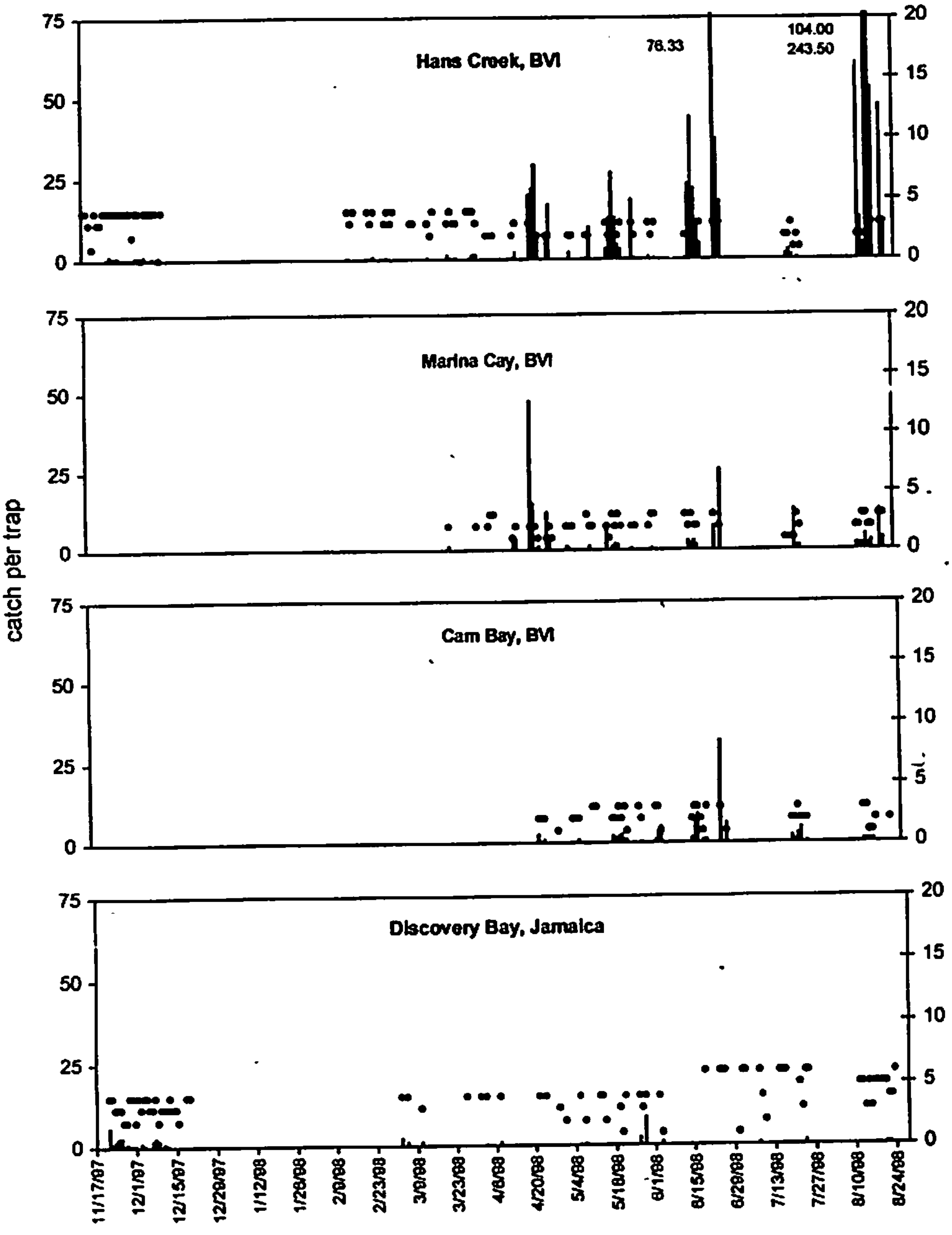


Fig. 2a. Light trap catches of settlement stage reef fishes from commercially exploited families (Acanthuridae, Balistidae, Carangidae, Lutjanidae, Mullidae, Scombridae, Serranidae and Sphyraenidae) from three sites in the British Virgin Islands and one site in Jamaica over the same time scale. Bars represent total catch of commercial species divided by number of traps set (left hand axis). Where a catch exceeds the scale, the actual number is noted on the figure. Dots represent number of funtioning light traps set per night (right hand scale). Note sampling at Marina Cay and Cam Bay (BVI) started in April 1998.

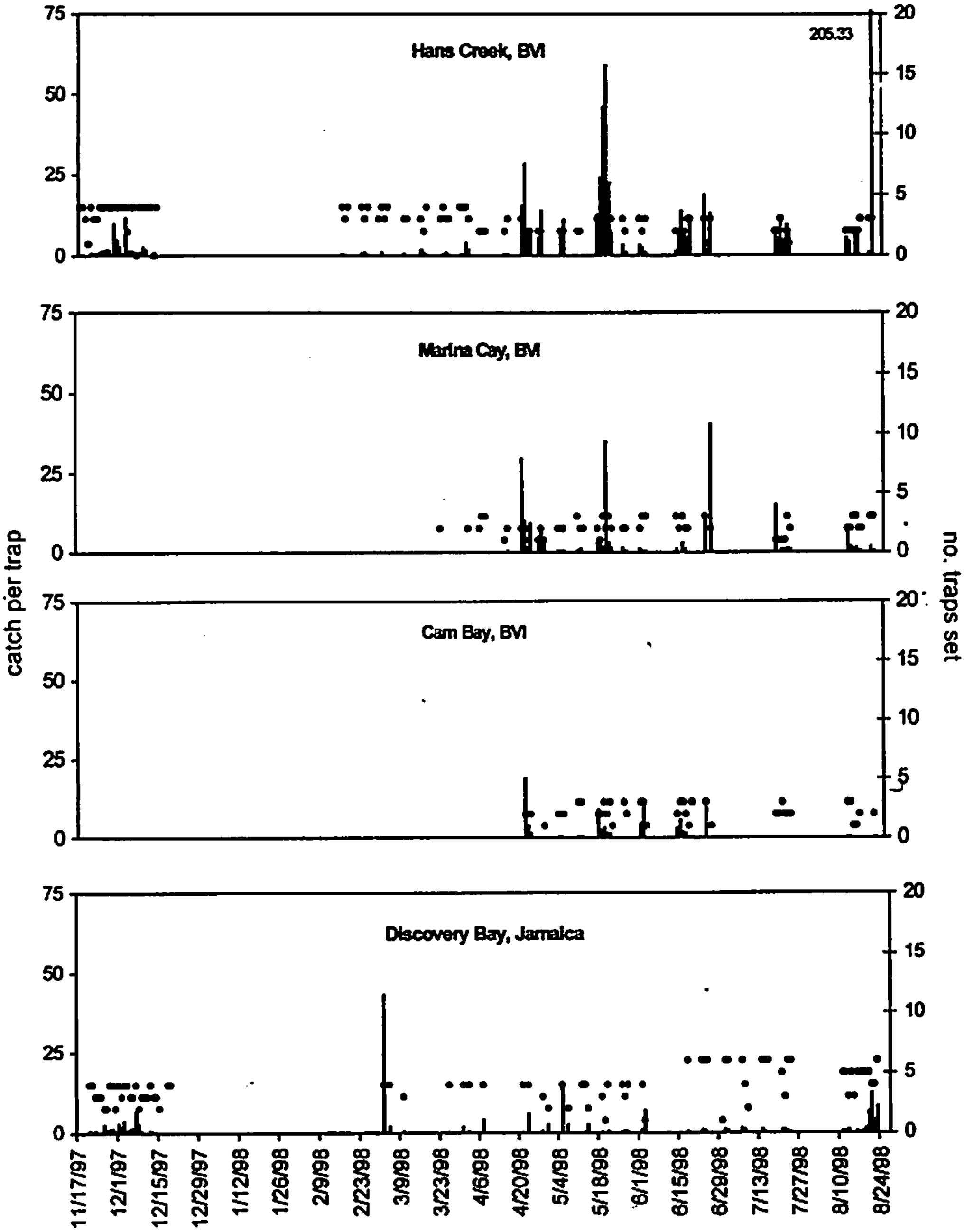


Fig. 2b. Light trap catches of settlement stage reef fishes from unexploited families from three sites in the British Virgin Islands and one site in Jamaica over the same time scale. Bars represent total catch of commercial species divided by number of traps set (left hand axis). Where a catch exceeds the scale, the actual number is noted on the figure. Dots represent number of funtioning light traps set per night (right hand scale). Note sampling at Marina Cay and Cam Bay (BVI) started in April 1998.

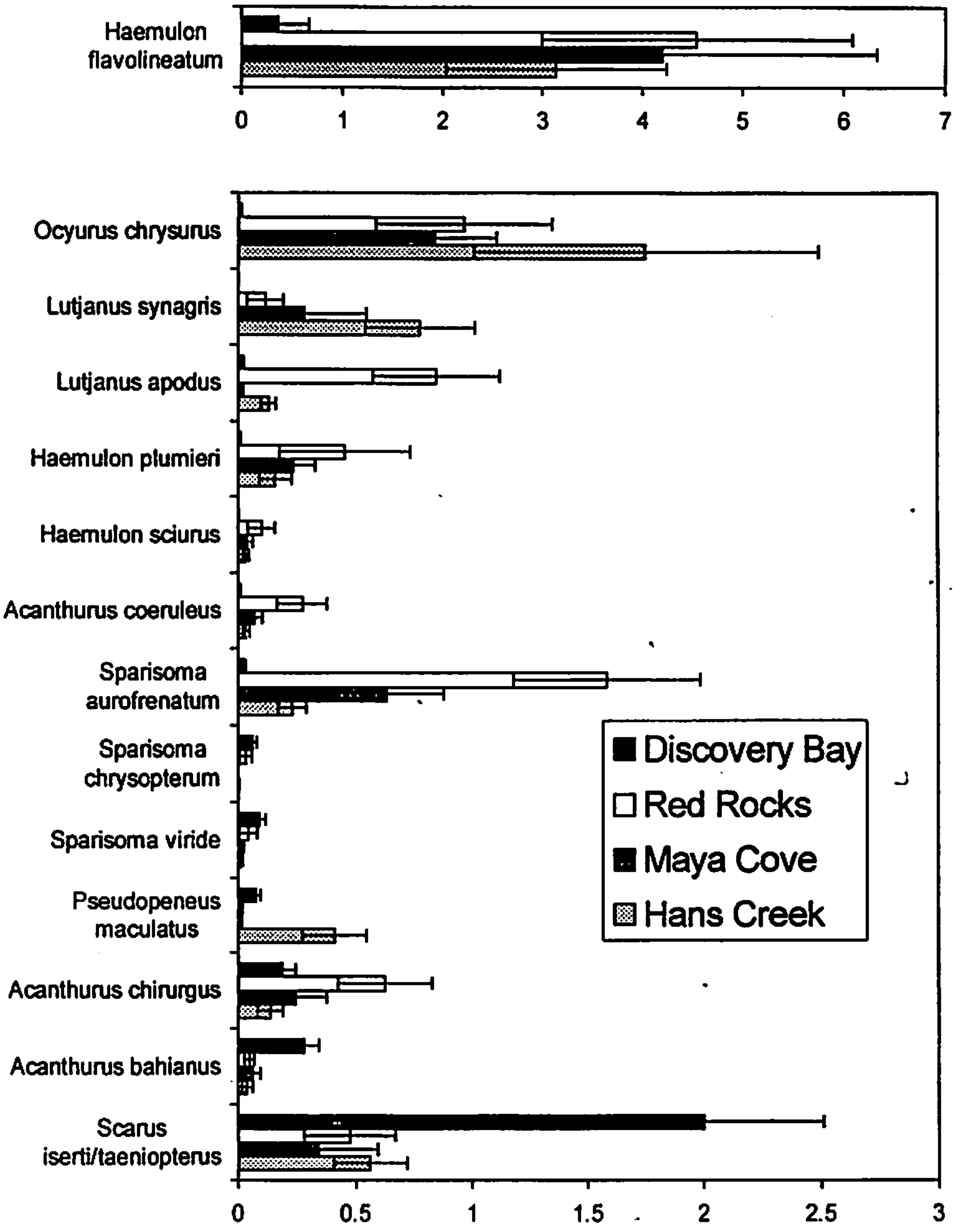


Fig. 3. Average catch per trap night of fishery speices taken in 0.5 mesh fish traps at Discovery Bay (Oct. 1996 to Mar. 2000), Red Rocks and Maya Cove (Jul. 1997 to July 1999) and Hans Creek (Jul 1997 to Mar 2000). Full sampling details in the text. Error bars represent 95% confidence intervals. *H. flavolineatum* shown separately to accomodate different scale.

than those from BVI but in contrast, the catch rates of predatory species in Discovery Bay were usually significantly reduced.

Table 1. Total catch of commercially important snappers divided by total effort (number of effective samples) for four sites.

	Hans Creek (n=284) BVI	Marina Cay (n=109) BVI	Cam Bay (n=87) BVI	Discovery Bay (n=314) Jamaica
O. chrysurus	4.77	1.49	1.29	0.00
L. synagris	1.72	0.61	0.31	0.01
L. apodus	0.20	0.08	0.31	0.00
L. griseus	0.31	0.15	0.18	0.00

DISCUSSION

In April 1998 increased light trap catches marked the beginning of the summer recruitment period. Summer recruitment peaks in reef fish have also been reported by Thorrold *et al.* (1994) Tupper and Hunte (1994), Beets (1997), Miller *et al.* (in press). Our light trap samples show that larval supply of commercially important species was far lower in Discovery Bay than at all sites in BVI. This, combined with low catches in wire mesh traps set for juvenile fish over three and a half years, suggest most of the larger high-valued species (snappers; grunts and jacks) have almost disappeared from the Discovery Bay ecosystem. Note that *L. griseus* was not included in the wire mesh trap analysis although settlement stage fish were taken in the light traps in BVI. The preferred juvenile habitat for this species is mangroves (Thayer et al. 1987, Mackey 1998). Although we set traps in mangroves in BVI, insufficient mangrove areas are found in Discovery Bay for a comparison and these data were subsequently excluded. The only species of commercial importance which were relatively abundant in Discovery Bay were small species which mature before recruitment to the fishery (e.g. *Scarus iserti, Sparisoma aurofrenatum*), or which have extended pelagic stages (e.g. Mullidae, Acanthuridae) and might be derived from distant spawning stocks. By contrast, all sites in BVI (but particularly Hans Creek) had high settlement and recruitment of exploited species. However, when unexploited species are considered, no clear difference emerges between Discovery Bay, Marina Cay and Cam Bay, although Hans Creek stands out as an exceptional site and may be an area of particularly high settlement.

Currently, there is no established "baseline" to identify "normal" rates of settlement and recruitment for reef fishes. There have been some multi-year studies in the Caribbean (Shulman and Ogden 1987; Hunt von Herbing and Hunte 1991; Robertson 1992; Tupper and Hunte 1994; Eggleston 1995; McGehee 1995; Sponaugle and Cowen 1996 a,b, 1997; Caselle and Warner 1996; Miller *et al.* in press), however, differing methodologies and target species make comparisons difficult. For example, many researchers have systematically removed settlers from habitat (e.g. Sponagule and Cowen 1997), some have used artificial habitat units or otherwise modified the environment (e.g. Beets 1997), while others have censused natural habitat (e.g. Robertson 1992). Other researchers looking for temporal trends have used end of season recruitment surveys which do not account for interannual variation in seasonality nor separate the effect of post settlement processes from larval supply, and may not be appropriate in the Caribbean (Robertson and Kaufmann 1998). Most recruitment studies in the Caribbean, as elsewhere, have concentrated on small, easily censused or territorial reef species (Luckhurst and Luckhurst 1977, Robertson 1992, Wellington 1992, Booth and Beretta 1994, Forrester 1995, McGehee 1995, Sponaugle and Cowen 1997). Few studies have been aimed at commercially important species, other than grunts (McFarland *et al.* 1985; Shulman and Ogden 1987) and groupers (Shenker *et al.* 1993; Eggleston 1995).

Nonetheless, considerable spatial variation in settlement and recruitment rates has been recorded (Robertson and Kaufman 1998 and references therein). For example, Sponaugle and Cowen (1996a) investigated three sites on the west shore of Barbados, and found that the central site had fewer settling fish than the other two sites. They attributed this to reduced onshore tidal transport. Caselle and Warner (1996) found spatial variation was greater than temporal variation over two summer recruitment seasons in St. Croix, and attributed this to physical oceanographic processes.

Differences in settlement of commercially important reef fishes to Discovery Bay and sites in BVI might also be caused by temporal variation in larval supply. The largest catches of settlement stage fish in Discovery Bay were in early March, after a break in sampling. It could be argued that our sampling might have missed an early settlement period in Jamaica. However, Forrester (pers. comm.) also set light traps for two weeks around new moon periods in late January 1997 and 1998 at Discovery Bay. His catches were dominated by atherinids with very few reef fishes. Additionally, one fish, the blenny Ophiblennius atlanticus, which made up 45% of the catch, dominated our March peak. Furthermore, spring and summer settlement and recruitment peaks have been recorded from other Caribbean locations including the Bahamas (Thorrold *et al.* 1994), Barbados (Tupper and Hunte 1994, Sponaugle and Cowen 1996 a and b) as well as by other studies in the Virgin Islands (Beets 1997; Miller *et al.* in press).

Interannual differences in settlement can be several fold, or orders of magnitude (Doherty and Williams 1988, Robertson and Kaufman 1998). Our own ongoing data collection has found significant interannual variation in settlement to reefs in BVI, with settlement to all three sites substantially reduced in 2000 (Watson *et al.* in prep). Perhaps the sampling period of this study was simply 'good' for BVI, 'bad' for Discovery Bay or even a combination of extremes. However, settlement in Discovery Bay appears to be selectively reduced for exploited species, whereas the reduced settlement rates currently being monitored in BVI are consistent across all reef fish species. Furthermore, data from wire mesh traps provide multi-year / year-round monitoring data recommended to avoid such problems (Robertson and Kaufman 1998). Consistently low abundances of older juvenile commercial species were taken between 1996 and 2000 at Discovery Bay compared with two sites (Maya Cove and Red Rocks) in BVI between 1997 and 1999 and one site (Hans Creek) between 1997 and 2000. The data suggest that the abundance of exploited species (especially snappers and grunts) at Discovery Bay has been low throughout this period.

An explanation for the differences may be the significant ecological and habitat changes that have occurred at Discovery Bay since Hurricane Gilbert in 1980, and the

Caribbean-wide die-off of the urchin, *Diadema antillarum,* in 1984. Coral cover has decreased, and algal and seagrass cover has increased in recent years (Liddell and Ohlhorst 1992, Hughes 1994). However, it is unlikely that this alone would have caused the decline in abundance of fish particularly in numbers of settling late stage pelagic juveniles on reefs at Discovery Bay. Certainly, nursery habitat including the shallow inshore seagrasses which are important for juvenile reef fishes in the Caribbean (Weinstein and Heck 1979, Ogden and Gladfelter 1983, Eggleston 1995, Van der Velde *et al.* 1992), are not lacking. Furthermore, although small-scale settlement patterns can be influenced by microhabitat choice, such habitat effects do not usually influence large-scale variation in recruitment (Tolimieri 1995, Caselle and Warner 1996). The north shore of Jamaica is considered to have one of the most heavily exploited nearshore fisheries in the Caribbean (Sary *et al.* 1997) and this exploitation itself has probably contributed to the ecological changes described above (Hughes 1994). The low numbers of commercially important species are most likely to be the direct result of recruitment overfishing, either in "upstream" source areas, locally retained populations, or both.

We know of no other study that has demonstrated such a selective settlement failure for exploited coral reef fishes. The data suggest that, as a result of settlement limitation, stocks of commercially exploited species such as snappers and grunts will increase very slowly in the small reserve at Discovery Bay. MPAs are increasingly recommended as simple management tools for multi-species fisheries (e.g. Roberts and Polunin 1991, Bohnsack 1996). In addition, Roberts (1998) suggests that creating a no-take MPA will automatically create a source for dispersal, whether or not the site provides propagules when designated. This is because biomass recovery will eventually cause the site to become a source of postlarvae (however, the dispersal and hence survival of such larvae may vary from place to place). Recent surveys do show increases in biomass of some species within the reserve at Discovery Bay, notably *S. viride*, *S. chrysopterum* and *S. aurofrenatum* (Munro 1999), suggesting that it may be partially successful as an improved source of larval fish, and hence an aid to population recovery (sensu Pulliam 1988). But simply stopping fishing will not provide a remedy for other over-exploited species if no larvae are arriving to settle. Stock enhancement with late stage larvae collected from light traps at other sites (first suggested by Doherty 1994) might provide a means of accelerating biomass recovery of over-exploited stocks within the reserve provided fishing bans are maintained. Certainly, the long term success of reserves depends on compliance with such bans, and this in turn often depends on perceived benefits to local fishers. It is important to be realistic about what those benefits are likely to be, and their expected time scale, in order to avoid subsequent loss of local support.

In contrast to Jamaica, there is little pressure to implement MPAs as a fisheries improvement tool in BVI. Hans Creek has been one of a series of MPAs proposed since 1984. During our study, the area received substantially more settlement stage fishes than nearby reefs, and may even act as a sink in this sense. These high inputs may not necessarily be consistent over a longer time scale however. For example, the average catch of juvenile fish in half inch mesh traps was not consistently higher at Hans Creek than at the other two sites across the range of exploited species. Thus, there may be temporal variation in recruitment levels among sites. Nonetheless, based on available data, protecting the area from fishing should create the defacto source that Roberts (1998) envisages. Perhaps most importantly, the site has abundant shallow mangrove, seagrass and coral habitats in close proximity to each other, and is at present free from most land-based pollution problems. Thus an MPA could be expected to act as a nursery ground for many species and subsequently supply adjacent reefs and fisheries through outmigration as well as larval dispersal.

Our study sites in BVI showed evidence of substantial variation in settlement and recruitment over a few kilometers. Thus our findings for Discovery Bay should not be extrapolated to other locations in Jamaica or even to neighbouring areas without further study. Similarly, Edmunds and Bruno (1996) investigated kilometer-wide variation in coral communities within ~9 km of Discovery Bay, and at several sites on St. John, United States Virgin Islands. They recorded substantial and significant variation in coral cover and abundance of juvenile corals, and cautioned against 'scaling-up' observations to cover spatial scales not sampled. Nonetheless, in Jamaica as a whole, the creation of fishery reserves in up current areas such as the Morant Cays and around the easternmost part of Jamaica, at Morant Point, would probably have the greatest beneficial effects on settlement and recruitment rates for over exploited fish stocks. Importantly, the degree of local retention expected for coral reef fish is hotly debated (Cowen *et al.* 2000). If retention is considerably more localised than previously thought, establishing fisheries reserves in areas not yet severely impacted (such as Hans Creek, BVI) should mostly benefit nearby rather than distant populations. Local recruitment failure, such as reported here for Discovery Bay, would also be more common.

Acknowledgments

The Inter-American Development Bank and the U.K. Department for International Development provided funding for this project. Many staff and interns at ICLARM's office in the British Virgin Islands, at the BVI Conservation and Fisheries Department and at the Discovery Bay Marine Laboratory assisted with data collection. Particular thanks to J. Levy, V. Murray, A. Roberts, R. Power, M. Leonard and F. Gell.

This is ICLARM contribution number 1600.

Literature Cited

Beets, J. 1997. Effects of a predatory fish on the recruitment and abundance of Caribbean coral reef fishes. Mar. Ecol. Prog. Ser. 148: 11-21.

Bohnsack, J. A. 1996. Maintenance and recovery of reef fishery productivity. *In* Reef Fisheries, vol. 20. Fish and Fisheries Series (ed. N. V. C. Polunin and C. M. Roberts), pp. 283-313. Chapman and Hall, London.

Booth, D. J. and Beretta, G. A. 1994. Seasonal recruitment, habitat associations and survival of pomacentrid reef fish in the US Virgin Islands. Coral Reefs 13: 81-89.

Caselle, J. E. and Warner, R. R. 1996. Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. Ecology 77: 2488-2504.

Connell, J.H. 1985. The consequences of variation in initial settlement vs. post settlement mortality in rocky intertidal communities. J. Exp. Mar. Biol. Ecol. 93(1-2): 11-45

Cowen, R. K., Lwiza, K. M. M., Sponaugle, S., Limouzy-Paris, C. B. and Olson, D. B. 2000. Connectivity of marine populations: open or closed. Science 287: 857-859.

Doherty, P.J. 1994. A potential role for light-traps in enhancement of coral reef fisheries. ICLARM Conf. Proc. no. 44: 92-93. Manila, Philippines.

Doherty, P. J. and Williams, D. M. 1988. The replenishment of coral reef fish populations. Oceanogr. Mar. Biol. Annu. Rev. 26: 487-551.

Edmunds, P. J. and Bruno, J. F. 1996. The importance of sampling scale in ecology: kilometer wide variation in coral reef communities. Mar. Ecol. Prog. Ser. 143: 165-171.

Eggleston, D. B. 1995. Recruitment in Nassau grouper *Epinephelus striatus*: post settlement abundance, microhabitat features, and ontogenetic habitat shifts. Mar. Ecol. Prog. Ser. 124: 9-22.

Forrester, G. 1995. Strong density-dependant survival and recruitment regulate the abundance of a coral reef fish. Oecologia 103: 275-282.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265: 1547-1550.

Hunt von Herbing, L. and Hunte, W. 1991. Spawning and recruitment of the bluehead wrasse *Thalassoma bifasciatum* in Barbados, West Indies. Mar. Ecol. Prog. Ser. 72: 49-58.

Keough, M.J. and Downes, B.J. 1982. Recruitment of marine invertebrates – the rôle of active larval choices and early mortality. Oecologia 54(3): 348-352

Liddell, W. D. and Ohlhorst, S. L. 1992. Ten years of disturbance and change on a Jamaican fringing reef. Proc. 7th Int. Coral Reef Symp. Guam 1: 144-150.

Luckhurst, B. E. & Luckhurst, K. 1977. Recruitment patterns of coral reef fishes on the fringing reef of Curaçao, Netherlands Antilles. Can. J. Zool. 55: 681-689.

Mackey, G. (1998). Juvenile nursery grounds in the British Virgin Islands, Eastern Caribbean: Two sampling strategies reveal complex interactions between mangroves, seagrass beds and backreef habitats of juvenile coral reef fishes. M.Res. In Ecology and Environmental Management Dissertation thesis, University of York.

McFarland, W. N., Brothers, E. B., Ogden, J. C., Shulman, M. J., Bermingham, E. L. and Kotchian-Prentiss, N. M. 1985. Recruitment patterns in young French grunts, *Haemulon flavolineatum* (Family Haemulidae) at St. Croix, U.S.V.I. Fish. Bull.U.S. 83: 413-426.

McGehee, M. A. 1995. Juvenile settlement, survivorship and in situ growth rates of four species of Caribbean damselfish in the genus *Stegastes*. Env. Biol. Fish. 44: 393-401.

Miller, J., Beets, J. & Rogers, C. (in press). Monitoring fish recruitment on a fringing reef in Virgin Islands National Park, St. John, U.S. Virgin Islands. Proc. 51st Gulf and Caribbean Fisheries Institute .

Munro, J. L. 1999. Marine protected areas and the management of coral reef fisheries, pp. 40. Technical Report. ICLARM Caribbean / Eastern Pacific Office, British Virgin Islands.

Ogden, J. C. & Gladfelter, E. H. 1983. Coral reefs, seagrass beds and mangroves: their interaction in the coastal zones of the Caribbean. pp. 133. UNESCO.

Pomeroy, R. S. 1999. Economic Analysis of the British Virgin Islands Commercial Fishing Industry. Research Report. ICLARM Caribbean / Eastern Pacific Office. Tortola, British Virgin Islands pp. 37.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. Am. Natur. 132: 652-661.

Roberts, C. M. 1997. Connectivity and management of Caribbean coral reefs. Science 278: 1454-1457.

Roberts, C. M. 1998. Sources, sinks and the design of marine reserve networks. Fisheries 23(7): 16-19.

Roberts, C. M. and Polunin, N. V. C. 1991. Are marine reserves effective in management of reef fisheries? Rev. Fish Biol. Fish. 1: 65-91.

Robertson, D. R. 1992. Patterns of lunar settlement and early recruitment in Caribbean reef fishes at Panamá. Mar. Biol. 114: 527-537.

Robertson, D. R. and Kaufmann, K. W. 1998. Assessing early recruitment dynamics and its demographic consequences among tropical reef fishes: Accomodating variation in recruitment seasonality and longevity. Aus. J. Ecol. 23: 226-233.

Sary, Z., Oxenford, H. A. and Woodley, J. D. 1997. Effects of an increase in trap mesh size on an overexploited coral reef fishery at Discovery Bay, Jamaica. Mar. Ecol. Prog. Ser. 154: 107-120.

Shenker, J. M., Maddox, E. D., Wishinski, E., Pearl, A., Thorrold, S. R. and Smith, N. 1993. Onshore transport of settlement stage Nassau grouper *Epinephelus striatus* and other fishes in Exuma Sound, Bahamas. Mar. Ecol. Prog. Ser. 98: 31-43.

Shulman, M. J. and Ogden, J. C. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. Mar. Ecol. Prog. Ser. 39: 233-242.

Sponaugle, S. and Cowen, R. K. 1996a. Larval supply and patterns of recruitment for two Caribbean fishes, *Stegastes partitus* and *Acanthurus bahianus*. Mar. Freshwat. Res. 47: 433-447.

Sponaugle, S. and Cowen, R. K. 1996b. Nearshore patterns of coral reef fish larval supply to Barbados, West Indies. Mar. Ecol. Prog. Ser. 133: 13-28.

Sponaugle, S. and Cowen, R. K. 1997. Early life history traits and recruitment patterns of Caribbean wrasses (Labridae). Ecol. Monogr. 67: 177-202.

Stobutzki, I. C. and Bellwood, D. R. 1997. Sustained swimming abilities of the late pelagic stages of coral reef fishes. Mar. Ecol. Prog. Ser. 149: 35-41.

Thayer, G. W., Colby, R. R. and Hettler, W. F. 1987. Utilization of the red mangrove prop root habitat by fishes in south Florida. Mar. Ecol. Prog. Ser. 35: 25-38.

Thorrold, S. R., Shenker, J. M., Mojica Jr., R., Maddox, E. D. and Wishinski, E. 1994. Temporal patterns in the larval supply of summer recruiting reef fishes to Lee Stocking Island, Bahamas. Mar. Ecol. Prog. Ser. 112: 75-86.

Tolimieri, N. 1995. Effects of microhabitat characteristics on the settlement and recruitment of a coral reef fish at two spatial scales. Oecologia 102: 52-63.

Tupper, M. and Hunte, W. 1994. Recruitment dynamics of coral reef fishes in Barbados. Mar. Ecol. Prog. Ser. 108: 225-235.

Van der Veld, G., Gorissen, M. W., den Hartog, C., van't Hof, T. and Meijer, G. J. 1992. Importance of the Lac-lagoon (Bonaire, Netherlands Antilles) for a selected number of fish species. Hydrobiologia 247: 139-140.

Watson, M., Nemeth, R. & Munro, J. L. in prep. Spatial, seasonal and interannual variation in settlement of coral reef fishes to neighbouring Caribbean islands. .

Watson, M., Power, R., Simpson, S. & Munro, J. L. in press. Low cost light traps - designs for coral reef fisheries research and sustainable ornamental fisheries. Naga .

Weinstein, M. P. & Heck Jr., K. L. 1979. Ichthyofauna of seagrass meadows along the Caribbean coast of Panama and the Gulf of Mexico: composition, structure and community ecology. Marine Biology 50: 97-107.

Wellington, G. M. 1992. Habitat selection and juvenile persistence control the distribution of two closely related Caribbean damselfishes. Oecologia 90: 500-508.

Use of Light-attracted Zooplankton for Rearing Post-settlement Coral Reef Fish

MAGGIE WATSON, ROBERT POWER, and JOHN L. MUNRO
ICLARM, Caribbean Marine Protected Areas Project
Suite 158, Inland Messenger Service
Road Town, Tortola, British Virgin Islands

KEY WORDS: Juvenile mortality, light attracted plankton, recruitment

ABSTRACT

Settlement stage *Lutjanus synagris* and *Ocyurus chrysurus* were caught in light traps set off fore reefs in the British Virgin Islands and raised in floating mesh cages tethered in water 1 - 2 m deep. Lights were designed to attract plankton into the cages and provide live natural food for the fish. Plankton taxonomic composition around lights was compared with samples from plankton tows in adjacent water, as well as with gut contents of cage reared and wild fish. Fish mortality and growth were followed over the first few weeks of life and compared with results from a field trial assessing natural mortality and growth. Cage rearing reduces the exceptionally high early post-settlement mortality typical of *Ocyurus chrysurus* from approximately 80% to 40% within the first month. We suggest two uses for this technique, a) to help speed recovery of over-exploited stocks within no-take marine reserves b) to rear settlement stage ornamental species until they are large enough to survive on artificial food. Light traps and cage culture in combination could replace destructive fishing practices on reefs exploited for the aquarium trade.

INTRODUCTION

Light attracted plankton has previously been investigated for culture of freshwater pike-perch (*Stizostedion lucioperca*) fry (Schlumpberger and Ziebarth 1981, Jaeger and Nellen 1983, Jaeger et al. 1984, all cited in Hilge and Steffens 1996). This paper reports preliminary investigations into the feasibility of collecting settlement stage reef fish and rearing them past their initial mortality hurdle by using light attracted zooplankton as food. High post settlement mortality is typical of many coral reef fishes. Shulman and Ogden (1987) found >90% natural mortality in French grunts *Haemulon flavolineatum* during the month after settlement, and this rate may be characteristic for species that settle in pulses, and/or form schooling aggregations of juveniles (Roberts 1996, and references therein).

We discusses potential uses for this rearing technology both to enhance recovery of recruitment overfished reef fish stocks within protected areas and to provide a non-destructive alternative income for fishers raising ornamental species for the aquarium trade.

MATERIALS AND METHODS

Settlement stage reef fishes were caught using light traps modified from a design by Stobutzki and Bellwood (1997). The traps consisted of 40 x 40 x 40 cm aluminium 'angle-iron' frames supporting transparent plexiglas panels. On each side of the trap a clear funnel ran the height or width of the cube, (two vertical and two horizontal) each with an opening of 12mm. The light was a 'stand alone' system inserted into the top of the main trap. It consisted of an O'ring sealed plastic box, housing two six volt rechargeable batteries and connected to a clear plastic tube containing an 8 watt fluorescent bulb. A light sensitive switch mounted on the top of each light box turned the trap on at dusk and off at dawn. An advantage of this modular design is that changing batteries and mending equipment did not require the entire light trap to be taken ashore. Buckets set beneath the main trap retained the fish as traps were hauled. Traps were set at a depth of 2 m, 100 - 200 m offshore of three fringing reefs on Tortola, British Virgin Islands around new moon periods in 1998 and 1999. Commercially important yellowtail and lane snappers (*Ocyurus chrysurus*, *Lutjanus synagris*) caught in light traps were reared in floating cages (125 L, mesh size 3 mm) tethered in 1 - 2 m of water for approximately one month to investigate the feasibility of rearing reef fish on light attracted plankton. At night, each cage was lit with either an 8 watt light module from the light traps or a 9 watt mains powered light sealed with silicone into plastic drinks bottles and appropriately fused. All cages were regularly scrubbed of algae. The order and variety of experiments described below were unavoidably constrained by unpredictable availability of fishes in monthly settlement pulses over the recruitment season.

Early Mortality in Caged and Wild Fish

Survival of *Lutjanus synagris* reared under two different stress regimes was examined to isolate the effect of handling stress on survival. For two cages (both with 45 fish initially) handling stress at first capture from the light trap was minimised by not touching the fish and by keeping them in extra large aerated buckets until placing them in the cage as the earliest opportunity. One group was counted and measured every week, while the other was sampled only fortnightly. *L synagris* reared in two other cages (with initial numbers of 35 and 40) received no special treatment at capture and were both sampled weekly. Survival of *O. chrysurus* in two cages (initial n = 35 and 63) was recorded weekly to investigate density dependence in mortality.

As part of a parallel study, early juvenile natural mortality of *O. chrysurus* was estimated from daily censuses of an area of seagrass 25 x 50 x 1-1.5 m in depth. The area was divided into 5 x 5 m squares. One observer swum concentrically around each individual section until the entire area of each square was covered. Each census took a total of 2 - 2.5 hours. Daily censuses were performed during the 11 days leading up to peak settlement in September 1999 and for six days following. Over the next nine days a different observer conducted censuses. Resumption of observations by the original observer identified bias in numbers of fish observed (but not the proportion of size classes – see section on growth below) and nine days data were dropped from the analysis of mortality. Observations then continued every other day for a further 11 days until the pulse of settlement became indistinguishable from other juveniles. Temporal patterns in abundance were assumed proportional to the processes of settlement and natural mortality (as in McGehee 1995). We also assume disappearance of fish represented mortality rather than movement, and that any emigration from the census area would be balanced by immigration. We base this assumption on the enormous size of the census area relative to observed home ranges of settlement stage *O. chrysurus* (Watson and Gell in prep and see discussion), and on results from a preliminary mark recapture experiment which found elastomer tagged *O. chrysurus* moved only a few metres after settlement (Watson and Gell in prep). The day when the number of settlement size fish peaked (91 compared to only four 10 days earlier) was assumed to represent the settlement event, and numbers of fish remaining over time were expressed as a percentage of that number for comparison with mortality in cage reared fish.

Estimates of Early Juvenile Growth for *L. synagris* and *O. chrysurus*, and Comparison of *O. chrysurus* Growth in Cage Reared and a Natural Population

Early juvenile growth was estimated from weekly measurements of two groups of *O. chrysurus* (n = 35 and 63) and three groups of *L. synagris* as in the mortality section above (n = 45 'low stress', n = 35 and n = 40). Data from the 'low stress' trial measured fortnightly were excluded as there were only two data points. Total lengths of wild fish from the September settlement peak were estimated (to the nearest 0.5 cm) during daily censuses of the seagrass grid until the cohort could no longer be clearly distinguished (about 25 days). Modal length from field observations was plotted against modal length of *O. chrysurus* (grouped to the nearest 0.5 cm) reared in two cages in order to compare growth of captured and wild fish.

Food Availability and Feeding Preferences

Zooplankton was sampled from water adjacent to floating cages using a mini-plankton net (30 cm diameter aperture) towed at approximately one knot for five minutes. Zooplankton attracted into cages was sampled with two swipes of a dip-net in an empty cage every five minutes over a 25 minute period. Gut contents were analysed for seventeen cage-reared *O. chrysurus* (total length 20-40mm) caught at night. Gut contents were also analysed for ten wild *O. chrysurus* (22 - 50 mm total length) caught during the day. Percent composition by volume in the water samples and in fish guts (individuals within each sample pooled) were compared to examine selective feeding behaviour.

RESULTS

Early Mortality In Caged and Wild Fish

Survival of *L. synagris* was greater in 'low stress' higher density cages (n = 45) than in 'high stress' lower density cages (n = 35 and n = 40) (Figure 1.). Two cages where initial handling stress was minimized had approximately 80% survival after three weeks, compared to cages stocked at lower initial densities (23% and 12% less fish) where survival was around 50% within two weeks. After initial capture, weekly measuring did not appear to have a marked affect on survival. Thus a large part of early mortality of *L. synagris* (and probably *O. chrysurus*) in cages appears to be due to initial handling stress.

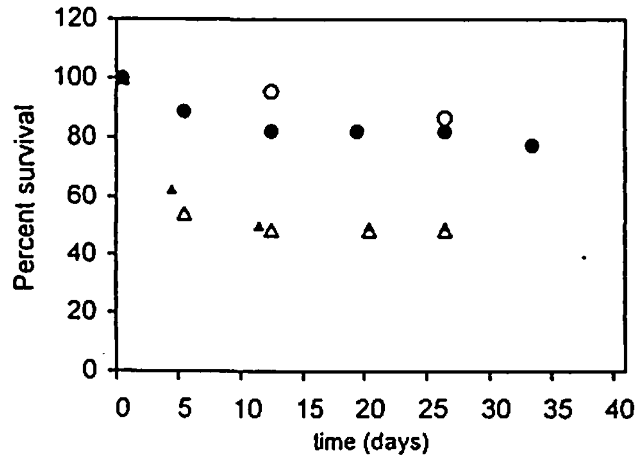


Figure 1. Percent survival of *Lutjanus synagris* against time in cages for four rearing regmines; triangle, initial n = 40; no special treatment; open triangle initial n = 35, no special treatment; circle initial n = 45, 'low stress' regime, sampled weekly; open initial n = 45, 'low stress' regime sampled fortnightly

Survival of *O. chrysurus* at initial densities of n=35 and n=63 over approximately one month were very similar (Figure 2) suggesting that mortality is not density dependent up to at least 0.5 fish per litre. Survival in these two cages was approximately 30% higher than estimates of survival from wild fish after one month (Figure 2). Daily censuses estimated mortality of *O. chrysurus* to be 80% within one month in the wild. Cage reared fish had a mortality of approximately 30-40% over the same time period. Mortality in all three groups fitted exponential curves (see equations on the graphs), i.e. 'type three' mortality. The curve fitted through the wild population was not forced through an intercept of 100% since the actual number of settlers is not known because settlement took place over a number of days during which mortality was already operating.

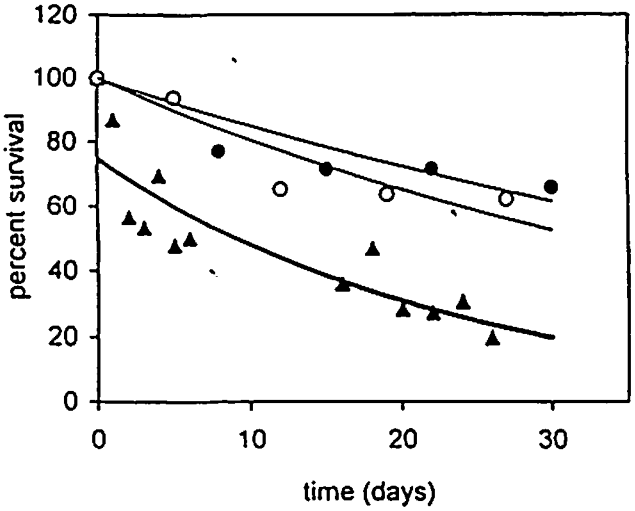


Figure 2. Percent survival against time for *Ocyurus chrysurus* < 1 month since settlement and reared in floating cages (closed circles initial n = 35, $y = 100e^{-0.0162x}$, $r^2 = 0.71$, open circles initial n = 63, $y = 100e^{-0.0125x}$, $r^2 = 0.80$) compared with percent survival in the wild estimated from daily field censuses of one monthly cohort (triangles, $y = 74.831e^{-0.0445x}$, $r^2 = 0.83$)

Comparison of Growth in Natural and Cage Reared Fish.

Early juvenile growth in cages was linear for both *O. chrysurus* and *L. synagris* and shows no signs of density dependence between 0.28 and 0.5 fish per litre (Figure 3 and Figure 4.). Modal length of *O. chrysurus* in cages was not significantly difference to modal length of the September 1999 cohort censused in the wild over the first month (Figure 5).

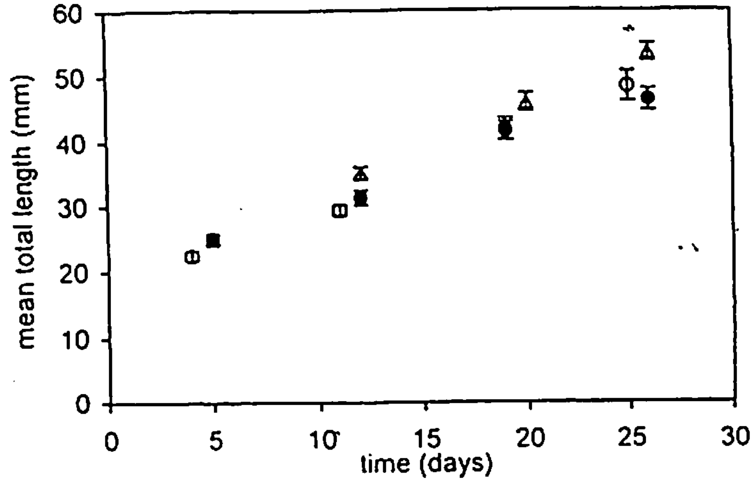


Figure 3. Mean total length (mm) of *Lutjanus synagris* against time in cages for three rearing regimes; closed circle initial, n = 45, 'low stress' y = 1.05*X + 19.7, r^2 = 0.98; triangle initial, n = 35, 'high stress' y = 1.35*X + 18.5, r^2 = 0.99; open circle initial n = 40, 'high stress' y = 1.275*X + 16.72, r^2 = 0.99. Error bars represent 95% confidence levels.

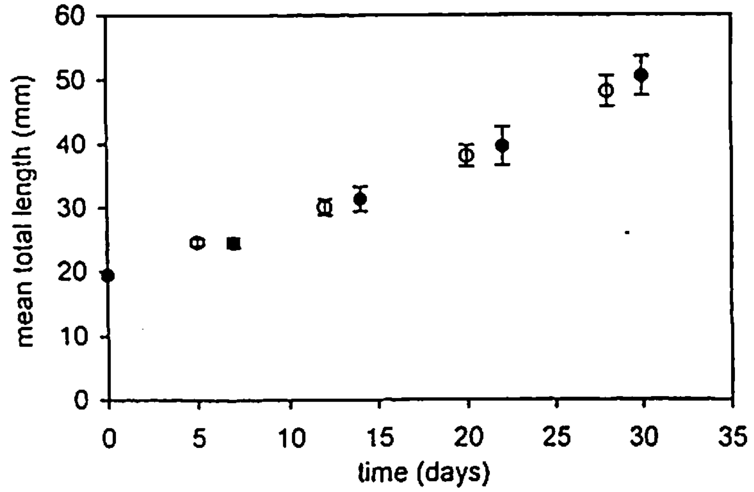


Figure 4. Mean total length (mm) of *Ocyurus chrysurus* against days in cage for two groups; closed circles initial n = 35, y = 1.0383*X = 17.99, r^2 = 0.99; open circles initial n = 63, y = 1.0081*X + 19.01, r^2 = 0.99. Error bars represent 95% confidence levels

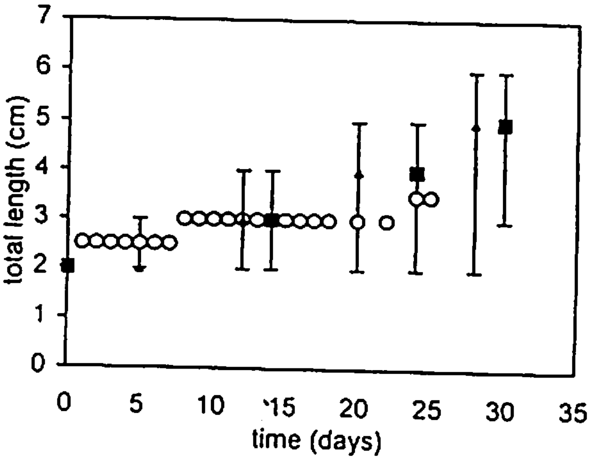


Figure 5. Modal total lengths of *Ocyurus chrysurus*, (less than one month since settlement) estimated to the nearest 0.5 cm from field observations (open circles) and two cage culture experiments (square and triangle) against time in days from peak settlement and from date of capture in light traps, respectively. Error bars for caged fish indicate size range.

Food availability and feeding preferences

Zooplankton samples taken from tows in water adjacent to floating cages and from dip-net sweeps inside lighted cages show zooplankton attracted to the lights is similar to that in open water (Figure 6). Both wild and cage reared *O. chrysurus* fed selectively, and included fish (mostly juvenile 'bait fish' - Atherinidae and Clupeidae) in their diet (34% and 13% respectively). These fish, which are attracted to lights, avoided dip-nets and the plankton tow. Malacostraca make up very similar volumes in the diet of both wild and caged fish (43% and 40% respectively). Caged fish also ate annelid worms (23%) attracted up off the bottom by the light. Combined with growth estimates, the data suggest zooplankton provides an adequate food source comparable with a natural diet for early juvenile snappers.

DISCUSSION

Our results demonstrate that the 'low tech', low maintenance technique of rearing reef fish using light attracted plankton supports growth at least equal to that in the wild, and substantially reduces mortality over the first month. We suggest two potential uses of this technique. In coral reef areas where recruitment over-fishing has diminished the supply of new recruits, recovery of fish populations may be extremely slow even if fishing ceases. For example, identical studies comparing reef fish settlement to the heavily exploited reefs on the north Jamaican shelf, and to the moderately exploited reefs in the British Virgin Islands found orders of magnitude differences in settlement rates (Munro and Watson 1998; Munro and Watson 1999), implying that stock recovery will take many years. If reefs are self-seeding recovery may not occur without intervention. Light traps may be a means of catching juvenile reef fish for stock enhancement (Doherty 1994). Using the techniques described here, settlement stage fish could be collected from a relatively large area, reared for several weeks, and concentrated within a marine protected area.

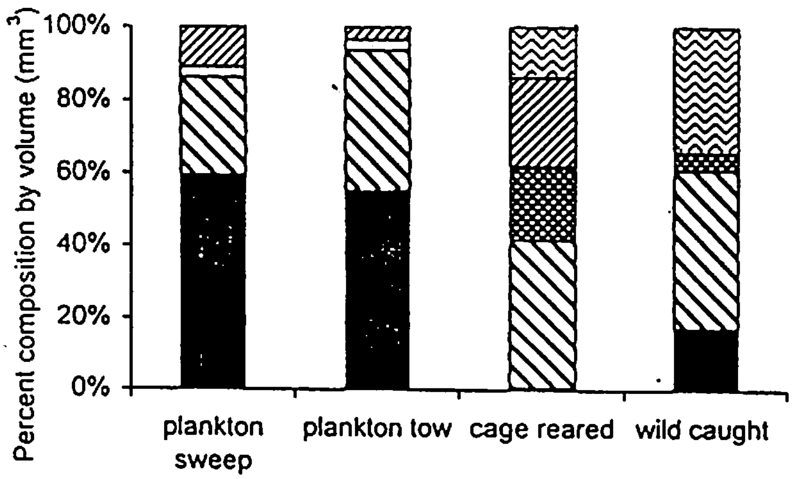


Figure 6. Percent composition by volume for plankton sweeps inside floating cages, a plankton tow in water adjacent to floating cages, and cages reared (n = 17, total length 20 - 40 mm) and wild (n = 10, total length 25 - 53 mm) *Ocyurus chrysurus*. Key: black = Copepoda, grey = Ostracoda, wide hatching = Malacostraca, thin hatchin = Annelida, wavyline = fish, dotted = Crustacean debris

This technology is intended for heavily exploited populations where even a slight increase in juvenile survival from small releases would be valuable. Stock enhancement has been heavily critizised as uneconomic (Hilborn 1998), inappropriate (Scarnecchia 1988, Meffe,1992), difficult to evaluate (Leber et al. 1996, Hilborn 1998), and potentially harmful to wild populations through introduction of disease or through genetic selection for inappropriate characteristics (Schramm and Piper 1995). However, most enhancement efforts have been large scale, expensive 'high tech.' programs raising up to several million fish from eggs to fingerlings. The present approach is low cost, low maintenance, and rears only wild caught stocks on site. Fish are fed with natural food before release to an unfished native habitat. The methods might be suitable for small scale marine protected areas projects in developing countries were coral reef fisheries resources are under the greatest threat.

In this study, cage rearing had the potential to decrease mortality in the first month after settlement from approximately 80% to around 40%. This estimate is probably conservative due to inaccuracies in the censuses of wild fish. It was not possible to measure the true natural settlement rates both because visual observations may miss many fish and because numbers of settling fish increased rapidly over several days and mortality before the settlement peaked was ignored in our analysis. For many reef fishes, mortality is thought to be highest soon after settlement (Victor 1986, Doherty and Sale 1986, Sale and Ferrell 1988). Furthermore, we compared natural mortality with *O. chrysurus* reared in cages before development of faster, low stress handling techniques at capture. Results from *L. synagris* suggest cage mortality can be reduced to around 20% with careful handling.

Perhaps one of the most important criticisms of stock enhancement is that artificially reared fish lack the behaviour necessary to ensure survival in the wild. A parallel study of 'early juvenile' snapper behaviour in seagrasses (Watson and Gell in prep) found that recently settled *O. chrysurus* and *L. synagris* (approximately 2 - 3 cm) remain almost stationary near the bottom and pick plankton from the water column. They rarely move more than 20cm from their initial position and tolerate conspecifics of the same size. However, from approximately 3 - 3.5 cm their range becomes considerably bigger (several square metres), they switch to feeding on benthic invertebrates and act aggressively towards similarly sized conspecifics. Thus cage rearing is probably most suited to rearing fish to approximately 3 - 3.5 cm (3 - 4 weeks).

The present study, which was designed to test the feasibility of the technology, has not addressed the question of whether cage reared fish subsequently released have a higher overall survival than wild fish from the same cohort. High mortality in the first few days after settlement (or release) may be due to unfamiliarity with the habitat. However, rearing in semi-natural environments (Masuda and Tsukamoto 1998 and references therein) and conditioning to the habitat (Olla et al. 1994) have been shown to reduce post release mortality. An evaluation phase is planned for 2000. Despite his many criticisms, Hilborn (1998) concedes that stock enhancement programs are most likely to succeed where wild stocks are essentially gone. This is the case for commercially fished stocks on many overexploited reefs. Even where high mortality makes cost per surviving individuals substantial, the value should be considered in terms of survivor reproductive potential rather than the contribution to stock numbers (Stoner and Glazer 1998).

The second application we suggest for rearing fish on light attracted plankton is to supply ornamental reef fish to the aquarium trade. Widespread use of destructive collecting techniques,,such as sodium cyanide, often leads to high mortality in captured fish, does substantial harm to the reef ecosystem, and has made development of sustainable collection techniques an international concern. However, growing consumer demand for 'eco-labled' fish suggests sustainable aquarium fisheries could provide a valuable alternative income for fishers, particularly where overfishing is currently degrading coral reef resources. We suggest fish could be reared on light attracted plankton from late pelagic/settlement size until they are big enough to thrive on artificial food. Catching fish before they reach the 'wall of mouths (Kaufman et al. 1992) on the reef provides an opportunity to avoid high post-settlment mortality. Where natural populations are already overexploited, a proportion of the fish caught for the aquarium trade could also be grown past their initial 'mortality hurdle' and used to enhance natural populations

LITERATURE CITED

Doherty, P.J. 1994. A potential role for light-traps in enhancement of coral reef fisheries ICLARM Conf. Proc., Manila. 44:92-93.

Doherty, P.J. and P.J. Sale. 1986. Predation on juvenile coral reef fishes: an exclusion experiment. *Coral Reefs* 4:225-234.

Hilborn, R. 1998. The economic performance of marine stock enhancement projects. *Bull. Mar. Sci.* 62: 661-674.

Hilge, V. and W. Steffens. 1996. Aquaculture of fry and fingerling of pike-perch (Stizostedion lucioperca L.) - a short review. *J. Appl. Ichthyol.* 12:167-170.

Jaeger, T. and W. Nellen. 1983. Die aufzucht von fischlarven in beleuchteten netzgehegen. *Fischwirt* 33:38.

Jaeger, T., W. Nellen, and H. Soll. 1984. Beleuchtete netzgehegeanlagen zur aufzucht von fishbrut bis zur setzlingsgröße. Eine bauanleitung und aufzuchtbeschreibung. *Ber. Inst. Meereskd.* Christian-Albrechts-Univ. Kiel 126:72.

Kaufman, L., J. Ebersole, J. Beets, and C.C. Mcivor. 1992. A key phase in the recruitment dynamics of coral reef fishes: post settlement transition. *Environmental Biology of Fishes* 34:109-118.

Leber, K.M., S.M. Arce, D.A. Sterritt, and N.P. Brennan. 1996. Marine stock-enhancement potential in nursery habitats of striped mullet, *Mugil cephalus* in Hawaii. *Fishery Bulletin* 94:452-471.

Masuda, R. and K. Tsukamoto. 1998. Stock enhancement in Japan: review and perspective. *Bull. Mar. Sci.* 62:337-358.

McGehee, M.A. 1995. Juvenile settlement, survivorship and in situ growth rates of four species of Caribbean damselfish in the genus *Stegastes*. *Environmental Biology of Fishes* 44:393-401.

Meffe, G.K. 1992. Techno-arrogance and halfway technologies: salmon hatcheries on the Pacific coast of North America. *Conservation Biology* 6:350-354.

Munro, J.L. and M. Watson, 1998. Comparative settlement and recruitment rates of coral reef fishes in moderately-exploited and over-exploited Caribbean coral reef ecosystems. International Society for Reef Studies. European Meeting. Perpignan, France September 1998. Unpubl. MS.

Munro, J.L. and M. Watson. 1999. *The rôle of marine protected areas in fisheries management and biodiversity conservation in coral reef ecosystems*, pp. 47. ICLARM Caribbean Marine Protected Areas Project. Phase 1. Technical report. ICLARM, Road Town, British Virgin Islands.

Olla, B.L., M.W. Davis, and C.LH. Ryer. 1994. Behavioural deficits in hatchery-reared fish: potential effects on survival following release. *Aquacult. Fish. Manage.* 25:19-34.

Roberts, C.M. 1996. Settlement and beyond: population regulation and community structure of reef fishes. Pages 85-112 in: N.V.C. Polunin and C.M. Roberts (eds.) *Reef Fisheries*. Chapman and Hall, London.

Sale, P.F. and D.J. Ferrell. 1988. Early survivorship of juvenile coral reef fishes. *Coral Reefs* 7:117-124

Scarnecchia, D.L. 1988. Salmon management and the search for values. *Canadian Journal of Fisheries and Aquatic Science* 45:2042-2050.

Schlumpberger, W. and G. Ziebarth. 1981. Produktion von vorgestreckten zandern in beleuchteten gazekäfigen. *Z. Binnefisch. DRR* 28:143-144.

Schramm, H.L.J. and R.G. Piper. 1995. Uses and effects of cultured fishes in aquatic ecosystems. In *American Fisheries Society Symposium 15*. 608 pp.

Shulman, M.J. and J.C. Ogden. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the

Caribbean reef fish *Haemulon flavolineatum*. *Mar. Ecol. Prog. Ser.* 39:233-242.

Stobutzki, I.C. and D.R. Bellwood. 1997. Sustained swimming abilities of the late pelagic stages of coral reef fishes. *Mar. Ecol. Prog. Ser.* 149:35-41.

Stoner, A.W. and R.A. Glazer. 1998. Variation in natural mortality: implications for Queen conch stock enhancement. *Bull. Mar. Sci.* 62: 427-442.

Victor, B.C. 1986. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecol. Mongogr.* 56:145-160.

Watson, M. and F. Gell. Settlement, early mortality and juvenile behaviour of the yellowtail snapper, *Ocyurus chrysurus*. In prep.

A Pump for Feeding Post-Settlement Coral Reef Fish with Light Attracted Zooplankton, with Possible Applications in the Fisheries for Marine Ornamentals[1]

R. M. Power and M. Watson[2]
International Center for Living Aquatic Resources Management (ICLARM),
Caribbean and Eastern Pacific Office,
158 Inland Messenger, Road Town, Tortola, British Virgin Islands.
email: rpower@surfbvi.com or fishpowerbvi42@hotmail.com

[1] ICLARM Contribution No. 1635

[2] Current address: Natural Environment Research Council, Polaris House, North Star Avenue, Swindon, UK. e-mail: Maggie@Xpertext.com

keywords: postlarvae, coral reef fish, cage-rearing, planktonic food.

Abstract

Late pelagic stage coral reef fishes experience very high predation when they settle to the substratum. Capture of some species of reef fish with light traps or crest nets before settlement may be a sustainable method for harvesting fish for the aquarium trade. Potentially, capture of fish at settlement could replace some existing commercial methods for collecting aquarium fish, which can be destructive to reefs and damaging to reef fish populations. However, because late pelagic stage reef fishes are fragile and prone to stress-related mortality, a short rearing program is likely to be useful to grow them to a size where they would be robust enough for sale to the aquarium trade. Another problem to be overcome is that very young fish often require live food, which can be technically difficult or expensive to supply. This paper describes a simple airlift pump with a light attraction component, which can be used to supply naturally occurring plankton for rearing very young fish in floating cages or tanks. Composition of plankton collected by this 'plankton pump' was compared with plankton in the surrounding habitat and composition of stomach contents of wild-caught and cage-reared fish. An example of blast fishing in Indonesia is used to discuss costs and feasibility of applying this technology to support an alternative reef fishery.

Introduction

In view of the current rate of global tropical reef degradation, there is growing interest in the development of sustainable, alternative, industries to divert pressure from artisanal reef fisheries (Doherty 1994; Pet-Soede and Erdmann 1998; Bell and Gervis 1999).

One possible area for development is the capture of settling late pelagic stage coral reef fishes for sale to the aquarium trade using light traps (Doherty 1994), crest nets (Dufour et al. 1996) or channel nets (Shenker et al. 1993). Collection by these methods has the potential to harvest large numbers of fish whilst avoiding the high mortality, recorded as > 90%, associated with the settlement period (Shulman and Ogden 1987; Roberts 1996 and references therein).

If reared to a marketable size, these fish could represent a substantial source of income for artisanal fishing communities (Baquero 1999 and references therein; Hair et al. in press). Before this can become a realistic economic alternative, however, there are certain factors that need consideration. For example, size or age of fishes at transportation can have a two-fold influence on the viability of this industry: postlarval stage fish are fragile and prone to stress-related mortality (Olla et al. 1998), whereas larger fish are more robust and less likely to die during transportation. Size of fish may also influence market price as larger individuals often fetch higher prices (Baquero 1999 and references therein). Another factor affecting the price of aquarium fish is the relative abundance of the species, so there is great incentive to keep very young specimens of rare and valuable species. In such cases, it may be technically difficult or expensive to supply the live food needed by these fish. However, light can be used to attract plankters for this purpose (Schlumpberger and Ziebarth 1981; Kuronuma and Fukusho 1984). Preliminary rearing trials with lutjanids in simple floating cages illustrate the potential for fast growth and high survival rates of fish reared in this way (Watson et al. in press, a).

The capture and culture of postlarval fish also has scope for aiding the recovery of over-exploited reef fisheries through the release of juveniles that have been reared to a size where natural mortality is far lower than during settlement (Masuda et al. 1998; Bell et al. 1999).

In this paper, we describe a relatively simple system for supplying live planktonic food for rearing late pelagic stage coral reef fishes.

Development and operation of the plankton pump system

Catches of postlarval fish from light traps, described by Watson et al (in press, b), were placed in 50cm cubic cages made from stiff 4 mm black plastic mesh. A large zipper opening across the top, extending halfway down two sides of the cage, provided access. Cages were moored to floating frames in 1.5 m of water close to backreef habitat. Initially, low energy household florescent lights (8W, 115V, 0.5A) were carefully waterproofed and placed inside each cage to attract planktonic food for the fish. Preventing the lights from leaking represented the most challenging technical problem for this rearing system and encouraged us to develop a "plankton pump" that only required one light for several cages.

The 'plankton pump' used a single waterproof light combined with an airlift pump and a plankton attraction chamber (Fig. 1). Air was supplied by a 2.24kva, 115V electric 'blower', which had the power to serve several plankton pumps, depending on the drag created by the length and diameter of the supply pipe (we used a pipe of 75 m and 4 cm internal diameter). Plankton attracted to the light was entrained in the flow of the airlift and pumped into four outflow pipes which emptied onto exposed mesh on the top of floating cages. The light was secured to the system well below the surface to dampen the movement of the light and electric cable due to wave action, thus reducing the chances of leakage and ensuring that floating cages were illuminated to facilitate feeding. The blower was operated for 30 minutes every hour throughout the night. Shorter time intervals might have been preferable, however, the choice was constrained by the availability of relatively inexpensive switches. The top mesh of the floating cage dried out during the day when the pump did not operate, which prevented colonization of that part of the mesh by fouling organisms. Plankton supplied by each outflow pipe could be easily monitored and measured by attaching a plankton net of appropriate mesh size and collection bottle to an outflow. The resulting catch of plankton was usually still alive the following day, making identification easy and calculation of volume for each item of plankton more accurate.

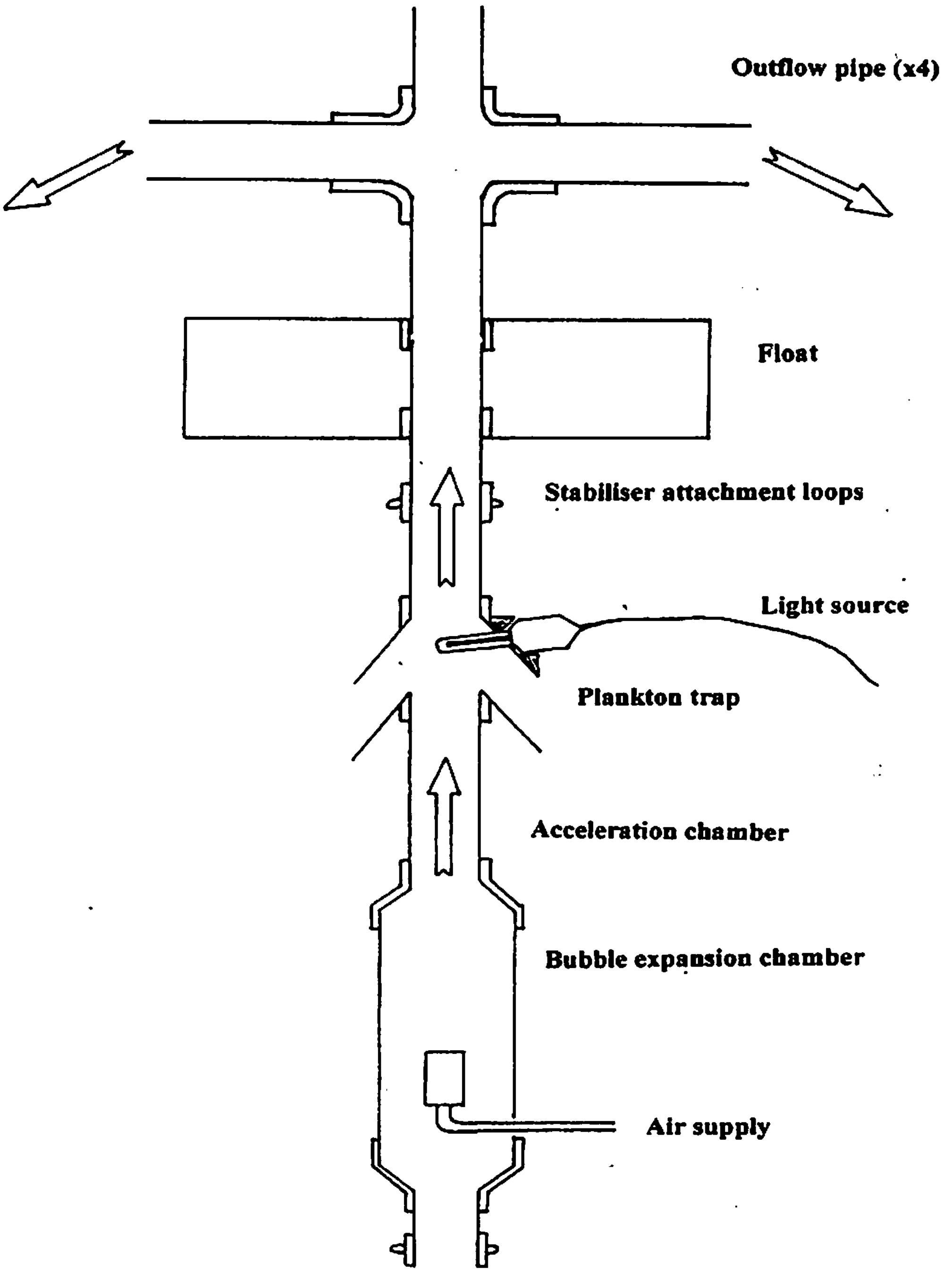


Figure 1. Schematic diagram of a device for attracting zooplankters to light and pumping them to floating cages stationed adjacent to the pump or to shore tanks. The plankton pump is made from standard PVC plumbing fittings and combines a simple airlift with a light attraction chamber (double inverted funnel) to entrain and pump plankton.

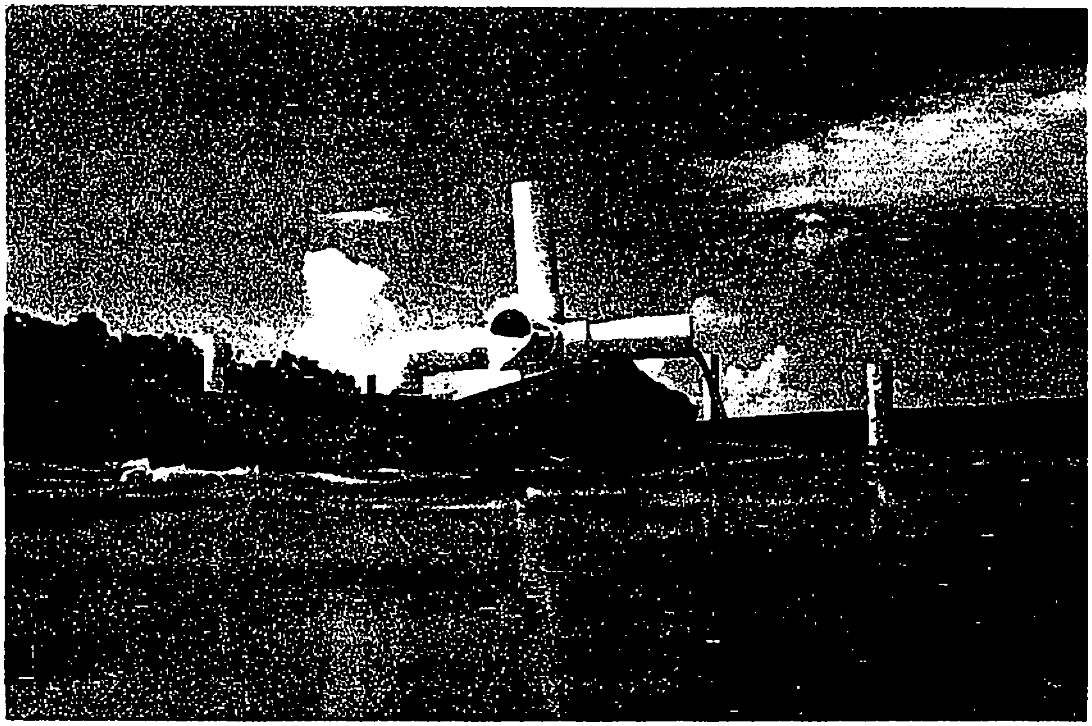


Figure 2. Operating plankton pump positioned so that outflow pours into floating mesh cages.

Feeding preferences of wild-caught and cage reared fish

To determine the diet of wild Yellowtail snapper (Ocyurus chrysurus) we caught ten individuals of 19-30 mm (< five days post-settlement) from shallow back-reef habitats approximately four hours after sunrise. The fish, which had been observed feeding, were chased into enclosures of 4 mm mesh, anaesthetized with clove oil solution and then killed immediately. They were preserved in 10% formalin in seawater and the abdominal cavity was injected with formalin solution.

The diet of O. chrysurus of the same size range, reared in cages supplied by a plankton pump, was determined by taking them from the floating cage four hours after dark and preserving them in the same way as the wild-caught fish. These fish had been in the cage for six days.

Prey items in the stomachs of fish were identified and volumes estimated under a microscope by measurement on a 1mm^2 grid. Plankton collected by the pump were compared with plankton in the nearby habitat by sampling: 1) inside an illuminated floating cage two hours after dark, 2) with a 15 minute plankton tow over seagrass (depth < 2 m, 200 μm plankton net), and 3) using a 200 μm net to collect the output from one of the outflow pipes of the plankton pump. The latter sampling was done for one night each fortnight (new moon and full moon) for four months. Plankton samples were preserved in isopropyl alcohol. The content of plankton in each sample was estimated from ten random sub-samples, each 1% of sample volume. Plankters were identified and their volumes estimated under a microscope using a 1mm^2 grid, as with the fish stomach contents. Plankton were grouped into the following categories: Mysidacea and Euphausiacea, unidentified crustacean larvae, Anomura, Annelida, Ostracoda, Amphipoda, Cumacea, Isopoda, Stomatopoda, Calanoida, Harpacticoda (after Todd and Laverack 1991). For each sample, total volumes of plankton in each category were estimated from the mean volume in the sub samples. Plankters larger than 2 mm^3 were excluded from the analysis.

The electivity of food categories (Ivlev 1961) was calculated using the following equation:

$$E = (2C/(A+C))-1$$

In which A is the percentage composition of food categories available to fish and C is the percent composition of food categories consumed by fish. A result between -1 and 1 for each category gives the relative preference (electivity) of food types, where 1 indicates that all available food was eaten and -1 that none of the available food was consumed.

Table 1. shows the electivity for categories of food items in the stomach contents of wild and cage-reared O. chrysurus. Cage-reared fish exhibited a strong preference for mysid and euphausid shrimps, while harpactacoids and calanoids had the highest electivity in wild fish. Percent composition of food categories in the stomach showed that mysids and euphausids made up more than half of the stomach contents of wild fish, whereas crustacean larvae and annelida accounted for more than half of stomach volume for cage-reared fish. Mean stomach volume was 10.4 mm^3 and 19.8 mm^3 for wild fish and cage-reared fish, respectively. The stomachs of cage-reared fish contained an average of 8.76 mm^3 of crustacean larvae whereas wild fish had less than 1 mm^3 of this food item. Volume of fish larvae in the stomachs of wild fish was more than five times that for cage-reared fish (absence of this category from plankton tows and sweeps meant that it had to be excluded from electivity calculations). In general, cage-reared fish had a wider variety of plankton in their stomachs and greater overall volumes.

Table 1. Food preferences of cage reared and wild caught fish in terms of percentage composition of stomach contents calculated by volume, as compared with percent composition of available plankton. Electivity: 1 = all available food items consumed and -1 = none of available food items consumed.

	Cage reared fish			Wild caught fish		
Food item category	stomach comp. %	available plankton % comp.	Electivity	% stomach comp.	available plankton % comp.	Electivity
Mysidacea and Euphausiacea	17.02	2.99	0.70	60.29	34.87	0.56
Unidentified crustacean larvae	33.53	8.12	0.61	8.08	5.76	-0.61
Anomura	5.94	2.14	0.47	3.85	3.17	-0.21
Annelida	38.36	11.11	0.55	0.00	3.17	-1.00
Ostracoda	1.55	5.13	-0.54	0.10.	2.31	-0.88
Amphipoda	1.74	4.27	-0.42	0.48	4.32	-0.57
Cumacea	1.17	8.12	-0.75	0.00	0.00	-1.00
Isopoda	0.16	4.27	-0.93	0.19	1.44	0.10
Calanoida	0.22	32.48	-0.99	2.12	8.93	0.81
Harpactacoida	0.32	21.37	-0.97	24.90	36.02	0.97

Based on the average volume of crustacean larvae in fish stomachs, supply from one outflow pipe was sufficient for 20 fish of 19-30 mm. Supply of annelid worms was sufficient for 80 fish of the same size. Note, however, that these estimates are likely to be conservative because of the exclusion of anything larger than 2 mm^3 from the samples.

Volume of plankton categories in pump samples (February to June 2000) was variable, but variation was far less than anticipated (Fig. 3). Effects of lunar illumination on relative light intensity of the plankton pump were expected to be more profound.

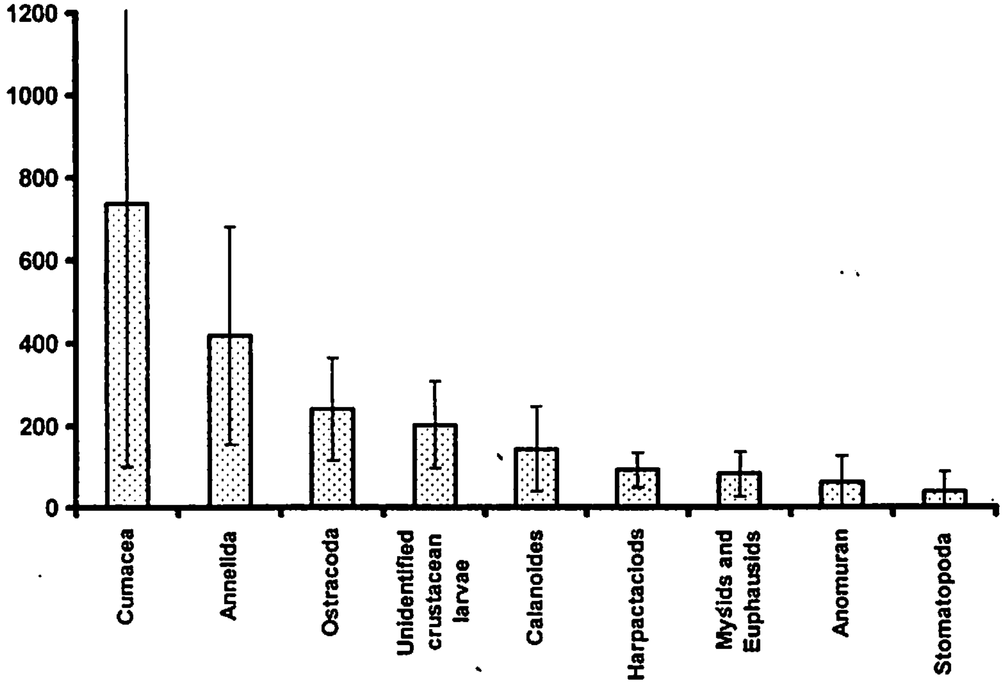


Figure 3. Mean volumes of food categories delivered per plankton pump outflow. Data gathered on eight nights (new moon and full moon, February to June 2000). Error bars indicate 95% CI.

Discussion

Although sample sizes were limited, analyses of stomach contents for wild and cage-reared fish indicated some similarities and differences in feeding behaviour between the two groups. Preferences for mysid and euphausid shrimps were similar for both groups of fish. The greater volume of this category in the stomachs of wild fish (Table 1) may well have something to do with the fact that they were feeding on settled, benthic, life stages of shrimp whereas caged fish fed on the juvenile and post-larval stages which are still planktonic and more likely to be attracted to light. For the same reasons, it is not surprising that caged fish had far higher volumes of crustacean larvae in their diets than wild fish. The necessity for small fish to avoid predators by associating with the substratum probably accounts for the far greater volume of harpacticoid copepods, which have a benthic distribution, in wild fish than in cage-reared fish. The much greater volumes of fish larvae in wild fish than in caged fish perhaps reflects similarities in settlement habitat usage by the post-larvae of other species which settle at a size where they may be vulnerable to predation by snappers that settle at a larger size, e.g., some species Haemulidae (McFarland et al. 1985) and Labridae, R.Power (ICLARM Caribbean and Eastern Pacific Office, personal communication) settle onto shallow back reef and seagrass habitat at approximately 8.5 mm (TL).

Stomach contents of cage reared fish were greater than wild fish, so growth rates should be greater than in the wild, with fish reaching more than twice their total length at settlement within the first 20 days (Watson et al. in press, a).

The catch from the plankton pump included large food items such as clupeoids (1-4 cm TL) and annelid worms (1-6 cm TL). These were not considered in the analysis as this study was intended to focus on the requirements of late pelagic-stage and early settlement-stage fish . Nevertheless, the presence of large food items indicates that this system may be capable of feeding fish of a wider size range. Plankton could be pumped onshore to tanks, which would be an advantage where security or storm damage may present a threat. It may be possible to rear earlier larval stages of finfish in tanks (Kuronuma and Fukusho 1984) in addition to a range of invertebrates. A diversity of ecological requirements can be met for various species which might have a permanent need for live food, or which need particular substrate or segregation from aggressive conspecifics.

Costs

The total cost of the plankton pump system was US $665.50, including 100m of electrical cable, 120m of heavy duty tubing, PVC airlift pump components (standard plumbing hardware), light, four floating cages, Sweatwater 2.24 kva blower (US $388.00), and an electronic timer switch. This cost would be reduced if a small compressor, e.g. the kind used by 'Hookah divers', was available in place of the electric blower. A waterproofed solar powered light source may also reduce long term operating costs. To pump plankton to onshore tanks the costs would be US $40.75 for a Sweatwater MD2 water pump and US $62.70 for two 60 L polyethylene shore tanks and pipeline to shore. Low cost light traps may be constructed for around US $15 for the main body and US $85 for a modular electric light source (Watson et al, in press, b). Crest and channel nets are available at a range of prices, but may be made for little more than the cost of the mesh available from Aquatic Eco-Systems, Inc. for US $38 for a roll 1.5m x 17m.

A potential application of the 'Plankton Pump'

Settlement stage capture of reef fishes has been suggested as a potential alternative and sustainable fishery (Bell et al. 1999). Farm gate prices for ornamental reef fish start at around US $0.50 each and reach more than US $20 (Baquero 1999). Various settlement studies have shown that there is potential for catching large numbers of suitable fish (Shenker et al. 1993; Dufour et al. 1996; Hair et al. in press). This technology could be a valuable support to such an industry allowing for storage and growout of fish.

Estimated monthly earnings for small-scale blast fishers in Indonesia (one man, one small boat, 70-100 bombs per month) is US $55 (Pet-Soede et al. 1999). Based on a daily catch of ten suitable individuals with a mean value of US $1.50 per fish and assuming 70% rearing survival, the monthly earnings from sale of these fish could total US $315. The returns from a modest harvest of postlarval fish could pay-off the start-up cost relatively quickly. Furthermore, it is likely that ornamental products from this source will qualify for eco-labels such as those proposed by the Marine Aquarium Council. This would increase the value of products considerably. The long-term potential earnings could offer considerable economic incentive for fishers to switch from blast fishing or other destructive practices.

Acknowledgments

This work was done as part of the Caribbean Marine Protected Areas Project, funded by the United Kingdom Department for International Development. Special thanks to S. Frederick and N. Erihstee for assistance with fieldwork and the development of the rearing system technology. Additional thanks to C. Wabnitz and L. Pet-Soede for providing information and to J. Bell and J. Munro for comments on the draft manuscript.

References

Baquero, J. 1999. Marine ornamentals trade: Quality and sustainability for the Pacific region. South Pacific Forum Secretariat Report. 50 p. Suva, Fiji.

Bell, J., Doherty, P. and Hair, C. 1999. The capture and culture of postlarval coral reef fish: potential for new artisanal fisheries. Secretariat of the Pacific Community Live Reef Fish Information Bulletin 6, 31-34.

Bell, J.D. and Gervis, M. 1999. New species for coastal aquaculture in the tropical Pacific - constraints, prospects and considerations. Aquaculture International 7, 207-223.

Doherty, P.J. 1994. A potential role for light-traps in enhancement of coral reef fisheries. p 92-93 in J.L. Munro and P.E. Munro (eds.) The management of coral reef resource systems. ICLARM Conference Proceedings 44, Manila.

Dufour, V., Riclet, E. and Lo-Yat, A. 1996. Colonisation of reef fishes at Moorea Island, French Polynesia: temporal and spacial variation of larval flux. Marine and Freshwater Research 47, 413-22.

Hair, C.A., Doherty, P.J., Bell, J.D. and Lam, H. (in press) Capture and culture of pre-settlement coral reef fishes in the Solomon Islands. Proceedings of the 9th International Coral Reef Symposium.

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes (Translated by D. Scott). Yale University Press, New Haven. 302 p.

Kuronuma, K. and Fukusho, K. 1984. Rearing of marine fish larvae in Japan. International Development Research Center, Ottawa, Ontario IDRC-TS47e, 109 p.

Masuda, R. and Tsukamoto, K. 1998. Stock enhancement in Japan: review and perspective. Bulletin of Marine Science, 62 (2), 337-358.

McFarland, W.N., Brothers, E.B., Ogden, J.C., Shulman, M.J., Bermingham, E.L. and Kotchian-Prentiss, N.M. 1985. Recruitment patterns in young french grunts, *Haemulon flavolineatum* (family Haemulidae), at St. Croix, Virgin Islands. Fishery Bulletin, 83 (3), 413-426.

Olla, B.L., Davis, M.W. and Ryer, C.H. 1998. Understanding how the hatchery environment represses or promotes the development of behavioural survival skills. Bulletin of Marine Science, 62 (2), 531-550.

Pet-Soede, L. and Erdmann, M.V. 1998. Blast fishing in southwest Sulawesi, Indonesia. NAGA, ICLARM Quarterly, 21 (2), 4-9.

Pet-Soede, C., Cesar, H.S.J. and Pet, J.S. 1999. An economic analysis of blast fishing on Indonesian coral reefs. Environmental Conservation 26 (2), 83-93.

Roberts, C.M. 1996. Settlement and beyond: population regulation and community structure of reef fishes. p. 85 -112 in N.V.C. Polunin and C.M. Roberts (eds.) Reef Fisheries: Chapman and Hall, London.

Shenker, J.M., Maddox, E.D., Wishinski, E., Pearl, A., Thorrold, S.R. and Smith, N. 1993. Onshore transport of settlement-stage Nassau grouper *Epinephelus striatus* and other fishes in Exuma Sound, Bahamas. Marine Ecology Progress Series 98, 31-43.

Schlumpberger, W. and Ziebarth, G. 1981. Produktion von vorgestreckten Zandern in beleuchtenten gazekafigen. Z. Binnefisch. DRR. 28, 143-144.

Shulman, M.J. and Ogden, J.C. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. Marine Ecology Progress Series. 39, 233-242.

Stobutzki, I.C. and Bellwood, D.R. 1997. Sustained swimming abilities of the late pelagic stages of coral reef fishes. Marine Ecology Progress Series 149, 35-41.

Todd, C.D. and Laverack, M.S. 1991. Coastal Marine Zooplankton: a practical manual for students. Cambridge University Press.

Watson, M., Power, R. M. and Munro, J.L. a, (in press) Use of light- attracted zooplankton for rearing post-settlement coral reef fish. Proceedings of the Gulf and Caribbean Fisheries Institue Meeting. 52.

Watson, M., Power, R.M., Simpson, S. and Munro, J.L. b, (in press) Low-cost light trap designs for coral reef fishery research and sustainable ornamental fisheries. Naga, The ICLARM Quarterly.

In press: Naga, the ICLARM Quarterly

Low cost light traps - designs for coral reef fishery research and sustainable ornamental fisheries

M. Watson, R. Power. S. Simpson, and J.L. Munro

Abstract

Relatively inexpensive light sources and light traps for capturing pre-settlement reef fish and invertebrates are described. A trap made from a plastic bucket, some plastic bottles, a small plastic waste bin and two sheets of plywood that cost US$15 appeared to be just as effective as a large aluminium and plexiglass trap that cost $250.

Introduction

Almost without exception, coral reef fish spend the first few weeks of life as pelagic larvae. For reasons that are not well understood, many aquatic organisms, including coral reef fish larvae, are attracted to light. Light traps can selectively sample older larvae (Doherty 1987, Choat et al 1993), and have proved valuable in assessing spatial and temporal patterns of recruitment. Light traps are generally thought of as expensive scientific research equipment, but they also have more practical applications. They could provide a sustainable alternative to destructive fishing practices in the aquarium trade and offer a way of collecting juvenile reef fish for stock enhancement (Doherty 1994, Watson et at. 2000). However, cost is an issue. The design originally popularised for reef fish by Doherty (1987) costs approximately cost $3000 and would prove prohibitively expensive for any project requiring a large numbers of traps. Various researchers have produced cheaper versions, either for sampling very small freshwater fish or invertebrates (Faber 1981, Floyd et al 1984, Ponton 1994) or marine invertebrates (Holmes and O'Connor 1988) and fish (Riley and Holt 1993, Brogan 1994, Sponaugle and Cowen 1996, Stobutzki and Bellwood 1997, Hernandez pers. comm.). ICLARM's recruitment monitoring project in the Caribbean has received numerous queries asking how light traps are designed and built. In this article we describe one lower cost and one minimal cost light trap modified from published designs. Detailed construction diagrams are provided. Costs, where given, are intended only as a rough guide, since they will vary geographically.

Light trap designs and costs.

Design of light source

Creating a waterproof electrical tight at reasonable cost is the main challenge for most light traps. Although Holmes and O'Connor (1988) had some success catching invertebrates with chemoluminescence, our research found white 'glow sticks' caught negligible numbers of reef fish. Small, low power incandescent bulbs may be suitable for some applications (e.g. Floyd et al 1984) but are unlikely to be powerful enough for reef fish. Traps tested during the present study were fitted with a modular light source constructed from readily available components. Our light unit, including batteries, all circuitry and components, cost approximately US$85.

The separate light unit made recharging and repairs relatively straightforward. Early attempts to build a plexiglass (also called perspex) housing on top of a trap modified from designs by Stobutzki (Stobutzki and Bellwood 1997; Stobutzki pers. comm.) were abandoned due to leaks at the many joins. Electronics were therefore housed in a plastic box approximately 22.5 x 16 x 9 cm manufactured as a diver's dry box ours were made by Pelican or Underwater Kinetics. The box comes with an O-ring seal around the lid, which we coated in silicon grease and kept tight shut with hose clamps. The box cost approximately US$20. The electronics were taken from 12V fluorescent cabin lights commonly sold in yacht chandlers or available by mail order. These lights came complete with circuit board and ballast and cost around US$18. The 30.5 cm (12 inch) bulb was sealed into clear vinyl hose available from marine suppliers and attached to the bottom of the box with silicone sealant or epoxy resin. A slide switch was set on the lid and sealed under a flexible primer bulb from a garden strimmer. This allowed units to be switched off when not in use without opening the box. Earlier designs used a push switch mounted at the end of the bulb which was squeezed on and off through the vinyl hose. However, water pressure occasionally squeezed the hose enough to trip the switch.

A light dependant resistor mounted on the lid automatically turns the light on at dusk and off at dawn, providing an important time saving as traps can be cleared and re-set in one trip. The resistor was sealed under a plexiglass cover. All components for the resistor circuit were bought from a local electronics shop cost for approximately US$20. The circuit (Fig. 1) had positive and negative sides with a central operational amplifier switch (Op. Amp.). The current on both sides of the switch was maintained at an equilibrium by five resistors and the photoresistor, with the photoresistor wired to the positive side of the Op. Amp.. In darkness the Op Amp is positively activated and drives a Field Effect Transistor (FET), completing the ballast/capacitor circuit to power the fluorescent bulb. The circuit was mounted on copper heat sinks on the inside of the box lid and covered in silicone sealant to minimize damage to components in the event of flooding.

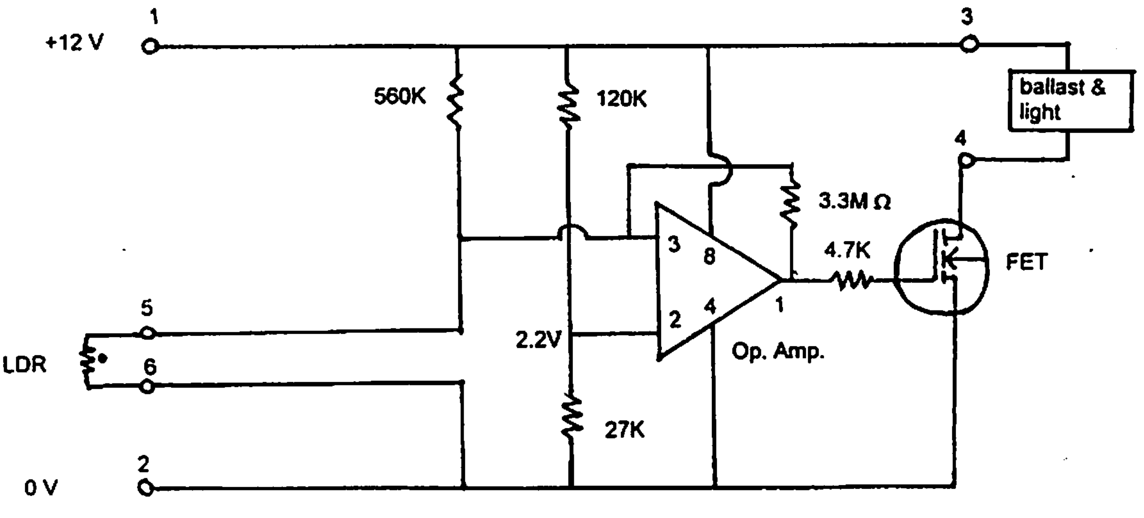


Fig. 1. Circuit diagram for light boxes. The numbers around the Op. Amp. are pin numbers of the of the IC itself. Thus; 1 is output, 2 inverting input, 3 non-inverting input, 4 ground and 8 supply. Pins 5, 6 and 7 are not used. The numbers 1-6 on the rest of the diagram refer to external connections. Thus; 1 power in, 2 ground, 3 power out to the load (in this case to the positive of the light PCB), 4 ground of the load (Note that this ground does not go directly to supply Ov but is switched by light sensitive switch), 5 and 6 are connections to the Light Dependant Resistor which is mounted on the external surface of the light box with a waterproof transparent cover and leads coming through two tiny holes.

Power was provided by 16 D-cell alkaline batteries or two sealed lead acid 10 amp-hour, 6 volt, rechargeable batteries. Alkaline batteries are more widely available, but proved more expensive. Despite a higher initial outlay, sealed lead acid batteries were at least five times cheaper than disposables. Sealed batteries resisted occasional partial floods better and required fewer error prone connections. This made changing batteries and finding faults easier. The positive and negative terminals connect to the waterproof switch and the photo switch circuit respectively.

Up to 18 lead acid batteries (9 sets) were re-charged simultaneously once using a low-tech connection board connected to an 8 amp car battery charger. The connection board was made up of a negative terminal connected to the charger lead and a positive connecting stub attached to an array of nine sets of paired car headlamp bulbs in series which acted as positive terminals, current limiters and charge indicators. The negative terminals of the nine sets of car lamp bulbs were connected via a bridge to the positive power supply from the charger. Pairs of batteries to be charged were wired in series. The free positive terminal from the battery pair was then connected to the positive terminal on the end of the bulb.

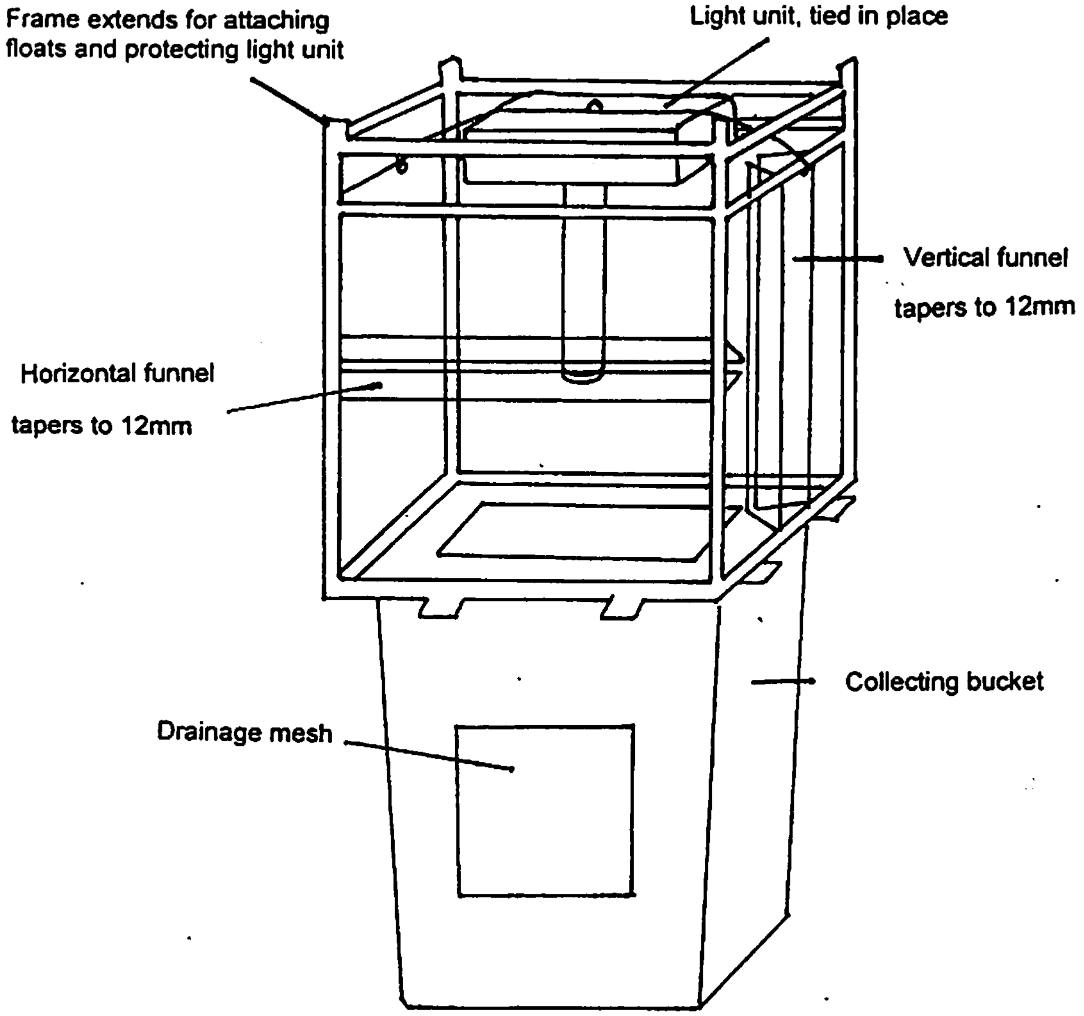


Fig. 2. Diagram of modified Stobutzki light trap. Only one horizontal and one vertical funnel shown for clarity. The main trap is 40cm on all sides. Funnels taper to 12mm. Frame extends 10 cm above the main trap. The collecting bucket is attached by shock cord looped tightly over tabs on the frame.

The free negative terminals of the battery set were connected to a common negative stub. Current exceeding that needed for optimum recharging illuminates the bulbs. Thus the bulbs glow brightly when battery charge is low, but dimly if at all as the charge is topped up. Faulty connections could be identified by dim bulbs at the start of charging. Battery sets were fully charged after 15 hours.

Light trap designs
Stobutzki and Bellwood (1997) built a smaller and simplified version of Doherty's light trap using moulded plexiglass and four horizontal entrance funnels. A single fluorescent bulb powered by 16 D-cell batteries is housed in a built-in plexiglass box and light tube. A collection bucket is strapped to the underside. We

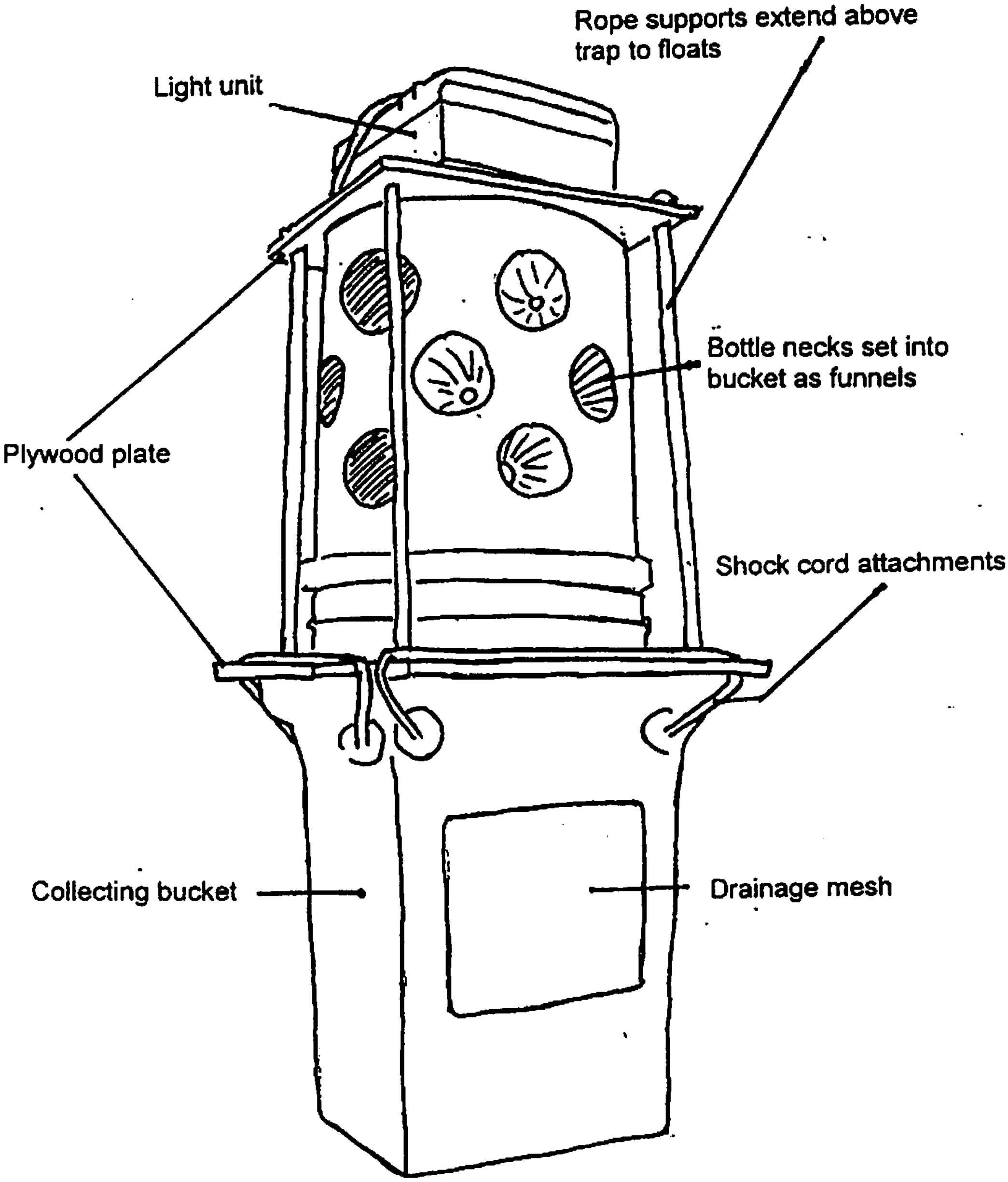


Fig. 3. Diagram of the bucket trap. Funnels are the necks of transparent plastic bottles set into the bucket. Collecting bucket is attached by shock cord to the plywood base plate.

have modified this design using flat sheets of plexiglass in a 40 cm x 40 cm x 40 cm aluminum frame. Two horizontal and two vertical entrance funnels taper to 12 mm (Fig. 2). We replaced the electrical compartment with a modular light unit as above. The collection bucket is a 23 litre (24 quart) waste paper bin with mosquito mesh drainage panels. Approximate cost per trap excluding the light is US$275, but might be less where components are cheaper.

Riley and Holt (1993) constructed a light trap for preflexion fish by setting four large plexiglass funnels into a frame cut from a 19 litre (five gallon) bucket. Sponaugle and Cowen (1996) made a trap from plankton mesh set with the necks of three plastic bottles as entrance funnels. We combined these two designs to reduce costs and increase robustness, setting the necks of 18 plastic bottles into a 19 litre (5 gallon) bucket (Fig. 3) to form the 'bucket' trap. The bucket itself was set between plywood top and base plates to which the light unit and collecting compartment were attached. This trap was quick to make, robust and cheap.

Comparison of designs

To compare the designs, two modified Stobutzki traps and one bucket trap were set five times over two nights around the new moon in August 1999. For each sample, a lottery draw was used to randomly position the traps on 6 moorings all within a few hundred metres of the reef crest. Traps were set for between 1 hr 45 min and 5 hr on the 15th and 4 hr 45 min and 6 hr 30 min on the 19th of August 1999. Light trap catches show strong lunar periodicity, so catches on different nights could not be combined.

Horizontal visibility at night was assessed by swimming away from the trap with a tape measure. To avoid burning an image of the trap on the observer's retina, the swimmer looked away every 5 fin kicks. Once the light was gone a further 5 m of tape was paid out and the trap approached until the light was seen. The average of the two measurements was taken.

Total catches are expressed as number of fish caught per hour including small pelagics (Clupeidae, Atherinidae and Engraulidae), which made up the bulk of the catch. On the 13th of August the Stobutzki and the bucket trap caught an average of 417 and 504 fish hr^{-1} respectively (n=6 and n=3). Actual catches ranged from 49 to 552 fish hr^{-1} and 34 to 1008 fish hr^{-1}. On the 19th the Stobutzki and the bucket trap caught an average of 29.4 and 29.8 fish hr^{-1} respectively. Actual catches ranged from 5.4 to 42.1 fish hr^{-1} for the Stobutzki trap (n=4) and were 30.4 and 29.1 fish hr^{-1} for the bucket trap (n=2). Peak catches did not correspond with any particular time of night. The results highlight the extreme spatial and temporal variability in catches. Despite more than an eight times more illuminated area in the Stobutzki trap compared with the bucket trap (5,184 cm^2 and 597 cm^2), traps were visible to the human eye at 47 m and 50 m respectively. The ratio of illuminated area to entrance area was 30.5:1 and 10.5:1 respectively. For comparison, Choat (1993) caught 293.2 fish hr^{-1} (>93% pomacentrids) using a Doherty light trap, whilst Brogan (1994) caught 313.5 fish hr^{-1} in a simpler two chamber light trap built from PVC piping. Brogan compared his trap with Doherty's design. Doherty traps caught more than twice the number of fish, however they were approximately 10 times as expensive (US$3000 and US$300 respectively).

Conclusions

Although both designs presented here worked, variable catches make it inappropriate to compare efficiency without a very large data set. Rather, the ease of construction and cost are considered more relevant. Whilst the modified Stobutzki trap cost approximately US$275 for a frame and plexiglass/ plexiglass, the bucket trap cost less than US$15, excluding the light box, collecting bucket and moorings.

The main advantage of a cheaper trap is that more can be deployed, and applications can extend beyond scientific research. For example, light traps could be used to supply sustainably caught ornamental reef fish to the aquarium trade (Fig.4,5). Catching fish in light traps before they reach the reef avoids losses from high post-settlement mortality. Thus, taking a few pre-settlement fish probably has less impact on the reef than removing settled fish. Widespread use of destructive collecting techniques such as sodium cyanide often leads to high mortality in captured fish, does substantial harm to the reef ecosystem, and

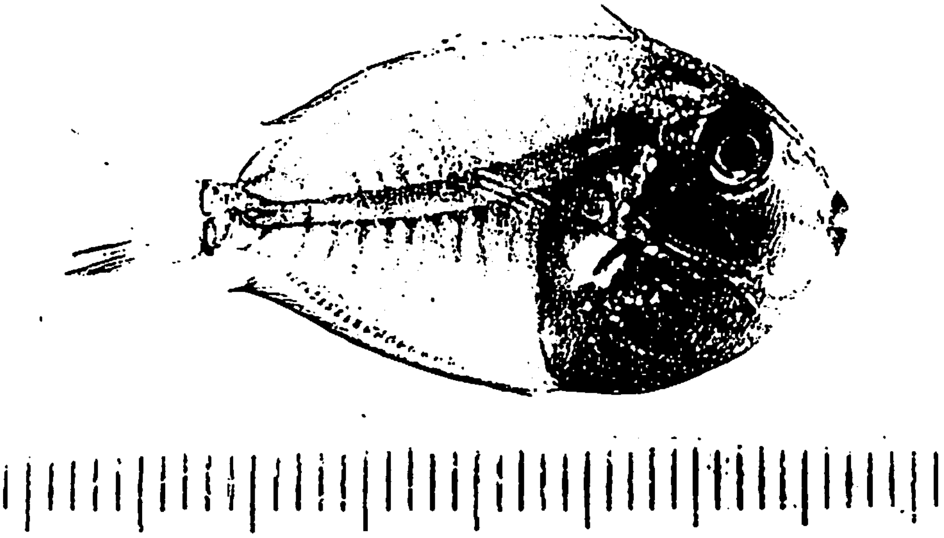


Fig. 4. Settlement stage surgeonfish caught during light trapping. Scale is mm.

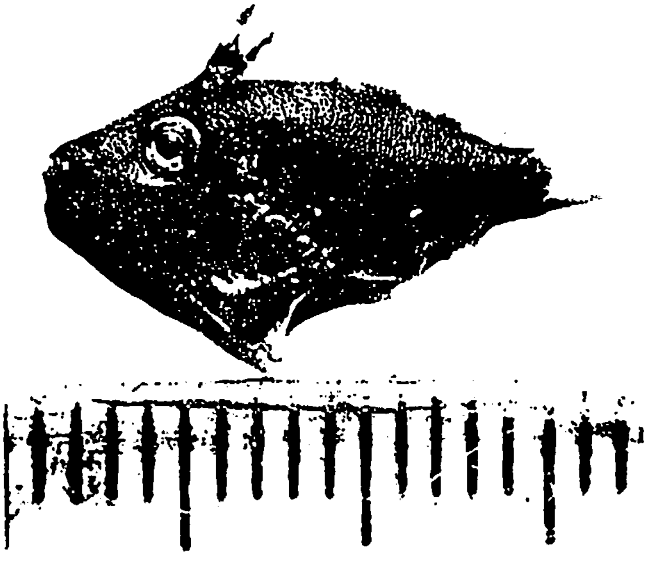


Fig. 5. Settlement stage filefish caught during light trapping. Scale is mm.

has made development of sustainable collection techniques an international concern. However, growing consumer demand for 'eco-labelled' fish suggests sustainable aquarium fisheries could provide a valuable alternative income for fishers, particularly where overfishing is currently degrading coral reef resources.

References

Brogan. M.W. 1994. Two methods of sampling fish larvae over reefs: a comparison from the Gulf of California. Mar. Biol. 118:33-44.

Choat. J.H., P.J. Doherty, B.A. Kerrigan. And J.M. Leis. 1993. A comparison of lowed nets. purse seine, and light-aggregation devices for sampling larvae and pelagic juveniles of coral reef fishes. Fish. Bull. U.S. 91:195-209.

Doherty, P.J. 1987. Light -traps: selective but useful devices for quantifying the distribution and abundances of larval fishes. Bull. Mar. Sci. 41:423-431.

Doherty, P.J. 1994. A potential role for light-traps in enhancement of coral reef fisheries. pp. 92-93 in: J.L. Munro and P.E. Munro (eds.) *The management of coral reef resource systems*. ICLARM Conference Proceedings 44, Manila.

Faber, D.J. 1981. A light trap to sample littoral and limnetic regions of lakes. Verh. Int. Verein. Limnol. 21:776-781.

Floyd. K.B., W.H. Courtenay and R.D. Hoyt. 1984. A new larval fish light trap: the quatrefoil trap. Prog. Fish Cult. 46:216-219.

Holmes, J.M.C. and J.P. O'Connor. 1988. A portable light-trap for collecting marine crustaceans; J. Mar. Biol. Assoc. UK 68:235-238.

Ponton, D. 1994. Sampling neotropical young and small fishes in their microhabitats: an improvement of the quatrefoil light-trap. Archiv fur Hydrobiol. 131:495-502.

Riley. C.M. and G.J. Holt. 1993. Gut contents of larval fishes from light trap and plankton net collections at Enmedio Reef near Veracruz, Mexico. Rev. Biol. Trop., Suplemento 41:53-57.

Sponaugle. S. and R.K. Cowen. 1996. Nearshore patterns of coral reef fish larval supply to Barbados, West Indies. Mar. Ecol. Prog. Ser. 133:13-28.

Stobutzki, I.C. and D.R. Bellwood. 1997. Sustained swimming abilities of the late pelagic stages of coral reef fishes. Marine Ecology Progress Series 149:35-41.

Watson. M., R. Power and J.L. Munro. 2000. Use of light-attracted zooplankton for rearing post-settlement coral reef fish. Proc. Gulf Caribb. Fish. Inst. 52:340-351.

M. Watson, R. Power. S. Simpson *and* **J.L. Munro** *worked in the Caribbean Marine Protected Areas Project, funded by the United Kingdom Department for International Development, at ICLARM's Caribbean/Eastern Pacific Office, 158 Inland Messenger, Road Town, Tortola, British Virgin Islands. E-mail: ICLARM-Caribbean@cgiar.org.*

Harvest of Settlement Stage Reef Fish for Small-scale Grow-out or Stock Enhancement; a Feasibility Study on the Family Haemulidae*

ROBERT M. POWER
ICLARM, Caribbean and Eastern Pacific Office,
158 Inland Messenger,
Road Town, Tortola, British Virgin Islands.
* ICLARM Contribution No. 1647.

ABSTRACT

Mortality rates of reef fishes are typically very high in the first few weeks after settlement. Capture, rearing and release of reef fish before or shortly after settlement may provide an opportunity to increase survival. Increasing survival at this stage could be a sustainable way of increasing fisheries resources. Visual censuses of juvenile grunts (Haemulidae) during settlement pulses from January to March 2001 and July to September 2001 in Tortola, British Virgin Islands were used to estimate local post-settlement mortality rates on a back-reef, seagrass/sand halo area. Concurrently, settling haemulids were captured from another location and reared in aquaria and sea cages. For fish smaller than 15 mm TL, aquarium-based rearing trials were used to compare the efficacy of feeding with wild-caught plankton or feeding with brine shrimp nauplii. Internally lit sea cages were tested against a plankton-pump food-delivery system for fish larger than 15 mm. Fish growth rates were rapid and mortality rates in sea cages were low for fish greater than 15 mm in size. Results are discussed in relation to potential applications for stock enhancement or mariculture.

KEY WORDS: Post-settlement mortality, post-larval fish feed, settlement-stage reef fishes.

INTRODUCTION

There now exists a wealth of information on the settlement and post settlement stages of coral reef fishes. In particular, the evidence demonstrating the population-limiting role of settlement stage mortality is considerable (Doherty et al in press, Roberts 1996 and references therein, Shulman et al 1987, Watson et al, in review). Exceptionally high mortality rates of many reef fish species during early settlement has led to interest in development of interventionist management strategies (Doherty 1994, Hair et al 2001, Watson et al in review). Harvest of fish before or shortly after settlement may provide an opportunity to increase the resource output from the settlement period. Capturing fish before they are subject to post-settlement mortality, and transferring them to rearing programs, has the potential to yield over 90% more fish than capture of the same cohort two weeks after settlement (Watson et al in review). Preliminary experiments, rearing settlement-stage lutjanids with light attracted plankton, showed that high survival rates and rapid growth is possible (Watson et al 2001). If significant numbers of settlement-stage fish can be reared successfully with low mortality, using low-technology systems, they may be a valuable source of "seed" for small-scale mariculture operations, or localized stock enhancement projects (Doherty 1994). While the economics of such an approach may not be appropriate for application in many commercial fisheries, the method may have application as a fisheries management tool in discrete, over-exploited artisanal fisheries.

This paper examines the mortality rates of haemulids shortly after settlement and the potential use of cheap and simple technology for rearing these fish to a size where mortality rates are much lower. As the recently settled fish are generally very fragile, and have restrictive food requirements, answers to the following questions are needed to assess the feasibility of early harvest and the use of simple rearing systems: What is the level of post-settlement mortality in the wild? Can it be reduced in captivity? How many fish settle each month? Is harvest of low-cost zooplankton food possible? Is it suitable for rearing haemulid fish?

Different species of haemulids often settle together and are indistinguishable from each other at this stage, however post rearing identification revealed that approximately 80% of settlement shoals were French grunt (*Haemulon flavolineatum*). White grunt (*H. plumieri*), Blue-striped grunt (*H. sciurus*) and Tomtate (*H. aurolineatum*) made up most of the remaining 20%. Fish of this family possess the following biological features which make them ideal candidates for such a study. First, they settle in large numbers virtually all year round (McFarland et al 1985), ensuring a constant supply of fish for small-scale grow-out or stock enhancement. Second, cohorts settle onto the same habitats and do not appear to move for two weeks, thereby providing an opportunity to quantify post-settlement mortality rates within this time period. Third, haemulids are planktivorous throughout most of their juvenile life phases, making them ideal candidates for rearing with simple and inexpensive plankton-attraction rearing systems. In addition, later juveniles will readily feed on chopped fish. Fourth, juvenile haemulids have been found to exhibit high site fidelity to daytime resting locations (Helfman et al 1982), a feature which would considerably simplify any stock enhancement experiments. Fifth, adult haemulids are of moderate economic value to small-scale artisanal fishers (Gaut & Munro 1983)

The disadvantages and challenges of working with haemulids lie in the small size of settling individuals (around 8.5 mm total length) (Helfman et al 1982). Fish this size present considerable challenges in rearing, as they are fragile and require very small, live food. They are also extremely sensitive to water temperature, chemistry, parasites and pathogens (Olla et al 1998, Montgomery-Brock et al 2001). Also, haemulids do not appear to be attracted to light (Watson and Munro, in review) and therefore have to be harvested after settlement. This means that some post-settlement mortality occurs prior to collection, reducing the scope for increasing production compared to species that can be caught in light traps prior to settlement.

MATERIALS AND METHODS

Mortality Rates of Settling Fish in the Wild.

This study focused on shallow habitats within the channel between Tortola and Beef Island in the British Virgin Islands because previous censuses showed that settlement-stage haemulids were present in large numbers between sand halo and seagrass habitats adjacent to back reef areas. A 170 m strip of back reef habitat, which was bordered to the east and west by land, was selected. About 200 m to the north, the fore reef dropped to island shelf at a depth of 20 m. To the south, it was bordered by dense seagrass at a depth of 1-3 m extending from the back reef for 50 m and ending in a sandy channel 5 m deep (Fig. 1). A pilot visual census was carried out for two weeks in December 2000 to determine likely settlement sites. Based on observations during the pilot survey, a 10 m by 6 m grid of 4 m^2 quadrats was laid out spanning the sand halo/seagrass interface, so that a line of five 4 m^2 quadrats covered each of three habitats; seagrass, seagrass/sand-halo interface and sand-halo (upper inset, Fig. 1). Numbers of fish on the grid were counted by visual census daily from January to April and July to September 2001 with few interruptions, giving 116 days of observations. Haemulid fish sizes were estimated and grouped into the following categories: 5-15 mm, 16-20 mm, 21-25 mm, 26-30 mm, >30 mm. In addition, the observations from July to September 2001 were extended to cover the whole back-reef area (170 m). Observations from the grid and wider back reef survey were used to generate mean settlement mortality estimates for the 5-15 mm and 16-20 mm size classes. The assumption was made that, if one of the three habitat categories was preferred, then any post-settlement movement of fish was likely to increase observed numbers on the preferred habitat, rather than decrease observed numbers. Thus estimates of mortality from this study may be conservative.

A one-way ANOVA, and post hoc Tukeys test, were used to test the null hypothesis: that there was no difference between the numbers of haemulids settling in sand-halo/seagrass interface habitats and in sand-halo or seagrass habitats.

Growth and Mortality Rates of Fish Fed with Brine Shrimp Nauplii and Plankton.

Haemulids which had settled over-night were carefully captured from a sand patch, 2.5 m deep, 500 m to the south of the settlement study site (Fig. 1). Fish of 6-15 mm could be captured easily by gently herding them towards a 0.3 mm mesh funnel net with a 1 m^2 aperture, which ended in a glass jar. All 'in water' movements of fish this size were done slowly and with great care being taken not to startle or stress the fish (earlier attempts at capture using a 1 mm mesh sweep net resulted in 98% mortality within the first two days). Once inside the glass jar, the fish were slowly brought to the surface and placed in a blue plastic bucket of fresh seawater. Fish were then transferred into a 95 l aquarium set up to simulate the sand-halo/seagrass habitat, with substrate and plants taken from the capture site (stocking density 1.58 fish l^{-1}) The aquarium had an under-gravel filter and was divided by a piece of plexiglass fitted with a 0.3 mm mesh window. This allowed for circulation and ensured that microbe content and water chemistry of both sides of the aquarium remained the same.

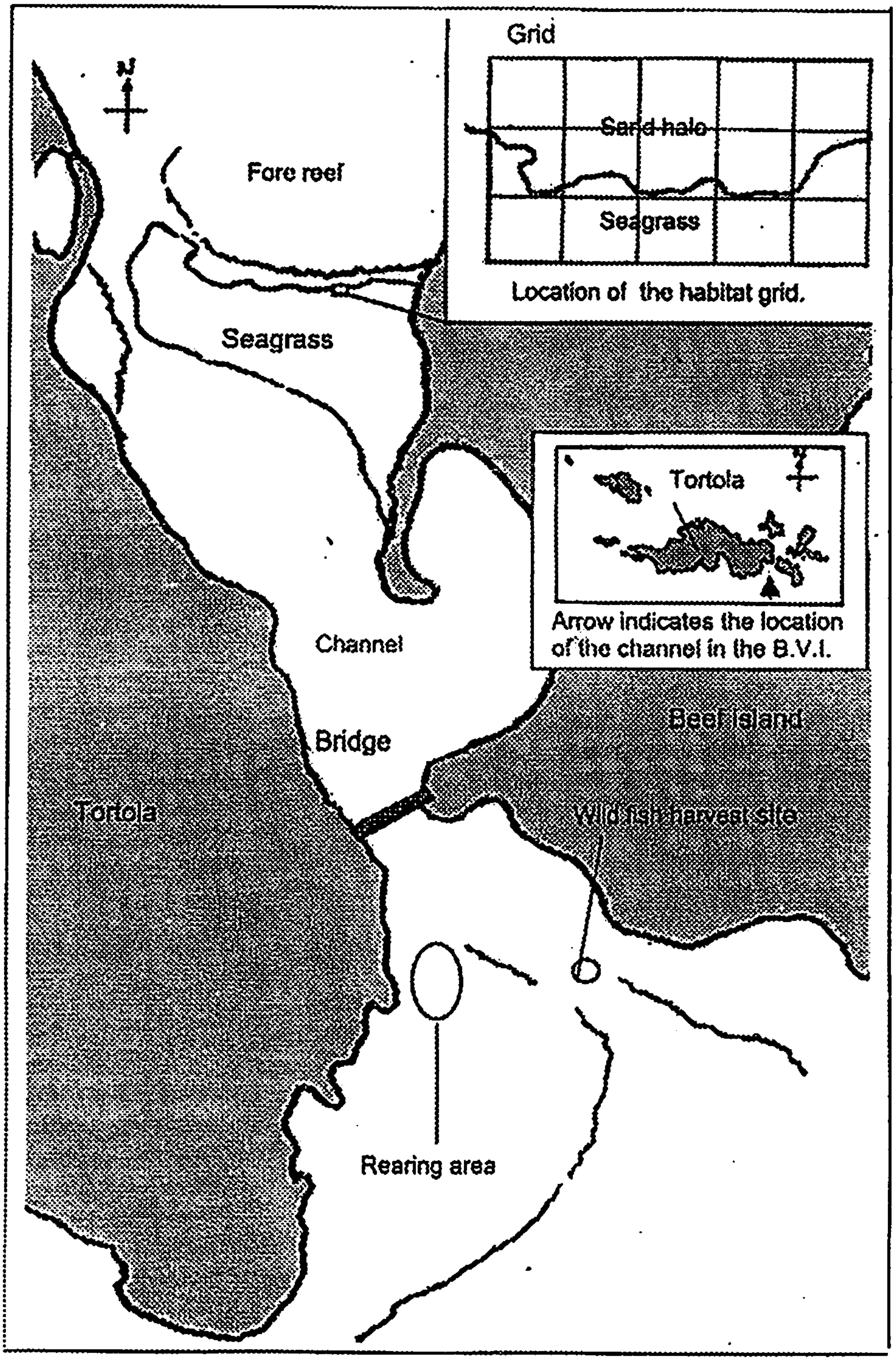


Figure 1: Map of the channel showing location of wild mortality study, rearing site for sea cage experiments and wild fish harvest site.

Fish in one side of the aquarium were fed brine shrimp nauplii whereas those on the other were fed live plankton harvested overnight by a plankton-attraction feeding-system (Power and Watson, in review). Prior to feeding the plankton was screened for parasitic isopods. Fish were fed until feeding behaviour ceased, morning, noon and evening. Aquarium water was exchanged with fresh seawater at a rate of ¼ tank day^{-1}. This experiment was run five times, twice for 8 days and three times for 16 days. Treatments were randomly swapped between sides of the aquarium each time. The aquarium was cleaned and reset with fresh substrate between the two, 8-day replicates, but left with the same substrate for the 16-day replicates. Fish were removed at the end of each experimental period, counted and measured against markings on the bottom of a transparent container. They were then transferred to the sea cage rearing experiments (see below). Thus, different fish were used for each of the five trials.

Growth and Mortality Rates of Fish Reared in Sea Cages.

To avoid some of the water quality and intermittent feeding problems associated with rearing the fish in aquaria, fish were also placed in small (6 l) "sea cages" fitted with the plankton pump system described by Power and Watson (in review). The plankton pump minimised water quality problems by providing a flow of water for half an hour of every hour on a 24-hour cycle. This flow of water not only reduced the buildup of waste and microbe populations within the cage, but was also likely to contain small quantities of suspended food during daylight hours to supplement the zooplankton attracted to the light at night. The pump also offered the opportunity to filter plankton before it reached the fish without severely restricting the flow of water through the cage.

Sea cages were situated over 2 m deep seagrass beds adjoining a channel (Fig. 1). Experiments were designed to test a variety of rearing strategies that may have potential for extensive application. The first sea cage experiment used fish that had been in aquaria for 8 days. Three treatments were set up, each with three 6 l cylindrical sea cages of 1mm mesh. Each sea cage was stocked with haemulids (mean TL 17.8 mm) at a density of 3.3 fish l^{-1}. The first treatment was designed to supply and retain plankton filtered by 1 mm mesh, at night, as well as exchange water and supply ambient plankton during the day. The outflow pipes from a plankton pump were fitted with 1mm filter bags and the sea cages were lined with ultra-fine mesh (<0.01mm). The cages were secured so that the outflow pipes delivered filtered plankton directly to the fish. The second treatment was designed to supply filtered plankton at night and exchange water and ambient plankton during the day, without any retaining mechanism. A second plankton pump was fitted with 1mm filter bags and cages as in the first treatment. The third treatment, a control, was designed to attract plankton to a light inside each sea cage, where fish could feed on them at night. This treatment had no water exchange or mechanism to retain plankton or supply it during the day. Three 1 mm mesh sea cages were each fitted with an internal light source (9W, 115V, 0.1 A) before being sealed and suspended one meter below the surface. These treatments were spaced 20 m from each other and run concurrently for a period of 8 days.

A second sea cage experiment was designed to investigate the potential for cheap automation of rearing newly settled haemulids. Fish were caught and transferred to nine 6 l cylindrical sea cages of 1 mm mesh, at a density of 1.6 fish l^{-1}. These cages were split evenly between three experimental treatments. The first treatment was designed to provide the correct size food for the smallest of the fish and retain it throughout the night and day. For this treatment, three outflow pipes from a plankton pump were each fitted first with 1mm and then 0.3 mm mesh filter bags. The three sea cages, which had been lined with ultra-fine mesh (<0.1mm) before being stocked with fish, were then secured to the outflow pipes so that filtered plankton of <0.3 mm diameter was delivered directly to the fish. The second treatment was designed to supply plankton which had passed through a 1mm filter, retain it at night with light attraction, as well as exchange water and ambient plankton during the day. A second plankton pump was fitted with 1mm filter bags and three sea cages with internal lights (9W,115V, 0.1A). In the third treatment, three sea cages were each fitted with an internal light source (9W, 115V, 0.1 A) before being sealed and suspended one meter below the surface. The lights attracted plankton through the 1 mm mesh, where fish could feed on them during darkness. This treatment had no water exchange or mechanism to retain or supply plankton during the day. All treatments were run concurrently for a period of 8 days and spaced 20 meters from each other.

Planktonic Food Supply.

Plankton pump output for the months February to December 2000 was sampled at full moon and new moon. A 200 µm plankton net and collection jar was attached to one of the outflows of the plankton pump, operated for half an hour each hour, throughout the night. Mean flow from each output was 0.85 l $minute^{-1}$. The volume of plankters collected each night was estimated from ten 1% sub-samples using a grid marked out with 1 mm squares. Plankters were grouped into the following categories: Copepoda, Mysidacea and unidentified crustacean larvae (after Todd and Laverack 1991). All other plankton forms were excluded from this investigation on the basis of their absence from fish stomach contents. Data were split between new moon and full moon samples and then further split into seasons, defined as the following periods: February-April, May-August and September-December. A two-way ANOVA was used to test the null hypothesis that there were no differences in the supply of plankton between seasons and within lunar cycles.

RESULTS

During a pilot visual census of the area, settlement-stage haemulids were observed in large numbers where the sand halo bordered the seagrass and on small sand patches within the seagrass. Numbers of fish observed further into the sand halo and in dense seagrass were minimal. Mean monthly settlement on the grid for January to June and August was 89.5 (+/- 204; max = 716) fish. Settlers showed a highly significant preference for the sand-halo/seagrass interface habitat ($p = <0.001$), accounting for 70.9% of total number of settlers recorded on the grid. Any movement of fish generally occurred within this habitat with shoals moving <2m overnight. Mean natural mortality after six days, calculated from the relative abundances at each settlement peak, was 65% (SD = 17.3). This correlated well with natural mortality calculated from the 37 day survey of the whole back reef area, which gave a mortality of 58.4% five days after peak settlement and 70% after six days. In addition, after 14 days a conservative mortality estimate of 67% was calculated by addition of surviving numbers of settlers to the subsequent peak in numbers for the succeeding size class (16-20 mm).

Table 1 gives a summary of the most significant results from the aquarium rearing experiments. The lowest mortality after 8 days was 10% for fish fed on brine shrimp and 25% for fish fed on plankton. Fish feeding behaviour between the two treatments appeared to differ little in duration. However, fish appeared to feed selectively on plankton, with prey being expelled after 29% of strikes. In contrast, fish rarely hesitated to consume brine shrimp. Mean mortality for both treatments was lower than 30% with no significant difference in sizes of fish by the end of the trial ($p = 0.32$). Mortality in the 16-day treatments was much higher than for 8 days, with the mortality rate increasing with each successive replicate. Forty percent of dead fish, removed from the final plankton-fed replicate, had spined crustacean larvae lodged in their throats.

Table 1. Summary of results from aquarium rearing experiments with haemulid fishes caught from the wild, shortly after settling.

Fish size	Treatment	Period	Feed time	Mean % mortality	Lowest % mortality	No. replicates	Rearing density fish l^{-1}
6-10 mm	Fed brine shrimp nauplii	8 days	Day	14 +/- 5.7	10	2	1.6
6-10 mm	Fed harvested plankton	8 days	Day	27 +/- 2.9	25	2	1.6
6-10 mm	Fed brine shrimp nauplii	16 days	Day	61 +/- 29.6	27	3	1.6
6-10 mm	Fed harvested plankton	16 days	Day	65 +/- 13.3	66	3	1.6

Stomach contents analysis of eleven plankton-fed fish (9.7 mm, mean TL +/- 1.03) contained 22% copepoda, 34% unidentified crustacean larvae and 44% mysids. Mean volume of stomach contents at satiation was 0.8 mm^3.

The lowest mortality rates from sea cage rearing experiments were achieved with the simple internally illuminated 1 mm mesh sea cage (Tables 2 and 3). Mean mortality rates of settlement size fish (Table 2) did not decrease when they were provided with filtered plankton or when plankton was retained during the day, although one replicate had 10% mortality. Mean mortality rates of fish pre-reared in aquaria (Table 3) and fed filtered plankton from the plankton pump was very high in the treatment where no retaining mechanism was provided, and not significantly lower than the wild mortality where food was retained.

Table 2. Summary of results from sea cage rearing experiments with haemulid fishes caught from the wild, shortly after settling.

Fish size	Treatment	Period	Feed time	Mean % mortality	Lowest % mortality	No. replicates	Rearing density fish l^{-1}
6-10 mm	Fed plankton: light inside cage	8 days	Night	29 +/- 25.4	7	3	1.6
6-10 mm	Fed plankton: Plankton pump, ultra fine mesh & 0.3mm filter.	8 days	Night & Day	60 +/- 45.8	10	3	1.6
6-10 mm	Fed plankton: Plankton pump, 1mm filter & light in cage.	8 days	Night	50 +/- 20	30	3	1.6

Table 3. Summary of results from cage rearing experiments with haemulid fishes which were pre-reared in aquaria for 8 days.

Fish size	Treatment	Period	Feed time	Mean % mortality	Lowest % mortality	No. replicates	Rearing density fish l^{-1}
16-20 mm	Fed plankton: light inside cage	8 days	Night	0	0	3	3.3
16-20 mm	Fed plankton: Plankton pump, ultra fine mesh & 1 mm filter.	8 days	Night & Day	83 +/- 10.4	75	3	3.3
16-20 mm	Fed plankton: Plankton pump, 1mm filter.	8 days	Night	92 +/- 2.8	90	3	3.3

Planktonic food supply varied throughout the year with significantly greater numbers of copepods and unidentified crustacean larvae being caught from September-December (p= <0.001 & <0.001 respectively), while mysid volumes were four times higher during May-December than in February-May. Differences in volumes of plankton between full moon and new moon were not significant for crustacean larvae (p= >0.9), but were significant for copepods and mysids (p = <0.001 and <0.001 respectively) with higher volumes at full moon. Interaction between moon phase and season was highly significant (p= <0.001). Comparison of mean volumes of plankton output for the three categories present in fish stomachs (Fig. 2), with mean volume of stomach contents, gave a crude estimate for the number of fish that may be reared with a plankton based diet from each plankton pump output (four to each pump). This estimate was based on fish feeding to satiation four times in an eight hour feeding period; double the feeding rate used for hatchery rearing lutjanid postlarvae (Turano et al 2000). This capacity was estimated at between 270 and 280 fish (9.7 mm mean TL).

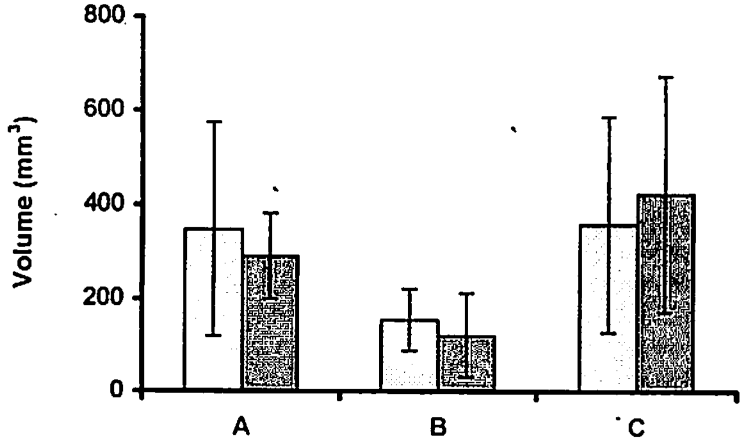


Figure 2. Mean total volumes of planktonic food per sample for 10 months February-December 2000. A Copepoda, B unidentified crustacean larvae and C Mysidacea. Full moon; dots and new moon; gravel. Error bars indicate 95% CI.

DISCUSSION

The greatest mortality of haemulid post-larvae in the wild occurs during the first six days after settlement, with only ~30% of fish surviving beyond 14 days. Whilst we cannot entirely rule out the effects of movement from this calculation it would appear that these results are consistent with estimates from other studies of settlement mortality (Doherty et al in press, Sulman & Ogden 1987, Roberts 1996 and references therein, Watson et al in review).

The results (Table 1) from feeding with brine shrimp nauplii and filtered plankton in aquaria show that the survival of recently settled haemulids can be increased substantially by rearing them in captivity. The best results from a combination of rearing strategies show that 10% mortality at 14 days can be achieved using a combination of feeding with brine shrimp nauplii and subsequent rearing in sea cages. Rearing fish in sea cages from settlement yielded 7% mortality. Mean mortality rates from each treatment present a slightly different picture with projected mortality at 16 days of around 30%. Even so, this still represents a large potential increase in production compared to natural rates of mortality. The high survival (100%) of fish reared from 8-16 days with internally illuminated sea cages, indicates that subsequent grow-out is likely to have low mortality. The same cannot be said for wild cohorts, where an average of 5% may reach maturity (Sulman et al 1987). Preliminary extended rearing trials of up to 40 days show mortality lower than 5% between day 16 and day 40 is possible, but observations indicate that interspecific aggression may increase with size. It would be advisable, therefore, to separate species as early as possible. The appropriate age for release of reared fish has yet to be determined. However, Helfman et al (1982) suggest that juveniles between 40 and 120 mm TL which have succeeded in learning the appropriate gregarious forage and resting behaviour, are far less likely to be preyed upon than smaller fish. If reared fish can be habilitated in a predator free environment with wild individuals at this size (Olla et al 1998), their mortality may be similarly low.

Some of the results point to areas for improvement and problems with the use of plankton as a cheap food. The fact that dead fish were found with spined crustacean larvae lodged in their throats appears to point to a breakdown in the normal prey selection behaviour. It is possible that early morning delays in supplying plankton to fish may disrupt their natural dawn feeding behaviour and result in hasty and inappropriate prey selection. While plankton supplies were variable, samples always contained more than enough food of the right size and variety. Interestingly, attempts to improve early sea cage rearing with various plankton filtering and retaining mechanisms, proved far less effective than a 1 mm mesh 6 l sea cage with an internal light. There appeared to be no adverse effects to fish from the reversal of the natural daylight feeding behaviour. Results from this rearing method may be improved by taking measures to control external parasites with techniques like hydrogen peroxide dips (Montgomery-Brock et al 2001).

This study shows that there is considerable potential for increasing the survival of fish at settlement, thereby creating a way to improve fisheries production by growing-out the additional fish in small-scale mariculture operations or in stock enhancement programs.

ACKNOWLEDGEMENTS

This work was completed as a component of the ICLARM Marine Protected Areas Project, funded by the United Kingdom Department For International Development. Special thanks to John Munro, Zolt Sary and Ivor Williams for assistance with experimental design and editing of the manuscript. Thanks also to Vanessa Bertenshaw, Karen Bech, Zsolt Sary and Newton Erihstee for assistance with fieldwork.

LITERATURE CITED

Doherty, P.J. 1994. A potential role for light-traps in enhancement of coral reef fisheries. pages 92-93 in: J.L. Munro and P.E. Munro (eds.) *The*

Management of Coral Reef Resource Systems. ICLARM Conference Proceedings 44, Manila.

Doherty, P.J., V. Dufour, R. Galzin, M.A. Hixon, and S. Planes. High mortality during settlement bottlenecks the abundance of a coral reef fish. Proc. Ninth Int. Coral Reef Symp. in press.

Gaut, V.C. and J.L. Munro. 1983. *Caribbean Coral Reef Fishery Resources.* ICLARM Studies and Reviews 7, Manila.

Hair, C.A., Doherty, P.J., Bell, J.D. and Lam, M. Capture and culture of presettlement coral reef fishes in the Soloman Islands. Proc. Ninth Int. Coral Reef Symp. In press.

Helfman, G.S., J.L. Meyer, and N.W. McFarland. 1982. The ontogeny of twighlight migration patterns in grunts (Pisces: Haemulidae). J. Anim. Behav. 30:317-326.

McFarland, N.W., E.B. Brothers, J.C. Ogden, M.J. Shulman, E.L. Bermingham and N.M. Kotchian-Prentiss. 1985. Recruitment patterns in young French grunts *Haemulon flavolineatum* (Family Haemulidae), at St. Croix, Virgin Islands. Fish. Bull. 83(3):413-426.

Montgomery-Brock, D., V.T. Sato, J.A. Brock and C.S. Tamaru. 2001. The application of hydrogen peroxide as a treatment for the ectoparasite *Amyloodinium ocellatum* (Brown 1931) on the Pacific threadfin *Polydactylus sexfilis.* J. World Aquac. Soc. 32(2): 250-254.

Olla, B.L., M.W. Davis and C.H. Ryer. 1998. Understanding how the hatchery environment represses or promotes the development of behavioural survival skills. Bull. Mar. Sci. 62 (2):531-550.

Power, R.M. and M. Watson. A pump for feeding post-settlement coral reef fish with light attracted zooplankton, with possible applications in the fisheries for marine ornamentals. J. World Aquac. Soc. In review.

Roberts, C.M. 1996. Settlement and beyond: population regulation and community structure of reef fishes. pages 85 -112 in: N.V.C. Polunin and C.M. Roberts (eds.) *Reef Fisheries.* Chapman and Hall, London.

Shulman, M.J. and J.C. Ogden. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum.* Mar. Ecol. Prog. Ser. 39:233-242.

Todd, C.D. and M.S. Laverack. 1991. *Coastal Marine Zooplankton: A Practical Manual for Students.* Cambridge Univ. Press.

Turano, M.J., A.D. Davis and C.R. Arnold. 2000. Observations and techniques for maturation, spawning and larval rearing of the yellowtail snapper *Ocyurus chrysurus.* J. World Aquac. Soc. 31(1):59-68.

Watson, M., R.M. Power and J.L. Munro 2001. Use of light-attracted zooplankton for rearing post-settlement coral reef fish. Proc. Gulf Caribb. Fish. Inst. 52:340-351.

Watson, M. and J.L. Munro. Settlement and recruitment of coral reef fishes in moderately exploited and overexploited Caribbean ecosystems: implications for Marine Protected Areas. Bull. Mar. Sci. In review.

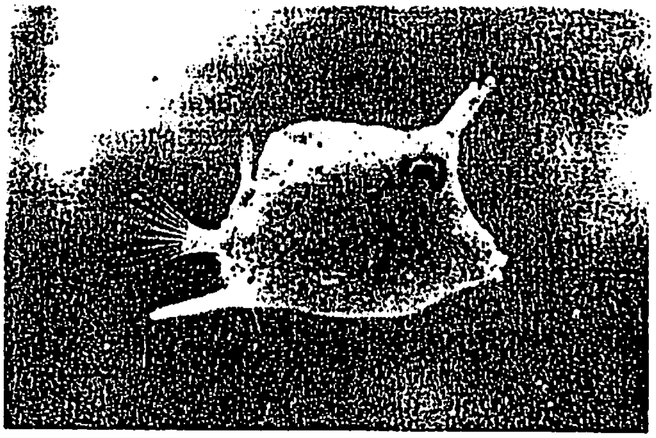
Watson, M., J.L. Munro and F.R. Gell Settlement, movement and early juvenile mortality of the Yellowtail snapper, *Ocyurus chrysurus.* Mar. Ecol. Prog. Ser. In review.

Juveniles Recruited to Sustain Aquarium Industry

A settlement stage yellow tail snapper (Ocyurus chrysurus) *hovers amongst seagrass (Photo: Maggie Watson)*

The chances of a fertilized egg making it all the way to become an adult reef fish are exceedingly small. Now researchers want to side-step some of that mortality in order to supply a sustainable aquarium trade and, at the same time, conserve coral reefs.

A damselfish swimming amongst the corals and rocks in a well kept aquarium seems a serene enough creature, but a few rough calculations will leave you marvelling at a journey of survival against tremendous odds. Now don't leap to conclusions about the villainous aquarium trade - the journey from reef to aquarium is only a small part of the tale. To begin with, unless our fish is one of only around 25 species of marine ornamental fish bred in captivity, it started life as a tiny larvae developing in open water. The vast majority, i.e. approaching 100%[1] of larvae, will perish before they return to shallow water. Then, often timing their arrival to the darkest nights of the month to avoid visual predators, the minute fish must negotiate a 'wall of mouths'[2] before settling to the bottom. Survival rates will vary, of course, both between species and over time. But for the few that make it to the end of their pelagic (open water) phase and then through the settlement process, around two thirds may die within a day of settlement[3]. After a month only 10% of the fish that settled may remain alive[3]. Those kinds of numbers have set researchers thinking - if you could harvest just a few fish before they meet their 'mortality hurdle' at settlement, your fishing impact should be minimal.



This tiny cowfish Lactophrys *spp. is only around 2cm long (Photo: Maggie Watson).*

*Blue tang (*Acanthurus coeruleus*) are yellow as juveniles. This fish settled less than 24 hours previously, and is still partly translucent (Photo: Maggie Watson)*

Baby fish aren't much good for eating, but juveniles are preferred by the aquarium trade. They cost less to ship, and they are often prettier than the adults. Researcher Vincent Dufour is so sure that there is a market that he has set up a company, AquaFish Technology (*www.aqua-fish.com*). Dufour found that 'crest nets' (shaped like funnels which catch the waves) set on reef crests around Pacific atolls will filter huge amounts of water flowing over the reef and through the lagoon. They can catch thousands of larval reef fish during a big settlement pulse. In one crest net on Moorea Atoll, Dufour's team averaged over 100 fish per night, many of which were ornamental species[4].

Aquafish hopes to contribute to a sustainable aquarium fishery, and Dufour and colleagues are not alone in thinking the idea has merit. Cathy Hair, Johann Bell and colleagues at the Coastal Aquaculture Centre in the Solomon Islands (run by ICLARM – The World Fish Centre) have been looking into village-based 'grow out' of larval fish. The idea is to provide coastal people with an alternative livelihood, and hopefully relieve some of the fishing pressure on coral reefs. Between November 1999 and June 2000 the team caught more than 1,170 fish from 70 species that were suitable for further rearing in on-shore tanks supplied with flowing seawater. The team use both light traps, based on designs developed in the 1990s by Peter Doherty at the Australian Institute of Marine Science (AIMS), and crest nets. The two methods both have their advantages. Light traps caught fewer kinds of fish than crest nets but more damselfish (Pomacentridae), many of which are ornamental species.

Sadly, ethnic violence in the islands has slowed research. Hair, an Australian, was evacuated in June

*Settlement stage filefish (*Monacanthus *spp.) like t hang out around weed or other floating objects The water here is so still you can see their reflection (Photo: Maggie Watson).*

last year and spent the next six months working u data at AIMS, where Doherty is a collaborator o the current phase of the project. Some research b local Solomon Islands staff has continued, but th constraints imposed by the political situation ar frustrating real progress.

Before the troubles began Hair and colleague were feeding their fish on eggs (roe) from a variet of large fish, on creatures the fish picked from liv rock, on plankton that came through the seawate pump, and on prepared food supplied by Mike Rim mer of the Queensland Department of Primary In dustries. Damselfish, surgeonfish, snappers and trig gerfish were all easy to rear. Painted cray *Panuliru versicolor* showed promise once cannibalistic indi viduals were isolated, and the delicate cleane shrimp *Stenopus hispidus* also showed potential fo rearing. But early juveniles are notoriously pick eaters and some families such as butterflyfish di not take well to the tanks.

About the same time, John Munro and colleague (including the authors) were working on anothe ICLARM research project investigating larval fis supply to islands in the Eastern Caribbean. When gluts of settlement stage snapper larvae were caught in light traps (up to 407 yellowtail snappers *Ocyurus chrysurus* in one light trap in a single night), Munro suggested keeping the fish in floating cages, illuminated at night by submersible lights. The lights would attract plankton for the fish to eat. The experiment was a first tentative step towards investigating the feasibility of helping restock new marine protected areas. The idea was that where previously overfished reefs suffer severely reduced natural recruitment, light trap caught larvae or juveniles could be reared in cages for several weeks. Once past their 'mortality hurdle' they could be released to help rebuild stocks. Whether the idea will work is still far from clear, and the team continues to investigate relative mortality rates in the wild and in captivity, feeding preferences, behaviour on release, etc. But several advantages were immediately apparent from the research. Floating mesh cages are cheap aquaculture tanks, and you don't need expensive equipment to maintain water quality. Plankton, much of which is attracted to light, is the natural food of many early juvenile fishes. Perhaps this low-tech approach would also be useful for village-based 'grow out' of fish larvae for the ornamental trade?

don't leap to conclusions about the villainous aquarium trade

harvest just a few fish before they meet their 'mortality hurdle' and your fishing impact should be minimal.

We experimented with solar powered and shore-powered lighting for floating fish cages, but waterproofing the lights can be tricky and expensive, and each floating cage needs a separate light. Biofouling can also clog the fine mesh needed for small fish, and exclude the light. Our most promising development is a simple 'plankton pump' (designed by Robert Power) which uses a single light to attract plankton at night, and then utilizes the same principle as the air lift pumps seen in many aquaria to circulate fresh, plankton rich water to floating cages or to tanks on nearby land. Alternatively, plankton rich water can be diverted to holding tanks, and fed to the fish the following day – so the natural cycle of day and night can be maintained for fish that use sight to catch food. So far, survival and growth rates have been promising for the snappers that we caught[5], and also for surgeonfish, filefish, damsels, butterflyfish and lobster larvae.

trading 50 individuals from common species per month would still provide more money than many dynamite fishers make

To make such 'grow-out' techniques more accessible to poor communities, we have also tried to reduce the cost of the light traps needed to catch the fish in the first place. Traps designed for scientific research are usually prohibitively expensive. We developed modular light units which are easily swapped between traps and are easier and cheaper to fix when they go wrong[6]. And together with Steve Simpson (now studying at AIMS), we investigated building the bodies of traps from five gallon buckets studded with funnels adapted from transparent drinks bottles[6]. The traps may not be quite as efficient as the expensive versions, but they cost a fraction of the price, and they do catch fish.

So is the idea of growing-out larvae for the ornamental fish trade viable? With the 'farm gate' prices of many ornamental fish starting at around $0.50 US for the more common species[7], trading 50 individuals from common species per month would still provide more money than many dynamite fishers make[8]. However, there are still plenty of drawbacks. For example, the most valuable species in the ornamental trade are usually the rarest, and these are not likely to be the species caught in great numbers in either light traps or crest nets. And in some parts of the Pacific very small fish, called tinies, fetch up to 30% less than adults. More importantly, supply of larvae is likely to be highly unpredictable in space and time. If collectors depend on ornamentals for their living they could be driven to destructive fishing techniques such as cyanide fishing when catches of larvae are low. The best way round this would probably be to use a wide variety of species and to make this kind of aquaculture just one part of a diverse livelihood. Most importantly of all, any fishery - even for tiny fish - will still need to have its fishing effort managed to avoid overfishing. Considering the patchiness of larval supply, it's not difficult to imagine batteries of light traps and crest nets making a substantial impact on natural populations, particularly if big settlement pulses are intercepted.

But, bearing in mind the colossal mortality rates for early juvenile fish, if a proportion of the reared fish were released to the wild as larger, less vulnerable individuals, the overall survival rate might still be higher than it would be without intervention. This remains an untested idea, but studies are currently underway. At least rearing natural stock provides some incentive to look after the environment, unlike more conventional captive breeding. If 'grow-out' can be made sustainable and profitable it could help both people and reefs. Farming reef fish larvae could be like selling corn seed for the price of the eventual harvest!

References

1 Leis JM (1991) The pelagic stage of reef fishes: the larval biology of coral reef fishes. In: Sale PF (ed) The Ecology of Fishes on Coral Reefs. Academic Press, San Diego: 183-230

2 Hamner WM, Jones MS, Carleton JH, Hauri IR, Williams DM (1988) Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. Bulletin of Marine Science 42: 459-479

3 Watson M, Munro JL, Gell FR (In review) Settlement, movement and early juvenile mortality of the Yellowtail snapper, *Ocyurus chrysurus*: implications for recovery interventions in severely overexploited stocks

4 Dufour V, Riclèt E, Lo-Yat A (1996) Colonisation of reef fishes at Moorea Island, French Polynesia: temporal and spatial variation in larval flux. Marine and Freshwater Research 47 413-22

5 Watson M, Power R, Munro JL (In press) Use of light-attracted zooplankton for rearing postsettlement coral reef fish. Proc. 52nd Gulf and Caribbean Fisheries Institute.

6 Watson M, Power R, Simpson S, Munro JL (In press) Low cost light traps - designs for coral reef fisheries research and sustainable ornamental fisheries. Naga. Preprint available from rpower@surfbvi.com

7 Baquero J (1999) Marine Ornamentals Trade: Quality and sustainability for the Pacific Region. South Pacific Forum Secretariat Report, Suva, Fiji 50 pp

8 Based on Pet Soede L, Cesar HSJ, Pet JS (1999) An economic analysis of blast fishing on Indonesian coral reefs. Environmental Conservation 26(2): 83-93

Maggie Watson and Robert Power worked together on ICLARM's Caribbean Marine Protected Areas Project in the British Virgin Islands. Their emails are Maggie@xpertext.com and rpower@surfbvi.com

A FISHY TALE!

by

M. Watson
ICLARM Caribbea/Eastern Pacific Office,
Tortola, British Virgin Islands

Visit the Wreck of the Rhone Marine National Park, or any of the fascinating coral reefs in the British Virgin Islands, and you will see a profusion of colourful fish. Butterflyfish take delicate nibbles from tiny coral polyps, parrotfish rasp algae from rocks, snappers drift serenely past. You can even see schools of bright blue tangs out to bully some poor damselfish off his carefully tended algal lawn, so they can graze themselves. On reefs like the Wreck of the Rhone, where fishing is banned, you might notice the fish are bigger. It seems obvious that the biggest fish produce the most young, but did you know that a big snapper can produce tens of times, maybe a hundred times the number of eggs produced by much smaller fish of the same species! So allowing at least a few fish to grow as big as possible free from fishing makes an enormous difference to how many fish you might get in the next generation, both inside the marine park and outside in the fishery.

This is just the beginning of an intriguing story. The fascinating thing about reef fish is that almost all species release their eggs into the open water to wash with the currents. Once hatched, the see-through fish larva spends anything between 14 days and three months adrift, feeding on minute planktonic animals. Away from hungry mouths on the reef, a baby fish is safer in empty, blue water, but it is still in a hostile and unpredictable environment. Even here, most will either get eaten or die of starvation. A fish that survives against these tremendous odds and makes it to a couple of centimetres long is ready to return inshore. It is getting too big to eat plankton, and needs shallow nearshore reefs, seagrasses and mangroves as nursery habitats. Now it faces an even greater challenge. Imagine the journey ahead! Our fish, which may be miles offshore, is still little more than a sliver of transparent muscle and a simple nervous system. How does it even know which direction to take?

The apparent impossibility of this task had ecologists stumped for years. People simply assumed that enough eggs must be spawned for a lucky few larvae to survive and find themselves back inshore - but probably many miles from where they started. Sometimes, enormous numbers of fish might settle from the ocean (for a few years in St. Croix USVI, tiny porcupine fish arrived in schools so big they could be seen from the air). In other years there may be almost nothing. In practical terms, this means keeping tabs on a fish population is difficult. From year to year you don't know how many fish you will get in the next generation, or where they might have come from. Those schools of snappers on the Rhone might have been spawned on a reef far upstream, and their offspring might drift far from the British Virgin Islands.

However, an interesting fact has opened a window on reef fish biology. When baby reef fish are ready to settle down from the ocean onto the bottom, they are attracted to light. No-one knows why, but it does mean ecologists can use light-traps to investigate patterns of settlement. Researchers from as far afield as Australia's Great Barrier Reef to the Caribbean have found that fish arrive on the reef around the new moon. Throughout the summer, fish settle on the darkest nights. It's their safest bet, since most predators hunt by sight, and the reef is a dangerous place if you are small.

So are these new settlers the lucky few, or can fish actively seek out shallow water? Reef researchers in Australia caught baby fish in light traps as the fish were about to settle on reefs. While watching them in aquaria the researchers made a startling discovery. These creatures are not the passive drifters once thought. In fact they are exceptional swimmers. Tiny surgeonfish only 3cm swam non-stop for several days, covering the equivalent of 98km. Now ecologists realised that larval fish had far more control over their destiny than previously thought. Even if currents tend to sweep them offshore, larvae might swim up or down in the water column to 'catch' currents going in different directions. More interestingly, when released in open water, fish which had not yet settled appeared to detect the direction of a reef almost 1km away. How? Sound travels well in water. Perhaps they hear waves crashing. Or perhaps water coming from the right habitat has a characteristic chemistry which makes it 'tastes' different.

But although fish which are about to settle may be good swimmers, larvae newly hatched from eggs are not so strong. Researchers in Barbados recently found water currents can 'diffuse' concentrations of recently spawned eggs and larvae before they are big enough to swim well. So patches of newly hatched fish may not travel far before becoming very 'dilute'. Looking at the situation from the other end, this suggests large groups of baby fish arriving at the reef may have been spawned fairly nearby. Once big enough, they may keep together and swim to stay close to shore. If that's true, it means populations may replenish themselves, rather than relying on an unpredictable rain of youngsters arriving out of the blue. It also means looking after coral reefs reaps local benefits (and by the same token, fishing too hard or destroying a reef will have local consequences).

Ecologists from ICLARM (the International Center for Living Aquatic Resources Management) are working together with the British Virgin Island's Conservation and Fisheries Department to find out more about the lives of baby fish. You might see the research boat on the water this summer, or come across light traps around the new moon. The research compares BVI to other areas in the Caribbean such as the United States Virgin Islands, and Jamaica, and the results may help decide where to put more protected areas.

Coral reefs and their fish communities are a treasure house of biological diversity, often described as the rain forests of the sea. Durable enough to last thousands of years, they are as intricate and delicate as a precision engineered watch. Whether you admire the beautiful electric blue chromis fastidiously picking a meal of plankton from the water or a ferocious looking moray eel lurking in a crevice, every cog in the machinery can be a fascinating character. Looking after these treasures makes us all richer. Whether in a designated protected area like the Wreck of the Rhone Marine National Park, or snorkeling on a less well known reef, look rather than touch. The saying is 'take only pictures, leave only bubbles…'.

And if those fish look as relaxed as your vacation and you're not looking forward to returning home, take heart – you will probably have the easier journey!

further reading:
Cowen et al. (2000). Science 287, 857-859..
Leis et al. (1996). Marine and Freshwater Research 47, 401-411.
Stobutzki & Bellwood (1997). Marine Ecology Progress Series 149, 35-41.

Printed in:
BVI Welcome Magazine., Tortola.
August/September 2000

Submitted to Marine Ecology – Progress Series (2

Settlement, movement and early juvenile mortality of the Yellowtail snapper, *Ocyurus chrysurus* *.

M. Watson, J.L. Munro** and F.R. Gell
ICLARM Caribbean/Eastern Pacific Office, 158 Inland Messenger, Road Town, Tortola, British Virgin Islands.

* ICLARM Contribution # 1615
** Corresponding author, e-mail: j.munro@cgiar.org

ABSTRACT: Visual censuses of recently settled Yellowtail snapper, *Ocyurus chrysurus*, were made within a grid measuring 50 x 25 m established in a <1m deep seagrass (*Thalassia testudinum*) bed in the British Virgin Islands, Eastern Caribbean, between September 1999 and July 2000. A peak of 92 newly-settled *O. chrysurus* were observed around the new moon in September 1999, followed by a decline of more than 75% over three weeks. Light trapping near adjacent fringing reefs documented a concurrent pulse of late pelagic stage *O. chrysurus*. Observations in April-May and June-July 2000 recorded much smaller supply events and lower settlement densities. The effects of post-settlement movement, as opposed to early mortality, were assessed and concluded to be negligible. First, fish <8cm total length were consistently observed in the seagrass but were never recorded in censuses of adjacent rocky habitat where older juveniles occurred. Thus, settlement stage fish were assumed to reside in seagrass for several weeks. Second, average home ranges for fish of 2-2.5 cm and 3-3.5 cm total length were estimated to be 2.3 m^2 and 6.3 m^2, respectively, indicating that movement of newly settled *O. chrysurus* was negligible compared to the size of the census area (1250 m^2). Third, late pelagic stage *O. chrysurus* caught with light traps in adjacent waters were tagged with fluorescent elastomer and released at the center of the seagrass grid the evening after their capture. Ninety-six individuals were released over three evenings in September 1999. Concurrent aquarium studies showed tagging mortality was 13%. Over the following eight days, 32 re-sightings were made. Only one fish was seen more than 2-3 m distant from where it was sighted on the first census after releases were completed, providing convincing evidence of site fidelity after settlement. Using a simple model, we conservatively estimated the coefficient of mortality, M, at settlement to be about 0.28 (equivalent to 76% survival per day) and to reduce by 0.042 per day thereafter.
KEY WORDS: Caribbean, coral reefs, fisheries, elastomer, recruitment

INTRODUCTION

The numbers of maturing individuals in a marine fish or invertebrate population is the cumulative result of pre-settlement and post-settlement mortality rates, but these rates are poorly known. Losses during the planktonic and pelagic stages of coral reef fish are thought to average about 20% per day (Cowen et al 2001). Post-settlement mortality rates have been better studied (Sale and Ferrell 1988, Caley 1998) and there is an increasing appreciation of the intense and often variable effects of post-settlement predation on subsequent population size (Shulman & Ogden 1987, Hixon & Beets 1989, 1993, Caley 1993, 1995, Carr & Hixon 1995, Forrester 1995, Beets 1997, Forrester and Steele 2000). Pluralistic models of fish population dynamics may be most appropriate (Menge & Sutherland 1987; Jones 1991; Hixon & Beets 1993; Doherty & Fowler 1994; Beukers & Jones 1997; Connell 1998; Levin 1998; Caselle 1999). However, there are relatively few direct estimates of early juvenile mortality, partly because it is difficult to separate early mortality from post-settlement movement (Frederick 1997a).

It is well established that fishes and other aquatic organisms can be recruitment limited and that settlers often do not seem to saturate their environments (reviewed by Doherty & Williams 1988, Booth & Brosnan 1995, Munro & Bell, 1997). In heavily fished regions, the effects of recruitment limitation on selected commercially exploited fish may be exacerbated as a result of recruitment overfishing (whereby adult stocks are fished so hard that their reproductive output is insufficient to sustain historic population levels) whether or not high post-settlement mortality obscures any obvious relationship between abundance at settlement and adult population size (Jennings & Lock 1996 and references therein). For fish stocks that may be recruitment limited, connectivity is important in determining recovery from disturbances including fishing (Doherty & Fowler 1994). In isolated stocks that only occasionally receive larval recruits from distant sources, severe overfishing can lead to recruitment collapse. For example, Munro & Watson (1999) and Watson & Munro (in review) show that the supply of commercially important fish larvae to heavily overexploited Discovery Bay in Jamaica is severely depressed and recruitment of juvenile fish has been consistently low in recent years. Such populations may take decades to recover even if no-fishing zones (such as one recently implemented in Discovery Bay) are established. Even where spawning stock biomasses appear to be relatively large, settlement and recruitment rates remain highly variable, temporally and spatially.

Recruitment limitation introduces the possibility of enhancing populations through artificial stocking (Doherty & Fowler 1994, Munro & Bell 1997, Doherty 1999). Alternatively, where mortality is high, measures aimed at boosting early juvenile survival may also help restore populations. Artificial stocking has been severely criticized in many fisheries as uneconomic (Hilborn 1998), inappropriate (Scarnecchia 1988, Meffe 1992), difficult to evaluate (Leber et al 1996, Hilborn 1998) and potentially harmful to wild populations through introduction of disease or through genetic selection for inappropriate characteristics (Schramm & Piper 1995). But despite these criticisms, stock enhancement may be the most appropriate option where wild stocks are essentially gone (Hilborn 1998), such as in reef fisheries suffering recruitment collapse. Doherty (1994) first proposed light traps as a means to gather larval reef fish for stock enhancement. Watson et al (2001) suggested gathering available late stage larval reef fishes with light traps and subsequently rearing fish for several weeks in order to by-pass the high mortality hurdle typical of early juvenile life (Roberts 1996 and references therein). Juveniles could then be released into no-fishing areas in order to accelerate population recovery.

However, assessing the feasibility of such an approach requires a good understanding of the juvenile life history of target species. Such information is scarce for many reef fishes (McCormick & Makey 1997) and especially for commercially important species such as snappers, grunts and groupers (but see McFarland *et al.* 1985; Shulman & Ogden 1987 for grunts and Shenker *et al.* 1993; Eggleston 1995 for groupers; Nagelkerken et al 2000a,b, 2001). Indeed, the majority of recruitment and early juvenile mortality studies have concentrated on small solitary and territorial species (McCormick & Makey 1997; Booth & Wellington 1998, Caley 1998).

The yellowtail snapper, *Ocyurus chrysurus*, is one of the most important and heavily targeted reef fishery species in the Caribbean. In this study, we investigate the first month of post-settlement life in shallow seagrass nursery areas with underwater visual census techniques. We separate early juvenile mortality from movement by answering the following specific questions: 1) Are settlement stage *O. chrysurus* resident in seagrass? 2) Do early juveniles maintain a home range and, if so, how does home range vary with fish size? 3) Is such a range stable? Using a simple model to explain changes in mortality over time, we provide the first experimentally derived estimates of natural mortality at settlement for this species and thus generate a natural mortality baseline against which to compare survival in short term rearing systems, and the likely success of release programs.

METHODS

Settlement. Settlement peaks and subsequent declines in abundance of Ocyurus *chrysurus* were monitored by censuses of a 50 x 25 m grid in a shallow seagrass (*Thalassia testudinum*) bed at the eastern end of Tortola, British Virgin Islands. Three surveys were made. The first two, in September-October 1999 and April-May 2000, started around the last lunar quarter. The third survey, in June-July 2000, started at new moon. The grid was marked into 5 x 5 m squares with thin nylon cord pinned to the substrate. One observer swam concentrically around each individual square until the entire area was censused, before moving on to the next square. If it was suspected that a fish had already been counted in a different part of the square or adjacent squares, the observer looked for the previously noted fish and only counted both if they could be seen simultaneously. Censuses of the total area took 2-2.5 hours.

The total length (TL) of each fish was estimated to the nearest 0.5 cm and its position within the square was noted. A scale drawing of the grid on the observer's slate (where 5 m was represented as 2.5 cm) provided a guide for length estimation. In addition, small fish usually remained stationary long enough to gauge their size against a background feature, allowing the observer to measure that if the size was uncertain. Estimates were probably less accurate for more mobile fish above 5 cm.

It was known from previous light trapping work (Watson & Munro in review) that *Ocyurus chrysurus* settles from the pelagic phase around new moon at 1.5 - 2.5 cm (modal size 2 cm) and this was confirmed by these observations. With the exception of the June-July data set, sampling began before new moon when very few fish were on the grid, confirming that cohorts did not overlap significantly. Sampling was most extensive in September-October when we censused until 26 days after peak settlement. We chose this cut-off to avoid biases due to new influxes, although in fact negligible new settlement was observed (October appears to be the end of the recruitment season in Tortola [Munro & Watson 1999]). Actual sampling frequencies ranged from daily around the new moons to 4 days approaching the last quarter moon but there was a ten-day break between moon ages 7-17 in September 2000 for logistical reasons (Fig. 1). So few settlement stage fish were recorded around the new moon at the end of May that sampling was discontinued until the following new moon period.

Temporal patterns in abundance were assumed proportional to settlement and natural mortality plus movement (as in McGehee 1995). The distribution of settlers at peak abundance for each of the three lunar cycles sampled was examined for random, clumped or uniform patterns using the Chi Squared test. Catches of *O. chrysurus* from light traps set in deeper water as part of a separate study during the 4-5 days preceding each new moon were examined for concurrent peaks in the supply of pre-settlement postlarvae.

Movement. Our assumption was that likely movements of newly settled *Ocyurus chrysurus* were negligible compared to the overall size of our sample area (1250 m^2) and that immigration across the boundaries equaled emigration. We tested this assumption with various techniques.

1) To assess whether settlement stage *O. chrysurus* were resident in the seagrass, length frequencies from the grid censuses were compared with concurrent visual censuses of an adjacent rocky habitat where older juveniles shoaled during the day.

2) To investigate the home range of early juvenile *O. chrysurus* in each of size classes 2-2.5, 3-3.5, 4-4.5 and 5-5.5 cm, individuals on the grid (n = 11, 7, 4 and 4 in each size class respectively) were monitored for 30 min each and their positions marked every minute by dropping a coloured coin. The coins were then mapped using the grid squares for reference and home range was estimated by the convex polygon method (Odum & Kuenzler 1955). This study was undertaken in September 1999. However, although daytime home range could be estimated, the study did not demonstrate whether individuals showed any site fidelity or whether they adopted a new but circumscribed home range erratically.

3) Therefore a third set of observations was made. In September 1999, pre-settlement *O. chrysurus* caught in light traps were tagged with fluorescent orange elastomer, injected behind the dorsal fin, following the methods described in Frederick (1997b). On the 6th, 7th and 8th of September, a total of 96 fish, approximately 2 cm TL, were put in a small mesh cage at the center of the grid at dusk on the night following capture in light traps. The fish initially schooled together in the water column. The cage was weighted so that one side regularly lifted off the ground in the current. Thus, as fish moved from the water column to the benthic habitat they could escape. The cage was removed the following morning, by which time any remaining fish had orientated to the substrate and they quickly dispersed when their cover was removed. The positions of elastomer tagged fish were recorded on subsequent censuses and compared between dates to determine whether settled fish were repeatedly seen at the same location. Forty-seven tagged fish were kept in aquaria for 48 hours to study tagging effects. Mortality was 13% over the first 24 hours and negligible in the subsequent 24 hours. This is very similar to Frederick's (1997b) study.

4) In a fourth set of observations 23 elastomer-tagged *Ocyurus chrysurus* were similarly released inside a 16 m^2 area, enclosed by a 45 cm high fence of 5 mm mesh, at the center of the experimental grid. The fence extended well above the seagrass, thus fish would have to re-enter the water column to cross it. The positions of elastomer-tagged fish either inside or outside the fence were recorded on 12 subsequent censuses up to 23 days later.

Mortality. Once we had separated any effects of movement from the census estimates (see results and discussion), abundance was considered proportional to survival, allowing us to calculate the proportion of fish surviving the first 3-4 weeks after settlement. Settlement was highly pulsed in the five nights preceding and including the new moon, when the numbers of fish in the 1.5 – 2 cm size classes peaked. Thereafter, no fish in the 1.5 cm size class were seen and very few fishes in the 2 cm size class were observed. Some large (>2 cm) new recruits probably arrived in the days after the numbers of fish in the study area had peaked and mortality rate calculations based on the apparent decline in abundance of a cohort will therefore tend to underestimate the actual mortality rate to some degree.

Extremely high rates of mortality of coral reef fish have been reported in the days following settlement from the plankton (Shulman & Ogden 1987; Sale & Ferrell 1988, Roberts 1996 and references therein, Planes & Lecaillon 1998, Caselle 1999) and the steady natural mortality rate, M, that is conventionally used to describe the death rates of adult fish is clearly inapplicable to early post-settlement fish. We postulated that mortality rates could be expected to decrease from a high initial value as post-settlement juvenile fish become adapted to their new environment and the survivors become more skilled in avoiding predators. If this is true and there is no abrupt ontogenetic change in mortality rates, the cumulative number of deaths would increase asymptotically until the entire cohort is dead, and the final mortality rate would be that of large, old, healthy fish. If there were an abrupt change in mortality rates, for example, with the change from juvenile to adult habitat, then a series of asymptotic curves would be expected.

Thus, if the cumulative number of deaths increases asymptotically over time,

$$D_t = N_r\,(1- e^{-(M+m.t)})$$

in which D_t is the cumulative number of deaths to time t, N_r is the initial number of fish in a single cohort that settles at t = 0, m is the amount by which the initial mortality rate, M, decreases each day. $D_t = N_r$ at t_{∞} when the last survivor dies.

This equation can be rearranged as

$$\log_e (1-D_t/N_r) = - M - m.t$$

or, because the fraction surviving to time t is $(1 - D_t/N_r) = S_t$,

$$\log_e S = - M - m.t \qquad \text{or} \qquad -(\log_e S) = M + m.t$$

Thus, if the natural logarithm of the fraction of N_r remaining after successive time intervals is plotted against the time intervals, t, the result should be a straight line with a slope equal to m and which intersects the y-axis at a value equal to M, the mortality rate at the time of settlement.

RESULTS

Settlement. In September 1999 a very marked peak in settlement was noted at new moon, with abundances of 1.5-3.5 cm *Ocyurus chrysurus* on the experimental grid going from five to 92 in nine days preceding new moon. A rapid decline followed (Fig. 1). In April-May and June-July 2000 peak abundance was much lower at 28 and 25 individuals, respectively. Note that in June-July the peak was either at or slightly before the new moon but no observations were possible during that period and our first census gave the peak abundance for this month. Thus actual peak abundance may have been underestimated. In all of the three lunar cycles, the distribution of new settlers at peak abundance appeared clumped and, in two, the distribution was significantly different from random. In September-October 1999, mean abundance at peak settlement was 1.84 fish per 25 m^2 sampling square (variance = 4.54, Chi squared goodness of fit $p < 0.01$). In April-May the mean was 0.56 per square (variance 0.78, p = 0.6) and in June-July the mean was 0.50 (variance = 0.43, p = 0.04).

Movement. As a general case, *Ocyurus chrysurus* of greater than 7.5 cm TL were not in the seagrass by day and were found in the adjacent rocky habitat. Fish of 2-2.5 cm TL hung in the water column amidst blades of seagrass and picked at passing plankton while fish from about 3.5 cm TL foraged for benthic invertebrates (pers. obs). We observed that 2-3 cm fish generally tolerated conspecifics of the same size, but fish >= 3.5 cm were aggressive to similarly sized fish and wary of larger individuals.

Fish less than 7.5 cm were always seen in the seagrass and never on the reef. Thus early juveniles were considered to be resident in the seagrass. Indeed, movement studies of individuals confirmed that even fish up to 5.5 cm TL had fairly restricted home ranges (Fig. 2) and recently settled fish <= 3.5 cm TL had mean home ranges of only 6.3 m^2, nearly 200 times less than the overall area regularly censused. We therefore considered the number of home ranges on the edge of the grid, where fish would be sometimes in and sometimes out of the census, likely to be insignificant compared to the overall number of fish with ranges completely within the grid.

To check if fish demonstrated site fidelity in their home ranges, we examined the distribution of re-sightings of elastomer tagged fish. Fig. 3 shows the positions of 32 re-sightings between 9 and 17 September. Of the 96 fish released on 6-8 September, only eight fish (the maximum seen on one day) were seen on the 9th. All but one of the subsequent re-sightings were within a few metres of a sighting on the 9th, suggesting that although on release many fish may have dispersed to areas outside the grid before settling (the grid extended only 12.5 m from the release spot in two directions), and not all tagged fish would have been spotted each census, home ranges remained in the same location.

Of the 23 elastomer-tagged fish released inside a 45 cm high fence in April-May, only 3 remained after two days. None were seen outside the fence on day 2 or on the twelve subsequent censuses, despite careful searching. One tagged fish remained inside the fence 23 days later. The tagged fish therefore either swam over the fence and moved out of the survey area or they were consumed by predators that entered the 16 m^2 enclosure.

Mortality. Since movement of recently settled *Ocyurus chrysurus* was found to be negligible in the first few weeks of life, abundances were assumed directly proportional to survival. We attempted to fit simple exponential and power curves to the data from all three lunar cycles (Fig. 1), but neither type provided a good fit when forced to go through the initial abundances observed.

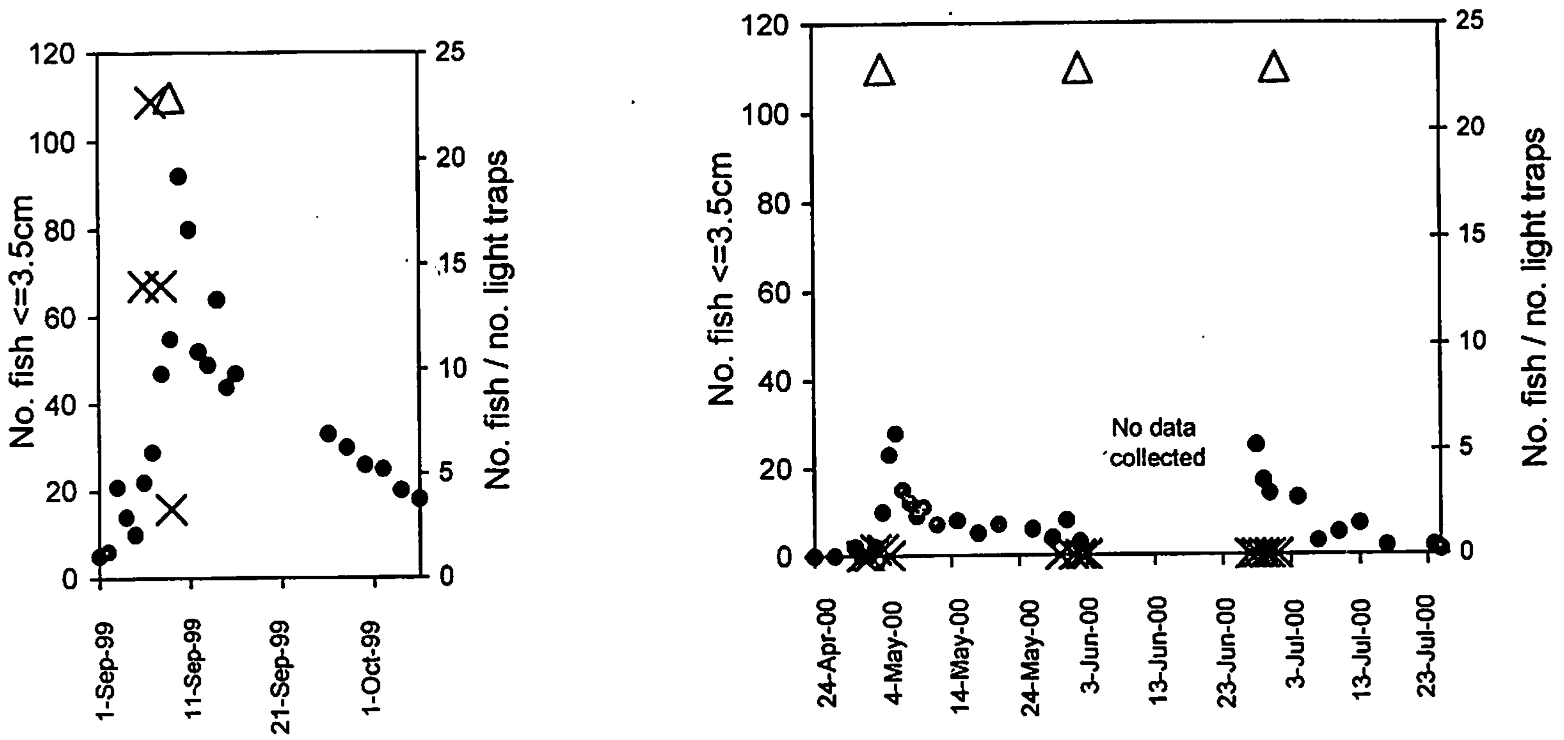


Fig. 1. Number of early juvenile *Ocyurus chrysurus* (solid dots, scale on the primary axis) observed within 1250 m^2 of shallow seagrass, and average catch of late pelagic stage *O. chrysurus* larvae taken in light traps at a neighbouring study site (crosses and scale on secondary axis), all plotted against date. Triangles represent new moon.

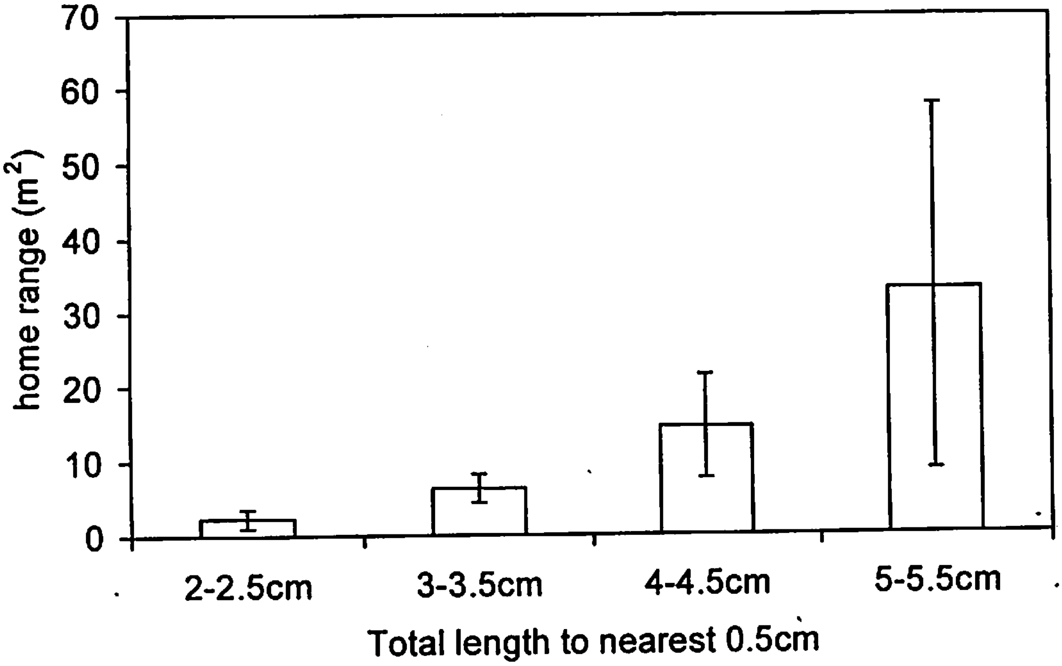


Fig. 2. Mean home range size for *O. chrysurus* total length 2-2.5cm, 3-3.5cm, 4-4.5cm and 5-5.5cm (n = 11, 7, 4 and 4 respectively). Error bars represent standard deviation.

Using the equation described in the preceding section, we plotted the natural logarithms of survival against time since peak settlement for each of the observed cohorts (Fig. 4). The data for the September-October cohort gives a good fit ($r^2 = 0.905$) and we derived estimates of m = -0.0423 and M = -0.2783. If the mortality coefficient M decreases at a constant rate as suggested by the straight-line relationship when log survival is plotted against time, the value of M derived from the intercept of this graph is an estimate of mortality at the moment of settlement. For the September cohort, the instantaneous daily mortality rate, M, at settlement is therefore -0.2783, equivalent to a fractional survival of 76% per day. The equation also predicts that survival to 7 days and 30 days would be about 56% and 21%, respectively. These estimates of the mortality rates are somewhat conservative because, as explained previously, a few additional settlers might have arrived in the study area in the period after new moon. These estimates of survival therefore represent maximum values.

Owing to the small numbers of fish that settled in April and June, the estimates are less reliable ($r^2 = 0.668$ and 0.691 respectively). For the April-May cohort, m = -0.0505 and M = -0.8026. Thus only 42% survived the first day after settlement and survival to 30 days would be about 10%. For the June cohort, m = -0.1023 and M = -0.2688. Post-settlement survival would be 69% after the first day and about 4% to 30 days.

The validity of these first estimates can be checked by using them to construct a matrix which estimates the fraction of the numbers of fish observed each day that would survive to successive days, starting seven days before new moon and ending seven days after new moon (the period for which continuous daily observations were made for the September-October cohort). From this, the number of fish actually settling each day can be calculated. These calculations suggest that about 240 fish settled into the study area over a 15-day period, of which only 23 (<10%) survived to 26 days after the new moon. This suggests that the mortality rates calculated from the data are conservative. However, the data are too variable to refine the estimates iteratively.

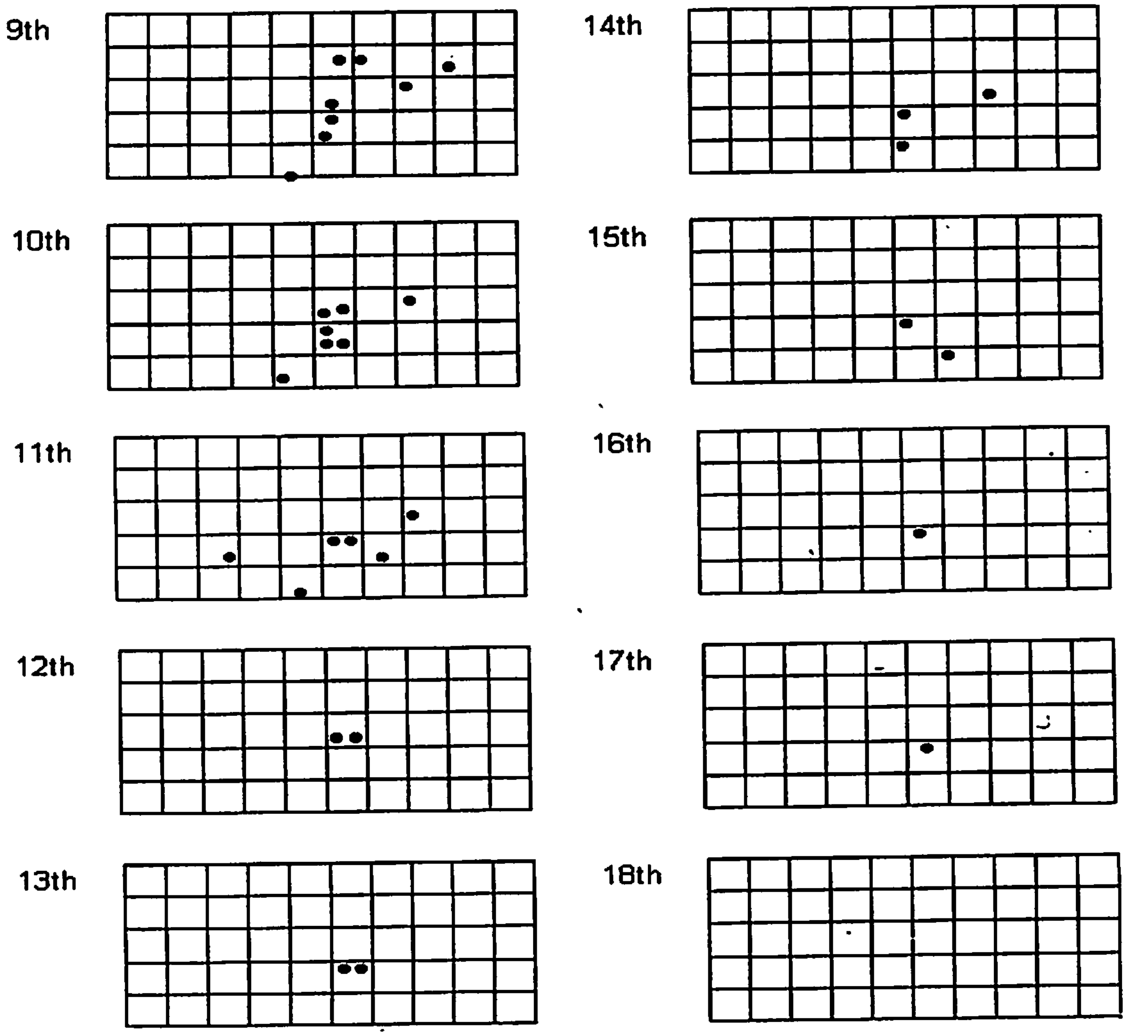


Figure 3. Schematic diagrams of a 50 m x 25 m grid in a seagrass bed where 96 elastomer-tagged, recently settled, *Ocyurus chrysurus* were released between the nights of 6 and 8 September 1999. Dots represent 32 resightings of tagged fish on subsequent censuses between 9 and 18 September 1999

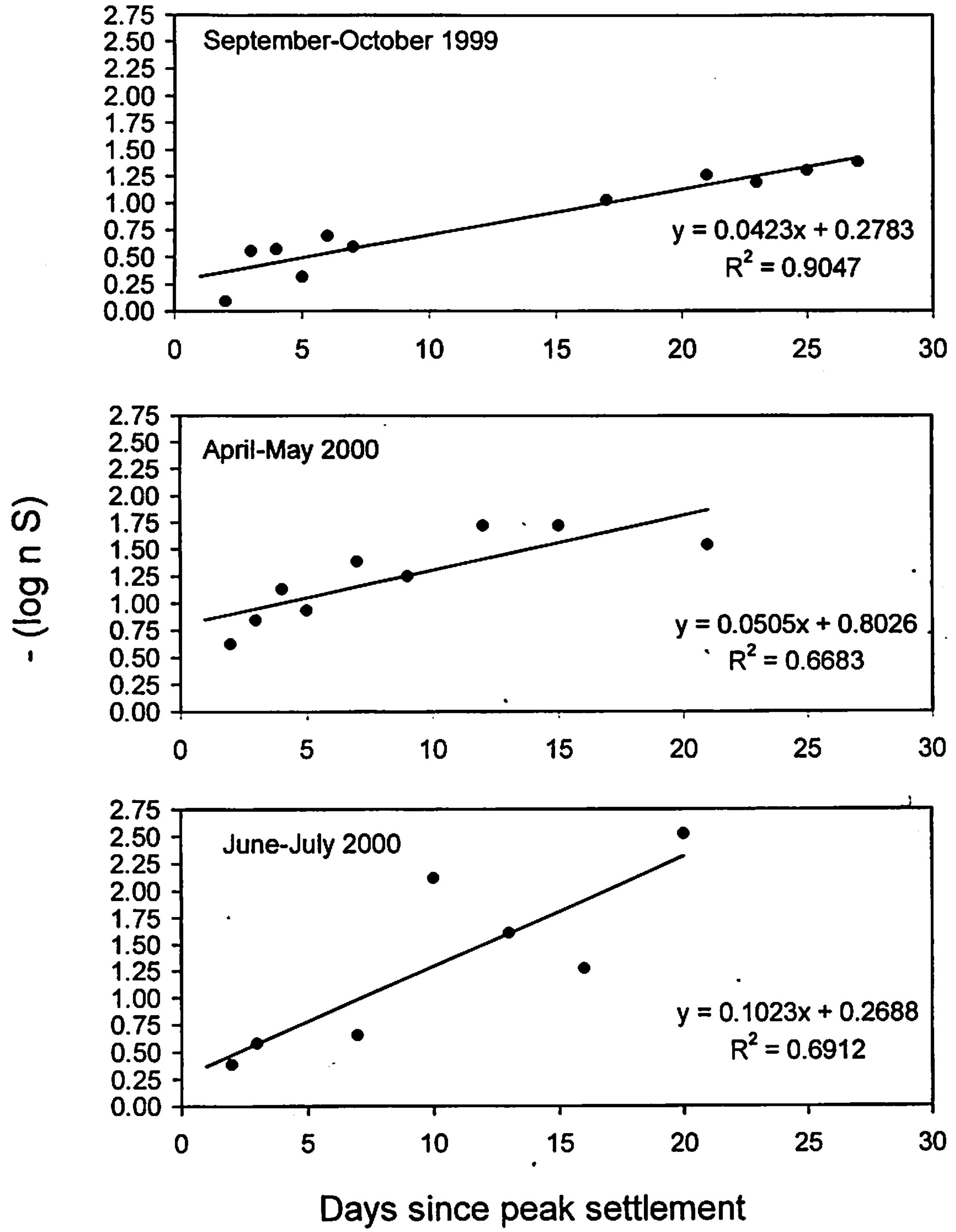


Fig. 4. Regressions of the natural logarithm of the survival rate to time t plotted against days since peak settlement. Slope is the daily amount, m, by which natural mortality decreases with increasing age and the y-axis intercept equals the natural mortality rate, M, at settlement

The tagging data also yield information on mortality rates. Allowing for 13% mortality induced by tagging and handling, the two experiments suggest 10-15% survival after two days, followed by a lower rate of attrition. This is a lower post-settlement survival than is indicated by the preceding analysis. However, the small numbers of fish involved preclude more detailed analyses. These were fish that were in the pre-settlement stage when caught and it is possible that they mostly dispersed in the water column when released.

DISCUSSION

Ocyurus chrysurus appeared to undergo a two-phase recruitment process (sensu Finn & Kingsford 1996) whereby early juvenile fish subject to high post settlement mortality are relatively sedentary in seagrass for several weeks, before moving to more rugose habitat as older juveniles. Ogden & Zieman (1977) considered *O. chrysurus* juveniles to be resident in seagrasses, and other researchers have found similar two-step patterns for various species and habitats (Baelde 1990, Eggleston 1995, Green 1996, McCormick & Makey 1997 and references therein, Nagelkerken et al 2000a,b, 2001). Nagelkerken (2000b) found that *O. chrysurus* uses seagrass exclusively up to 2.5 cm TL and thereafter moves progressively into mangroves and other habitats and suggested that they are obligate dependents on seagrasses and mangroves. This cannot be true in all situations, because they are found on oceanic banks with least depths of 30-40 m (Thompson & Munro, 1983) and modest numbers must be able to survive in relatively deep coralline habitats.

Bertenshaw (2001) also found that newly settled *O. chrysurus* settled preferentially into seagrass beds, but also stands of *Halimeda*, sand holes and coral rubble. Thus, settlement preferences may vary spatially and or temporally within species, perhaps as a function of settlement intensity (Booth & Wellington 1998). Further, there are both limitations and advantages to our methods of estimating settlement, movement and survival that should be considered.

Settlement. Visual censuses are unlikely to have recorded all settlement stage fish. Some will always be missed, and numbers observed may depend on a variety of factors. For example the sharp dip in abundance on the 12 and 13 October coincided with the close passage of a tropical storm, and decreased visibility. The apparent slight increases in abundance after about two weeks in the April-May and June-July data sets might be caused by a small influx of fish half way through the cycle but more likely are a chance variation in the small numbers observed.

It is possible that a few fish grew out of our size range, artificially inflating mortality estimates. However, from observing a rapid rather than a gradual transition of most fish between the 0.5 cm size classes, we consider this effect to be small. Further, it is likely to have been outweighed by a bias operating in the other direction. As numbers drop and an observer becomes more familiar with fish distribution it becomes easier to spot fish that one expects to see than to spot randomly re-distributed individuals. Thus, abundance in the middle of the surveys may be overestimated relative to the initial abundance at peak settlement.

Movement. Our observations of early juvenile movement are restricted to the period immediately after settlement to the benthic habitat and do not extend into the period when juvenile snappers and grunts typically start to undergo diurnal migrations (Ogden & Ehrlich 1977; Ogden & Zieman 1977; Weinstein & Heck 1979; Helfman et al 1982). Once settled, *Ocyurus chrysurus* appeared to establish consistent home ranges and did not move far. Fish did not appear to re-enter the water column once settled, although we cannot rule this out for fish that settle to other, perhaps less suitable, habitats.

Of the 92 elastomer-tagged fish released on the experimental grid over 6-8 September, only 32 were re-sighted and most of these are thought to have been multiple re-sightings of the eight fish (the maximum recorded) seen the day after the final release. If movement was so limited, what happened to the other fish? Tag related mortality (13%) would have accounted for some losses. In addition, marked fish may have suffered increased predation due to their increased visibility. Notably, the biggest batch of fish (released on 6 September was at large for two days before counts were started. Since mortality is highest immediately after settlement, these fish could have been disproportionately affected. Further, a significant proportion of fish presumably dispersed off the grid before choosing a settlement microhabitat, as the nearest two edges were only 12.5 m distant from the release point and at least one of the repeatedly re-sighted fish was seen at the edge of the grid. As mentioned previously, these were late pre-settlement fish that had not voluntarily settled and it is possible that a substantial proportion returned to the water column, dispersed and settled elsewhere.

There is little information on movement of early juvenile snappers for comparison with our results. Mori (1984) studied the early life history of *Lutjanus vitta* in the Sea of Japan and Frederick (1997a) studied transplanted *Lutjanus kasmira* on an array of isolated artificial reefs in Hawaii, and noted a strong tendency to move straight after release. Early juveniles clearly had the ability to move at least 100 m. However, fish were collected from outlying artificial habitats several days after settlement, and transplanted to the center of the array. Direction of movement was significantly correlated with the direction of home reefs and movement (and also survival) was strongly related to fish size. In addition, Frederick notes that *L. kasmira* schooled freely over arrays of artificial habitats of 2 and 5 m radius. Thus the behaviour of this fish appears quite different from *Ocyurus chrysurus*.

Since movement in our study was minimal, we feel confident in assuming decreases in observed abundance reflect mortality.

Mortality. Other researchers have used similar visual techniques to estimate mortality (e.g. Sale & Ferrell 1988, Booth 1991, Booth & Berretta 1994; McGehee 1995) and our study has advantages recognized by several authors, for example, frequent censuses (Booth 1991, Caley et al 1996, Levin 1998), at least one large cohort (Sale & Ferrell 1988), a relatively large census area to take account of varying predation between microhabitats (e.g. Beukers & Jones 1997, Nemeth 1998), and a lack of tagging artifacts (Bergman et al 1992) since tagged fish were not used for mortality estimates (see below). Additionally, most previous studies have used artificial or manipulated habitats (Shulman et al 1983, Risk 1998, Frederick 1997a, Finn & Kingsford 1996, Beets 1997, Connell 1997, but see Caselle 1999) that may not always accurately represent natural environments (Connell 1997).

Our study concurs with a growing body of research that emphasizes the importance of post settlement mortality in structuring populations (Shulman & Ogden 1987; Warner & Hughes 1988; Jones 1991; Connell & Gillanders 1997; Connell 1998; Caselle 1999). Our strongest data set is for September-October 1999, where mortality for recently settled *O. chrysurus* was estimated at 79% over 30 days. Data from April-May and June-July 2000 show a similar pattern in the plot of log survival against time (Fig. 4). However, the initially low abundance at peak settlement magnifies the effects of variation in counts when converted into proportions or percentages, reducing confidence in the slope of the fitted line. Mortality estimates from such small samples sizes may be seriously flawed (Caley 1998). Thus we have insufficient data for a full analysis of the effects of settlement density on survival. Nonetheless, in the simplest sense it is noteworthy that actual numbers surviving were higher in September when supply was approximately three times greater than in April-May and June-July, (peak abundances 92, 28 and 25 respectively), suggesting mortality may show density independence or under-compensating density dependence. Use of different habitats by early juvenile and older juvenile fish (here seagrass and high relief structures such as reefs and mangroves respectively) lowers the likelihood of density dependent feedback on early juvenile survival (Schmitt & Holbrook 1996).

Implications for recovery interventions in severely overexploited stocks. Post-settlement mortality is generally recognized as high for coral reef fish (Roberts 1996 and references therein). Actual mortality values can vary greatly between species and even sites. For example Sale & Ferrell (1988) estimated survivorship during the first week after recruitment for 17 coral reef species was as high as 90% or as low as 50%, and Beukers & Jones 1997 found juvenile mortality of the damselfish *Pomacentrus moluccensis* over the first year of life varied between 20 and 100% among sites. Caselle (1999) found very variable mortality of *Thalassoma bifasciatum* at eight sites around St. Croix, USVI. She found evidence for density dependent mortality during the first few days of benthic life above a threshold settlement density. After that, mortality was density independent. Shulman & Ogden (1987) estimated that post settlement mortality for Caribbean grunts is 90% within a month and concluded that, whether or not mortality is density dependent, factors controlling benthic mortality are more important in determining population dynamics than variations in settlement. Further, the mortality rates during the settlement process, i.e. while the fish are in the water over settlement habitat but before they actually switch to the benthic environment are presently unquantified but are probably extremely high (Kaufman et al 1992).

However, where density dependant effects are weak, both larval supply and early juvenile mortality will be important in controlling adult populations (Connell 1998). Thus, to effectively enhance severely depleted populations, a combined approach that increases supply of settlers and decreases early mortality may be most effective. Doherty (1994) suggested settlement stage reef fish caught with light traps could be used to supplement natural populations. Watson et al (2001) proposed a relatively simple rearing system to raise such fish beyond their early juvenile 'mortality hurdle' for subsequent release into 'no-fishing' marine protected areas. Preliminary tests of this system found mortality of snappers stabilized at approximately 20% after two weeks (Power unpub. data). This can be compared with the estimate of at least 60% loss in two weeks observed in the present study. Note that for increased survival to aid stock recovery, overall survival must be improved for all life history stages from release through to maturity (Heppell & Crowder 1998). This has not yet been demonstrated for such an approach. Importantly, if overfishing originally caused a stock collapse, any intervention must be in concert with reduction of effort, and habitat protection (e.g. through marine protected areas). It is essential that lawmakers and the public don't see enhancement as an alternative to improved stewardship (Scarnecchia 1988, Meffe 1992).

Nonetheless, even where fish mortality remains high and the per capita costs of interventions appear substantial, the value of enhancement should be considered in terms of survivor reproductive potential rather than a direct contribution to stock numbers (Stoner & Glazer 1998). Further, for new management regimes to gain long-term acceptance amongst communities depending on reefs, positive results need to be demonstrable within a few years. For recruitment overfished reef ecosystems without a reliable and productive upstream source of fish larvae, interventions to accelerate recovery may be the only alternative to waiting for decades for the meagre remnant local stocks to build up to the point where they can provide natural replenishment.

Acknowledgements. Funding for this study was provided by the United Kingdom's Department for International Development. R. Power, J. Lawn, S. Fredericke, S. Simpson, G. Hassidis and staff from the BVI Conservation and Fisheries Department assisted with light trapping.

LITERATURE CITED

Baelde P (1990) Differences in the structure of fish assemblages in *Thalassia testudinum* beds in Guadeloupe, French West Indies, and their ecological significance. Mar Biol 105:163-173

Beets J (1997) Effects of a predatory fish on the recruitment and abundance of Caribbean coral reef fishes. Mar Ecol Prog Ser 148:11-21

Bergman PK, Haw F, Blankenship HL, Buckley RM (1992) Perspectives on the design, use and misuse of fish tags. Fisheries 17:20-25

Bertenshaw VJ (2001) Settlement bahaviour and survivorship of *Ocyurus chrysurus* (yellowtail snapper) and other juvenile reef fish species of the British Virgin Islands. M.Sc. thesis, University of Plymouth

Beukers JS, Jones GP (1997) Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia 114:50-59

Booth DJ (1991) The effects of sampling frequency on estimates of recruitment of the domino damselfish *Dascyllus albisella*. J Exp Mar Biol Ecol 145:149-159

Booth DJ, Brosnan DM (1995) The role of recruitment dynamics in rocky shore and coral reef fish communities. Adv Ecol Res 26:309-385

Booth DJ, Wellington G (1998) Settlement preferences in coral-reef fishes: effects on patterns of adult and juvenile distributions, individual fitness and population structure. Aus J Ecol 23:274-279

Caley JM (1995) Reef-fish community structure and dynamics: an interaction between local and larger-scale processes? Mar Ecol Prog Ser 129:19-29

Caley MJ (1993) Predation, recruitment and the dynamics of communities of coral-reef fishes. Mar Biol 117:33-43

Caley MJ (1998) Age-specific mortality rates in reef fishes: evidence and implications. Aus J Ecol 23:241-245

Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. Ann Rev Ecol Syst 27:477-500

Carr MH, Hixon MA (1995) Predation effects on early post-settlement survivorship of coral-reef fishes. Mar Ecol Prog Ser 124:31-42

Caselle JE (1999) Early post-settlement mortality in a coral reef fish and its effect on local population size. Ecol Monogr 69:177-194

Connell SD (1997) The relationship between large predatory fish and recruitment and mortality of juvenile coral reef-fish on artificial reefs. J Exp Mar Biol Ecol 209:261-278

Connell SD (1998) Effects of predators on growth, mortality and abundance of a juvenile reef-fish: evidence from manipulations of predator and prey abundance. Mar Ecol Prog Ser 169:251-261

Cowen RK., Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000). Connectivity of marine populations: open or closed? Science 287:857-859

Doherty PJ (1994) A potential role for light-traps in enhancement of coral reef fisheries. In: Munro JL & Munro PE (eds) The management of coral reef resource systems. ICLARM Conference Proceedings 44, Manila. p 92-93

Doherty PJ (1999) Recruitment limitation as the theoretical basis for stock enhancement. In: Howell BR, Moksness E,Svasand T (eds) Stock enhancement and sea ranching. Blackwell Science, Oxford p. 9-21

Doherty P, Fowler T (1994) An empirical test of recruitment limitation in a coral reef fish. Science 263:935-939

Doherty PJ, Williams DM (1988) The replenishment of coral reef fish populations. Oceanogr. Mar. Biol. Annu. Rev. 26:487-551

Eggleston DB (1995) Recruitment in Nassau grouper, *Epinephelus striatus*: post settlement abundance, microhabitat features, and ontogenetic habitat shifts. Mar Ecol Prog Ser 124:9-22

Finn MD, Kingsford MJ (1996) Two-phase recruitment of apogonids (Pisces) on the Great Barrier Reef. Mar Freshwat Res 47:423-432

Forrester G (1995) Strong density-dependant survival and recruitment regulate the abundance of a coral reef fish. Oecologia 103:275-282

Forrester G, Steele M (2000) Variation in the presence and cause of density dependent mortality in three species of reef fishes. Ecology 81:2416-2427

Frederick JL (1997a) Post-settlement movement of coral reef fishes and bias in survival estimates. Mar Ecol Prog Ser 150:65-74

Frederick JL (1997b) Evaluation of fluorescent elastomer injection as a method for marking small fish. Bull Mar Sci 61:399-408

Green AL (1996) Spatial, temporal and ontogenetic patterns of habitat use by coral reef fishes (family Labridae). Mar Ecol Prog Ser 133:1-11

Helfman G, Meyer J, McFarland WN (1982) The ontogeny of twilight migration patterns in grunts (Pisces Haemulidae): Anim Behav 30:317-326

Heppell SS, Crowder LB (1998) Prognostic evaluation of enhancement programs using population models and life history analysis. Bull Mar Sci 62:495-507

Hilborn, R (1998) The economic performance of marine stock enhancement projects. Bull Mar Sci 62:661-674

Hixon MA, Beets JP (1989) Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. Bull Mar Sci 44:666-680

Hixon MA, Beets JP (1993) Predation, prey-refuges, and the structure of coral-reef fish assemblages. Ecol Monogr 63:77-101

Jennings S, Lock JM (1996) Population and ecosystem effects of reef fishing. In: Polunin NVC, Roberts CM (eds) Management of reef fisheries Chapman and Hall, London. p 193-218

Jones GP (1991) Postrecruitment processes in the ecology of coral reef fish populations: a multifactoral perspective. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego. p 294-330

Kaufman, L., J. Ebersole, et al. (1992). A key phase in the recruitment dynamics of coral reef fishes: post settlement transition. Env Biol Fish 34(2):109-118

Leber KM, Arce SM, Sterritt DA, Brennan NP (1996) Marine stock-enhancement potential in nursery habitats of striped mullet, *Mugil cephalus* in Hawaii. Fish Bull US 94:452-471

Levin PS (1998) The significance of variable and density-independant post-recruitment mortality in local populations of reef fishes. Aus J Ecol 23:246-251

McCormick MI, Makey LJ (1997) Post-settlement transition in coral reef fishes: overlooked complexity in niche shifts. Mar Ecol Prog Ser 153:247-257

McFarland WN, Brothers EB, Ogden JC, Shulman MJ, Bermingham EL, Kotchian-Prentiss NM (1985) Recruitment patterns in young French grunts, *Haemulon flavolineatum* (Family Haemulidae) at St. Croix, U.S.V.I. Fish Bull US 83:413-426

McGehee, M.A. (1995) Juvenile settlement, survivorship and in situ growth rates of four species of Caribbean damselfish in the genus *Stegastes*. Env Biol Fish 44:393-401

Meffe GK (1992) Techno-arrogance and halfway technologies: salmon hatcheries on the Pacific coast of North America. Cons Biol 6:350-354

Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition and predation in relation to environmental stress and recruitment. Am Nat 130:730-757

Mori (1984) Early lifre history of *Lutjanus vitta* (Lutjanidae) in Yuya Bay, the Sea of Japan. Jpn J Ichthyol 30:347-392

Munro JL, Bell JD (1997) Enhancement of marine fisheries resources. Rev Fish Sci 5:185-222

Munro JL, Watson M (1999) Caribbean Marine Protected Areas Project: The role of marine protected areas in fisheries management and biodiversity conservation in coral reef ecosystems. ICLARM Caribbean Marine Protected Areas Project Technical Report

Nagelkerken, I, Dorenbosch M, Verbeck WCEP, Cocheret de la Morinière E, van der Velde G. (2000a) Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. Mar. Ecol Prog. Ser 202: 175-192

Nagelkerken I, van der Velde G, Gorissen MW, Meijer GJ, van't Hof T, den Hartog C (2000b) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuar Coast Shelf Sci 51:31-44

Nagelkerken I, Kleijnen S; Klop T; van den Brand RACJ, Cocheret de la Morinière E, van der Velde G (2001) Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. Mar Ecol Prog Ser 214:225-235

Nemeth RS (1998) The effect of natural variation in substrate architecture on the survival of juvenile bicolor damselfish. Env Biol Fish 53:129-141

Odum EP, Kuenzler EJ (1955) Measurement of territory and home range size in birds. Auk 72:128-137

Ogden JC, Ehrlich PR (1977) The behaviour of heterotypic resting schools of juvenile grunts (Pomadasyidae). Mar Biol:273-280

Ogden JC, Zieman JC (1977) Ecological aspects of coral reef - seagrass bed contacts in the Caribbean. Proc 3rd Int Coral Reef Symp:377-382

Planes S, Lecaillon G (1998) Evidence of high predation in new fish recruits within the first night: a caging experiment. pp. 144, International Society for Reef Studies 1998 European Meeting, Perpignan, France.

Risk A (1997) Effects of habitat on the settlement and post-settlement success of the ocean surgeonfish *Acanthurus bahianus*. Mar Ecol Prog Ser 161:51-59

Risk A (1998) The effects of interactions with reef residents on the settlement and subsequent persistence of ocean surgeonfish, *Acanthurus bahianus*. Env Biol Fish 51:377-389

Roberts CM (1996) Settlement and beyond: population regulation and community structure of reef fishes. In: Polunin NVC,Roberts CM (eds.) Reef fisheries. Chapman & Hall, London. p. 85-112

Sale PF, Ferrel DJ (1988) Early survivorship of juvenile coral reef fishes. Coral Reefs 7:117-124

Scamecchia DL (1988) Salmon management and the search for values. Can J Fish Aquat Sci 45:2042-2050

Schmitt RJ, Holbrook SJ (1996) Local-scale patterns of larval settlement in a planktivorous damselfish - do they predict recruitment? Mar Freshwat Res 47:449-463

Schramm, HLJ, Piper RG (1995) Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society Symposium 15:608

Shenker JM, Maddox ED, Wishinski E, Pearl A, Thorrold SR, Smith N (1993) Onshore transport of settlement stage Nassau grouper, *Epinephelus striatus*, and other fishes in Exuma Sound, Bahamas. Mar Ecol Prog Ser 98:31-43

Shulman MJ, Ogden JC (1987) What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. Mar Ecol Prog Ser 39:233-242

Shulman MJ, Ogden JC, Ebersole JP, McFarland WN, Miller SL, Wolf NG (1983) Priority effects in the recruitment of juvenile coral reef fishes. Ecology 64:1508-1513

Stoner AW, Glazer RA (1998) Variation in natural mortality: implications for Queen conch stock enhancement. Bull Mar Sci 62:427-442

Warner RR, Hughes TP (1988) The population dynamics of reef fishes. Proc. 6th Int Coral Reef Symp 1:146-155

Watson M, Munro JL (in review) Settlement and recruitment of coral reef fishes in moderately exploited and overexploited Caribbean ecosystems: implications for marine protected.areas. Bull Mar Sci

Watson M, Power R, Munro JL (2001) Use of light-attracted zooplankton for rearing post-settlement coral reef fish. Proc Gulf Caribb Fish Inst 52:340-351

Weinstein MP, Heck KL Jr. (1979) Ichthyofauna of seagrass meadows along the Caribbean coast of Panama and the Gulf of Mexico: composition, structure and community ecology. Mar Biol 50:97-107

Proc. Gulf Caribb. Fish. Inst. 51: 557-568. (2000)

Outmigration and movement of tagged coral reef fish in a marine fishery reserve in Jamaica.

JOHN L. MUNRO
International Center for Living Aquatic Resources Management (ICLARM)
Caribbean/Eastern Pacific Office, c/o P.O. Box 3323, Road Town, Tortola
British Virgin Islands

ABSTRACT

Between December, 1996 and May, 1998, a total of 6 947 coral reef fish were marked and released within the Discovery Bay Fishery Reserve, on the north coast of Jamaica. Nearly 6 000 recaptures have been obtained (including multiple recaptures of the same individuals). Most recaptured fish were caught in the project's traps, fishing within the fishery reserve, and re-released. Additionally, several hundred fish have been returned by fishers operating in adjacent areas.

The Discovery Bay Fishery Reserve is comprised of 27.5 ha of backreef and seagrass beds with few patches of live coral and is mostly less than 2 m deep. It serves principally as a nursery habitat for coral reef fish. However, the mark-and-recapture program has shown that some species remain resident in the reserve for extended periods, and biomasses of these species appear to have increased substantially. Other species move out of the reserve with increasing size and two species of parrot fish have moved substantial distances (tens of km) along the narrow northern shelf of Jamaica.

It is concluded that for most species the fishery reserve serves to delay the age and size at recruitment to the trap and spear fisheries and is therefore enhancing catches in the fisheries in adjacent waters. Species which take up residence in the reserve have the potential to supplement the heavily depleted spawning stock biomasses.

KEY WORDS: catch rates, mark and recapture, recruitment,

INTRODUCTION

The coral reef fish resources of Jamaica have been heavily exploited for many years, particularly on the narrow northern shelf, where high population densities and limited employment opportunities make fishing an occupation of last resort for numerous people. The principal method of capture is by the use of wire-mesh Antillean fish traps (Munro, 1983) but spear fishing has become increasingly important, particularly as it offers opportunities for income for young men with minimal capital. The fishing intensity in all areas is extremely high. The small mesh of the traps ensures that almost all species become catchable captured well before maturity and that the larger species have negligible chance of survival to maturity (Munro 1983).

Catch rates have declined in recent years and the value of the catch has fallen markedly as the abundances of more valuable species such as groupers, snappers and large grunts have been reduced to negligible levels. In some cases these fish have virtually disappeared. Large species of parrotfish (Scaridae), triggerfish (Balistidae), angelfish (Pomacanthidae) are very rarely seen. Trap catches are dominated by small species of parrotfish and surgeonfish (Acanthuridae). Moray eels (Muraenidae) are the major piscivores and squirrelfish (Holocentridae), grunts (Haemulidae), goatfish (Mullidae), the small jack, *Caranx ruber*, and the snapper, *Lutjanus apodus*, comprise the other predatory species.

The coral reefs of Jamaica have been seriously overgrown by algae and coral cover reduced to a few percent in most areas. This has been attributed to the die-off of the sea urchin, *Diadema antillarum*, combined with the reduced abundance of herbivorous fish as a result of overexploitation (Hughes 1994).

The University of the West Indies has operated a Fisheries Improvement Project, based at their Discovery Bay Marine Laboratory, since 1988. This project has addressed the social and organisational problems of fishers in the vicinity of Discovery Bay, has persuaded them to increase the mesh size of their fish traps and helped to organise co-operatives and associations (Woodley 1994, Sary et al 1997). One outcome was a decision by the Alloa Fishermen's Association in Discovery Bay to set aside an area as a fishery reserve. These fishers operate from Old Folly beach in the south-west part of Discovery Bay and set fish traps mostly, but not exclusively, on the shelf to the west of the channel entrance to the Bay and in deep waters (>10 m) within the Bay.

The Discovery Bay Fishery Reserve consists of 27.5 ha of shallow backreef and bay margins on the western side of the Bay, adjacent to the Discovery Bay Marine Laboratory (Fig. 1). The reserve is largely less than 2 m deep, with substantial stands of seagrass in the seaward portion and mostly-dead patch reefs separated by stretches of sand elsewhere. An ancient circular sink hole in the middle of the reserve has a maximum depth of 12 m. The northern boundary of the reserve is marked by a crest of hurricane-generated reef rubble which has a few shallow openings to the ocean at the western end. The 10 m depth contour marks the eastern boundary within the Bay. The reserve has been operational since November 1996. The boundaries are marked by buoys and the reserve is patrolled intermittently. However, the Reserve does not yet have legal status and there is no legal means of preventing people from fishing within its boundaries. Nevertheless, the trap fishers generally respect the boundaries. Spear fishers, who roam up and down the coast, regularly traverse the Reserve but appear to be more interested in fishing on the fore reef.

Part of the activities of this project, which we operate on a collaborative basis with the Centre for Marine Sciences of the University of the West Indies, has investigated the rates of out-migration and biomass increase in the Fishery Reserve. The principal question addressed has been whether or not such a small and shallow fishery reserve would have any beneficial effect on the fish resources and the fishers.

Rakitin and Kramer (1996) found that trap catch rates for a number of species declined with increasing distance from the centre of the Barbados Marine Reserve. This effect was evident at distances of over 3 km and was attributed to outmigration from the reserve, but they were unable to document the same effect by underwater visual census. In contrast, Corless et al (in press) found that there was limited movement of all common reef species in a 70 day period after tagging in the Soufriere Marine Management Area in St. Lucia.

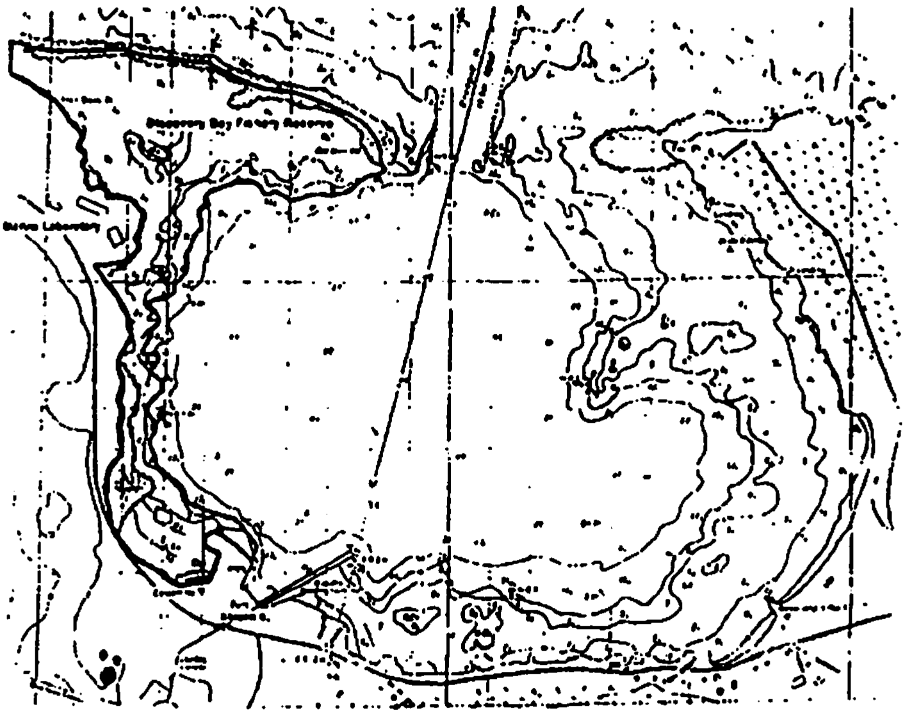


Figure 1. Discovery Bay, Jamaica, showing the location of the Discovery Bay Fishery Reserve.

METHODS

The project has undertaken a mark and recapture program since December 1996. A fleet of 10-15 double-arrowhead fish traps (Fig. 2), constructed with plastic-coated 1 inch (3.3 cm maximum aperture) hexagonal mesh, has been fished within the fishery reserve. The traps were usually hauled and reset twice per week. The catches were retained alive in large bins, and each fish identified, tagged and released in the same area where it was captured. Previously tagged fish were re-measured and released. Eels and non-marketable species were not tagged. The tagging operations were conducted from December 1996 to May 1998. The recovery program will continue, at least until June 1999.

Three types of fish tags have been used. T-bar anchor tags (Hallprint TBF-1 fine and TBA-1 standard), which are applied with a tagging gun, were used on medium and larger fish. Fingerling tags (Floy FTF-69), with individual needles which are used to pass an elastic vinyl thread through the anterior cartilage of the dorsal fin, were used on the smallest fish.

Discovery Bay and the adjacent fore reef was divided into a grid system using 3 seconds of longitude (92.5 m squared) to identify tagging and recovery stations. Recoveries by fishers operating along the coast were identified by reference to known local fishing sites.

Tagged fish captured by fishers were purchased at three times the market price. Additionally, after fifteen months of operations, all fishers who had captured tagged fish were invited to a social function at which tag numbers were entered in a lottery and numerous prizes were distributed to winners in various categories. This probably helped to maintain a degree of enthusiasm for the project. However, some tagged fish were undoubtedly overlooked by fishers and, in some cases, tags were pulled out and discarded by uncooperative fishers.

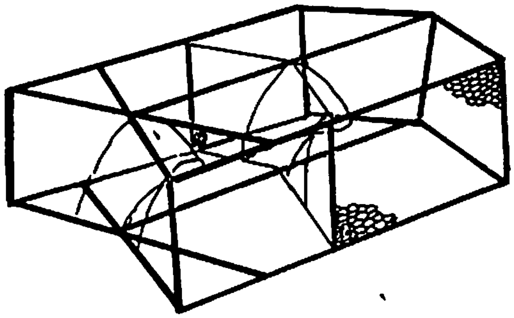


Figure 2. Double chevron fish trap constructed of 1-inch (3.30 cm maximum aperture) coated galvanised wire mesh and mangrove poles. Trap dimensions are 122 cm (48 in) along the side, 86 cm wide (36 in) and 61 cm (24 in) high.

RESULTS

A total of 6 949 fishes (48 species) were tagged and 5 919 recoveries (25 species) were obtained to 23 October 1998, including multiple recaptures of individuals. The principal species are listed in Table 1.

Clearly, there are substantial differences between species, but some generalisations can be made. Most of the smaller species remained in the reserve and many were repeatedly recaptured at the same trapping station. These included the small grunts, *Haemulon flavolineatum*, *H. aurolineautum* and *H. sciurus* and the mojarra, *Gerres cinereus*. Surgeonfish fell into an intermediate category and while most remained in or close to the reserve for extended periods, other individuals (e.g. *Acanthurus bahianus*) moved up to 3.5 km from the tagging station within a relatively short period (Fig. 3). The schoolmaster snapper, *Lutjanus apodus*, behaved in a similar fashion.

Surprisingly, parrotfish proved to be highly mobile. *Sparisoma aurofrenatum* was found in the reserve for extended periods (up to 380 days) but a number were recaptured between 0.5 and 3 km from the reserve (Fig. 3). Many of these were recaptured within Discovery Bay and had not moved onto the shelf.

The larger parrotfish, *S. chrysopterum* ($L_\infty = 45$ cm) and *S. viride* ($L_\infty = 60$ cm) moved freely from the reserve (Fig. 3). One individual *S. viride* remained within the reserve for over 400 days, while others moved several km from the reserve within 100 days and one individual was recovered 16 km east of the reserve. In contrast, *S. chrysopterum* mostly had left the reserve within 120 days and large numbers were recaptured 3-10 km from the reserve and two at 27-28 km to the east.

In contrast, the striped parrotfish, *Scarus iserti*, appeared to remain in the reserve for extended periods and, with one exception, all recaptures were within the reserve or on its fringes. The exception was a 26 cm fish captured 26 km east of the reserve after 405 days. The low number of returns of this species from outside the reserve is difficult to explain. Reeson (1975) found that above 16 cm total length this species was catchable in 1.25" mesh, the size used by most fishers, so gear selectivity does not explain the lack of returns.

Table 1. Principal species of fishes marked and recaptured within and outside of the Discovery Bay Fishery Reserve. Number of recaptured fishes includes multiple recaptures of the same individual.

Species	Number tagged	Number recaptured inside reserve	Number recaptured outside reserve
Sparisoma aurofrenatum	958	1 024	42
Scarus iserti	1 120	1 093	5
Sparisoma chrysopterum	1 050	651	131
Acanthurus bahianus	824	600	26
Holocentrus ascensionus	183	333	5
Sparisoma viride	356	234	25
Holocentrus rufus	248	246	10
Acanthurus coeruleus	165	217	10
Pseudupeneus maculatus	154	181	4
Acanthurus chirurgus	435	151	7
Haemulon flavolineatum	273	113	1
Haemulon aurolineatum	188	109	0
Lutjanus apodus	73	93	4
Gerres cinereus	193	92	0
Haemulon sciurus	145	80	1
Mulloidichthys martinicus	161	71	0
Caranx ruber	148	35	2
Other species	275	325	0
Totals	6 949	5 646	273

A comparison of the size frequency distributions of fishes recaptured within and outside the reserve shows that for the three parrotfish (*S. aurofrenatum, S. viride* and *S. chrysopterum*) the minimum sizes taken outside the reserve are substantially larger than within (Fig. 4). This is not accounted for by differences in mesh size used by the fishers since these species can be retained by 1.25" mesh at sizes of 14, 15 and 17 cm TL respectively (Reeson 1975). Therefore, it is concluded that the fish are mostly using the shallow waters of the reserve as a nursery and that for that part of the stock which is within the reserve recruitment to the fishery is delayed and yields correspondingly improved.

Our fishing operations in the reserve provide us with a record of relative abundance of all species, expressed as number of fish/trap/night. The records appear to fall into three groups:

a) Species in which changes in catch rates vary erratically with no significant changes over time. This group includes all three species of acanthurids, the French grunt, *H. flavolineatum*, and the squirrel fishes, *Holocentrus ascensionus* and *H. rufus*. These are species which occupy the reserve for extended periods as juveniles but which move out and perhaps return on an irregular basis.

b) Species in which there are marked seasonal variations in catch rates but without any increase in relative abundance within the reserve. This includes *S. chrysopterum*, *H. sciurus* and the two species of goat fish, *Mulloidichthys martinicus* and *Pseudupeneus maculatus* (Fig. 5 a-d). In each case there are one or two influxes of recruits per year which occupy the shallows of the reserve for several months and then move elsewhere.

c) Species in which there is a progressive increase in catch rates which can be attributed to increases in the numbers of fish resident in the reserve. This includes the parrotfish, *S. aurofrenatum*, in which catch rates have steadily increased from negligible levels, and *S. viride*, in which the trends are less clear because of the wide range in confidence limits (Fig. 5 e,f).

Catches of less abundant species were too small to permit any conclusions.

DISCUSSION

A number of species which were tagged in substantial numbers were never recovered outside of the reserve. These included *G. cinereus* and *H. aurolineatum* which appeared to be resident in the Discovery Bay Fishery Reserve. However, no tagged *M. martinicus* and only four specimens of *P. maculatus* were returned from outside the reserve despite the pronounced seasonal changes in abundance which must be accounted for by movement elsewhere.

All of the other common species were found to move out of the reserve (and perhaps return) frequently, on an irregular basis, seasonally or progressively. Where the movement is a seasonal movement of young fish into deeper water (Fig. 5 a-d) the harvests will certainly benefit from delayed recruitment of that portion of the stock which is protected by the reserve.

In the case of progressive movement out of the reserve the harvests will likewise be improved and, additionally, if the resident stock accumulates (Fig. 5 e,f) there can be a significant addition to the spawning stock biomass of those species. This is of very great importance as related work (Munro and Watson 1998) has shown that recruitment rates of most of the important species in the fishery at Discovery Bay is 2-3 orders of magnitude lower than in the relatively unexploited fish communities at Tortola, British Virgin Islands (BVI). The species in which recruitment rates are comparable with BVI are those which have extended pelagic larval phases (acanthurids, mullids) and which can be expected

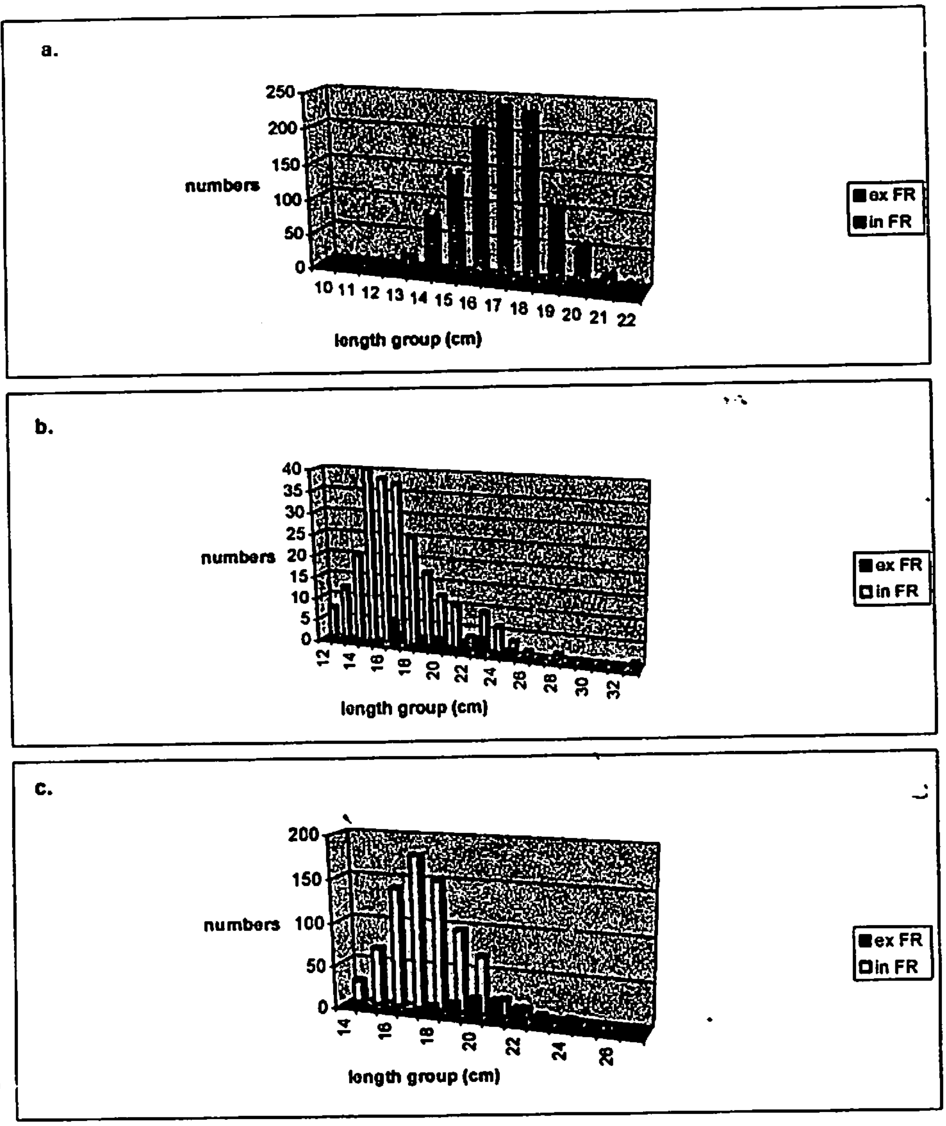


Figure 4. Size frequency distributions of three species of parrotfish captured within and outside of the Discovery Bay Fishery Reserve. a) Sparisoma aurofrenatum; b) Sparisoma viride and c) Sparisoma chrysopterum.

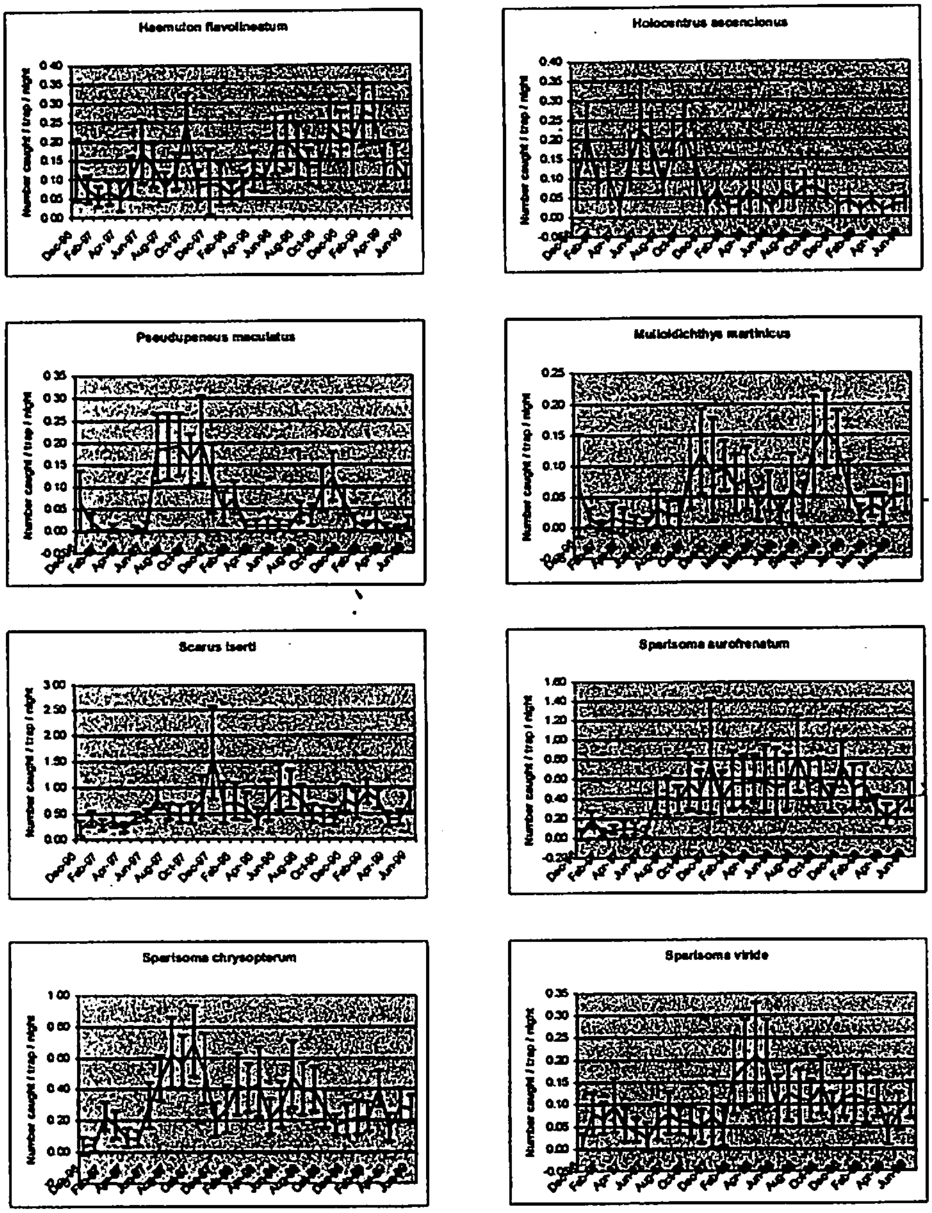


Figure 5. Changes in the relative abundance of six species of reef fishes within the Discovery Bay Fishery Reserve between December 1996 and October 1998. a) *Haemulon sciurus*; b) *Sparisoma chrysopterum*; c) *Mulloidichthys martinicus*; d) *Pseudupeneus maculatus*; e) *Sparisoma aurofrenatum* and f) *Sparisoma viride*.

to drift to Jamaica from elsewhere (Roberts 1997). Also, recruitment rates of small species which mature before recruitment to the trap fishery (*S. iserti, S. aurofrenatum, H. flavolineatum*, and *H. aurolineatum*) and which consequently have sufficient local spawning stocks are relatively undiminished.

As most of the tagged fish did not move very far from Discovery Bay, it can be concluded that the fishers who have contributed a part of their usual fishing grounds to the creation of the Discovery Bay Fishery Reserve will be the prime beneficiaries. These gains will be as a result of 3-6 month delays and hence larger sizes at recruitment for some species. Other species will have reduced mortality rates as a result of periodic residence in the reserve and hence larger average sizes. A third group, mostly of small species which mature before recruitment to the commercial fishery, will have increases in spawning stock biomass and resulting increases in recruitment rates.

These results suggest that a regulatory measure which could benefit all Jamaican fisheries would be to prohibit any fishing in depths of less than 6 m, except with hook and line. All shallow reef and seagrass beds are nursery grounds for a wide range of species. However, for Jamaican fisheries to recover, substantial areas of shallow and deep reef, particularly around the eastern, upcurrent, end of the island, will need to be turned into fishery reserves or marine protected areas. Additionally, meaningful steps will need to be taken to manage the fisheries and to improve the lot of the fishing communities.

ACKNOWLEDGEMENTS

This work has been funded by the Inter-American Development Bank and executed in collaboration with the Centre for Marine Sciences of the University of the West Indies, directed by Dr. Jeremy D. Woodley. The contributions of CMS staff, J.T. Levy, V. Murray, K. Samuels, K. Lankester and K. Black-Clark are gratefully acknowledged. The support of the Director of the Discovery Bay Marine Laboratory, Dr. Michael Haley, and his staff has been an essential element in the successful execution of this project.

REFERENCES

Corless, M. B. G. Hatcher, W. Hunte and S. Scott. Assessing the potential for fish migration from marine reserves to adjacent fished areas in the Soufriere Marine Management Area, St. Lucia. *Proc. Gulf Caribb. Fish. Inst.* 49 In Press.

Hughes, T.P. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547-1552.

Munro, J.L., Ed. 1983. *Caribbean Coral Reef Fishery Resources.* ICLARM Studies and Reviews. Manila 276 pp.

Munro, J.L. and M. Watson. 1998. Comparative settlement and recruitment rates of coral reef fishes in moderately-exploited and over-exploited Caribbean coral reef ecosystems. International Society for Reef Studies, European Meeting, Perpignan, September 1998. Abstract.

Rakitin, A. and D. L. Kramer. 1996. Effect of a marine reserve on the distribution of coral reef fishes in Barbados. *Mar. Ecol. Progr. Ser.* 131:97-113.

Reeson, P.H. 1983. The biology, ecology and bionomics of the parrotfishes, Scaridae. Pages 166-177 in: J.L. Munro (ed.) *Caribbean Coral Reef Fishery Resources*. ICLARM Studies and Reviews. Manila.

Roberts, C..M. 1997. Connectivity and management of Caribbean coral reefs. *Science* 278:1454-1457.

Sary, Z., H. A. Oxenford and J. D. Woodley. 1997. Effects of an increase in trap mesh size on an overexploited coral reef fishery at Discovery Bay, Jamaica. *Mar. Ecol. Prog. Ser.* 154:107-120.

Woodley, J.D. 1994. Facilitating changes in artisanal fishery practice at Discovery Bay, Jamaica. Pages 75-78 in: J.L. Munro and P.E. Munro (eds.) *The Management of Coral Reef Resource Systems.* ICLARM Conference Proceedings 44, Manila.

STATUS REPORT ON A JAMAICAN REEF FISHERY: CURRENT VALUE AND THE COSTS OF NON-MANAGEMENT*

ZSOLT SARY[1], JOHN L. MUNRO[1] and JEREMY D. WOODLEY[2]

[1]ICLARM Caribbean/ Eastern Pacific Office
158 Inland Messenger, Road Town, Tortola
British Virgin Islands
[2]Centre for Marine Sciences, University of the West Indies
Kingston 7, Jamaica
*ICLARM Contribution 1645

ABSTRACT

The reef fishery on the north coast of Jamaica is one of the most intensely overfished in the Caribbean. Discovery Bay lies in the center of the north coast and the reef fishery there is typical of the rest of the fishery on this coast, with a narrow, accessible fishing ground which provides food and employment to large numbers of people, despite its overexploited state.

Management measures that could rebuild fish stocks were suggested a quarter of a century ago. However, the central government has not been able to introduce the necessary measures. The University of the West Indies has implemented several management measures on a small scale around Discovery Bay but these have not been applied on a wider scale.

This paper provides an updated status report of the reef fishery on a segment of the north coast with a fishing area of about 12 km^2. We estimate current fishing effort to be over 7000 boat trips per year using traps, lines, or nets. In addition, over 5000 spear fishing trips are made per year. The average income is between US$13 and $29 per trip. The total catch in the study area is about 60 tons per year, worth about $300,000. Despite its overexploited state, the productivity of the reef remains high with an estimated yield of 5 tons km^{-2}.

We estimate that the cost to Jamaica over the past 25 years of not managing its fisheries on the north and south coast is around $1.3 billion. Managing small-scale multi-species fisheries is undoubtedly difficult, but the figures here suggest that it is surely worth the effort.

KEY WORDS: Jamaica, small-scale fishery, valuation.

INTRODUCTION

The reefs on the north coast of Jamaica are often recognized as one of the most intensively overfished shallow coralline reef areas in the Caribbean. This widespread recognition of the problem is largely due to over 30 years of research on the reefs of Discovery Bay and numerous publications reporting the lack of fish (Munro 1983, Aiken and Haughton 1987, Hughes 1994, Picou-Gill *et al.* 1996). This paper provides an updated status report on the fishery in the Discovery Bay area and compares current fishing effort and catch rates to historical figures.

Discovery Bay lies in the center of the north coast of Jamaica and the reef fishery there is typical of those along the entire coast. The coral reefs lie on a very narrow, accessible submarine shelf. The coral reef fishery here is an important source of food and employment, despite its overexploited state. Its open access nature, coupled with high human population growth and intense economic pressures, has drawn large numbers of people into the fishery.

There are a variety of strategies that have been suggested for the management of the Jamaican reef fisheries (Munro 1983) and there are several reviews of these options (Munro and Williams 1985, Mahon 1989). Some management measures have been implemented locally, with the assistance of the Discovery Bay Marine Laboratory of the University of the West Indies (UWI), on a small scale and in the short term. These included introducing a larger mesh size for fish traps and the establishment of a small fishery reserve. However, little has been done at a national level. Fishers all agree that the fishery is declining but economic factors have led them to intensifying fishing effort over the years (Aiken and Haughton 1987), rather than reducing it.

METHODS

Collection of Catch and Effort Data

Catch and effort data in the Jamaican north coast artisanal reef fishery were collected from 19 July 2000 to 18 July 2001 at five landing sites in and adjacent to Discovery Bay (Rio Bueno; Old Folly and Top Beach in Discovery Bay; Swallow Hole in Runaway Bay; and Salem; Figure 1) three or four times a week, on randomized pre-determined days. To encourage cooperation from fishers, inducements were offered in the form of one ticket in a raffle for every 10 kg of detailed catch data provided, or one ticket for 25 kg of aggregated catch data.

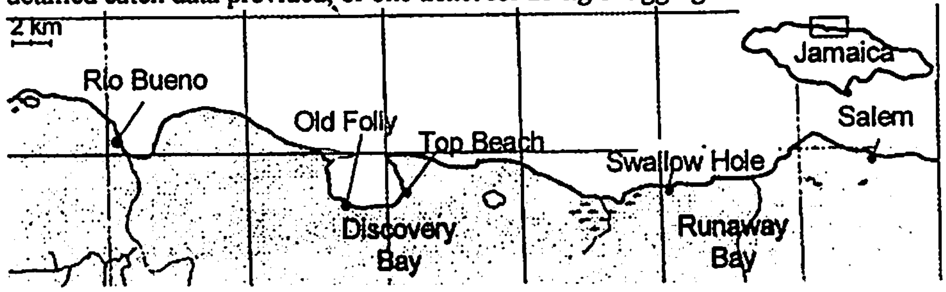


Figure 1. Map of Jamaica, showing study area and the five landing sites.

On each data collection day, the number of active boats (at sea that day), motorized and unmotorized, was enumerated by counting the incoming boats as they were landing on the beach, by counting the empty spaces among the rows of boats and from information from key informants.

From the active boats landing at the site, the number of fish and the total weight of each species (to the nearest 0.01 kg) in the catch were recorded separately for all consenting fishers. If sorting of the catch was not possible, an attempt was made to record the total number of fish and total weight of the catch. Fishing effort information (time spent at sea, number of crew members, the number of fish traps hauled, average soak time of gear, mesh size of each fish trap or net, depth fished) was also collected whenever possible.

The number of boats missed by the data collectors (due to unusual landing time, too many boats landing at once, or uncooperative fishers), was also counted and recorded; the type of fishing gear most likely used by the missed boats was noted.

A detailed formal survey was also carried out among the active fishers at the five landing sites using a standard questionnaire to obtain information on the age of the fishers, full/part time status, other occupations, number of dependents, primary and secondary gear used, the size of boats and engines used, and the number of fish traps of various mesh sizes and other gears in use in the fishery.

The survey area covered 26 km of shelf edge at a depth of 100 m and a fishing area of approximately 12 km^2. This excluded the central part of Discovery Bay >30 m deep, which is too deep to be fished and is not coralline. Full details of the survey and the data collection and analyses are provided by Sary (2001).

In addition, unpublished catch and effort data, obtained in a similar way to that described above from the same five landing sites, collected by the UWI's Fisheries Improvement Programme (UWI/FIP) from January 1996 to December 1997, was collated and used to examine changes in catch rates in the fishery over the last 5 years. Other sources of data concerning the fishery in the area are the works of Nembhard (1970), Sahney (1983), Munro (1983), Haughton (1988), Picou-Gill *et al* (1996) and Sary *et al* (1997).

RESULTS

The Fishers, Fishing Gear and Fishing Effort

Key characteristics of the fishing community, the fishing gear used and the effort expended are summarized in Table 1. There are about 130 active fishers in the area, almost 60% of them relying on fishing as their sole income earning activity. On average, each fisher supports another 4 people. The average age of fishers is 49 years.

There are approximately 85 boats (not including derelict boats or boats under repair/construction) that are based at the five landing sites and ten boats that are based at isolated locations along the coastline but operate in the fishing area, in a similar fashion to boats at the main landing sites. Almost two thirds of fishers own a boat. The average boat size is 6.5 m. The majority of the boats are small, usually unmotorized wooden canoes about 3 m in length, while the remaining third of the boats are the standard Jamaican 8 m reinforced fiberglass open canoes, which are powered by outboard engines (usually 35 to 65 hp).

Almost 70% of the fishers use fish traps as their primary or secondary gear. Three mesh sizes are used in wire mesh traps. The most common has 43 mm maximum aperture (32 mm or 1 ¼" between knots), and about 71% of the traps in the fishery are made of this mesh size. Larger 55 mm mesh (38 mm or 1 ½" between knots) are less often used (26% of traps) and 33 mm (25 mm or 1" between knots) are now uncommon (3%).

On an average day there are about 20 boats fishing on the narrow fringing reef along this 26 km shelf, about 12 of them non-motorized. They have approximately 29 people operating from them (captain, share fishers, and crew). In addition, about 15 spear fishers are also fishing in the area each day. This represents over 7000 boat days per year, and over 5000 spearfishing days per year. Many fishers operate more than one gear on each fishing trip.

Trap fishing boats haul an average of seven traps per fishing trip. Thus, during the estimated 5000 trap fishing trips (or boat days) in the area during the year, over 34,000 trap hauls were made. Nearly 90% of the trap hauls are of 43 mm (1.25") mesh traps and nearly all the rest of the hauls are of 50 mm (1 ½") mesh traps. These figures do not reflect the actual proportion of the various mesh size traps in the fishery simply because the smaller mesh traps are hauled almost twice as often as the larger mesh traps. Trap fishers set their traps 27 m deep on average.

Table 1. Characteristics of the fishers and the fishing fleet at five landing sites (Rio Bueno to Salem) on the north coast of Jamaica, 2000-2001.

		Number	Fishing effort year^{-1}	
Estimated number of active fishers		130		
Average age		49		
Primary gear:	Trap fishers	80	4900	boat days
	Line fishers	19	2400	boat days
	Net fishers	5	340	boat days
	Spear fishers	26	5000	fishing days
Functional boats (sea worthy)		95		
Boats motorized		45		
Average boat length (m)		6.5		
Average motor size (hp)		28		
Traps hauled	1" mesh traps		200	trap hauls
	1.25" mesh traps		30100	trap hauls
	1.5" mesh traps		4000	trap hauls
	TOTAL		34300	trap hauls
Mean soak time	1.25" mesh traps	2.8 days		
	1.5" mesh traps	5.2 days		

About 50% of the fishers use hook and line as their primary or secondary gear. Over 2000 boat trips are spent hook and line fishing, most of them for drop line fishing usually at night (targeting nocturnal reef fish and deep-slope snappers), or in the afternoon (fishing for parrotfish; a small but little known part of the fishery). Very few line fishing trips are for troll fishing. A small number of fishers use gill nets, about 1 boat per day, setting their nets in shallow reef areas. Net and line fishing boats appear to spend nearly twice as much time at sea per trip as trap fishing boats.

About 32 fishers are full- or part-time spear fishers. Their enumeration is difficult because they do not generally operate from boats and will enter and leave the water anywhere along the shore. A limited set of visual surveys along the coast provided the estimates of fishing effort.

Catch Rates

The catch rates in various gears are summarized in Table 2 and incomes from fishing are given in Table 3.

The average catch of a trap fishing boat is 6.1 kg per trip, and the average income is $29 per trip (all figures in US$); this is shared between the boat captain and his crew. The most important fish families in the trap catch are parrotfish and surgeonfish. The more valuable snappers are the third most important family. Other commercially valuable groups, such as groupers, jacks, and grunts are much less common. About 10% of the catch consists of unmarketable trash fish, much of which is nonetheless consumed. The total catch over the entire area by fish traps is about 30 tons per year, with a value of $140,000.

The most lucrative fishing activity appears to be net fishing, with an average income of $34 per boat trip, but the success of this activity may be partly seasonal when jacks are more common in the fishing area. Also, several net fishers are in fact spear fishers using nets and boats. They herd fish into the net and spear any fish too large to be gilled in the net. This activity is very labor intensive. Nonetheless, given the relatively high catch rates per boat, it is not clear why more fishers do not take up net fishing.

Dropline fishing is the least rewarding with fishers making less than $10 per trip, though this type of fishing may still be popular since it is the least gear and labor intensive of all the fishing practices. The estimated catch of all drop line fishers is about 4.7 tons per year, with a value of $25,600. Troll lines yield a total of 1.1 tons valued at $5,600. Net fishing yields 2.2 tons per year, with a value of $11,700. Spear fishers were estimated to land 23 tons, with a value of $122,000.

Costs, Catch Values and Incomes

The total catch by all fishing gears in the study area is about 60 tons per year, worth about $300,000. Shared among the approximately 130 active fishers in the area, it represents a yearly income of about $2,300 per year for the average fisher.

The value of the catch is relatively high because of the high demand for fish in Jamaica. Fish are generally sold on north coast fishing beaches directly to the consumers, or occasionally to vendors, in two categories. The "quality" fish are currently sold for $5.90/kg (J$120/lb) and these include groupers, snappers, goatfish, jacks, large grunts and most pelagic predators (Spanish mackerel and wahoo) and lobsters. Almost any large fish is rated as "quality" and small "quality" fish are downgraded to "common". "Common" fish include most of the other reef species, such as parrotfish, surgeonfish, angelfish, small grunt and crabs, which are sold for $4.90/kg (J$100/lb). Unmarketable species include moray eels, scorpion fish, filefish and very small fish. These are generally kept by the fisher for home consumption or given away to indigent persons or to people who help pull the boats up on shore.

The cost of entering and remaining in the fishery is high, except for spear fishing, primarily due to the capital needed to obtain and maintain a boat. The initial costs may range from $800 to $8000, depending primarily on whether a new or second hand boat and engine are bought (Polunin *et al*, 2000). Plywood boats are the least expensive at about $400 to $900, while fiberglass boats cost

Table 2. Estimated catches of traps, lines, nets, spears, and total catch, by fish family, at five landing sites (Rio Bueno to Salem) on the north coast of Jamaica, July 2000 to July 2001.

	Traps		Drop lines		Troll lines		Nets		Spears		All gears
Catch composition	kg boat^{-1} day^{-1}	kg yr^{-1}	kg boat^{-1} day^{-1}	kg yr^{-1}	kg boat^{-1} day^{-1}	kg yr^{-1}	kg boat^{-1} day^{-1}	kg yr^{-1}	kg trip^{-1} day^{-1}	kg yr^{-1}	kg yr^{-1}
Scaridae	2.34	11500	-	-	-	-	0.56	190	1.38	7050	18740
Sphyraenidae	-	-	0.16	330	3.04	820	0.15	50	1.4	7140	8340
Acanthuridae	0.97	4750	-	-	-	-	0.16	50	0.23	1170	5970
Lutjanidae	0.53	2600	0.36	760	-	-	0.43	150	0.12	610	4120
Serranidae	0.28	1360	0.44	920	-	-	-	-	0.31	1580	3860
Carangidae	0.17	850	0.67	1400	-	-	1.79	610	0.06	300	3160
Haemulidae	0.29	1430	-	-	-	-	0.88	300	0.18	910	2640
Mullidae	0.24	1180	-	-	-	-	-	-	0.23	1180	2360
Holocentridae	0.35	1710	0.2	420	-	-	-	-	0.063	320	2450
lobsters and crabs	0.16	780	-	-	-	-	-	-	0.16	840	1620
Muraenidae	0.23	1110	0.08	180	-	-	-	-	-	-	1290
Balistidae	0.13	620	-	-	-	-	-	-	-	-	620
Scombridae	-	-	0.1	210	0.67	180	-	-	-	-	390
Belonidae	-	-	0.1	210	0.41	110	0.12	40	-	-	360
others families	0.38	1880	0.15	310	0.01	4	2.25	760	0.50	1900	4850
TOTAL CATCH	6.07	29700	2.26	4740	4.07	1110	6.34	2150	4.50	23000	60770

over $4000 new. Dugout canoes are now rare due to the scarcity of large accessible cottonwood trees. Large fiberglass boats need large engines (35 to 65 hp) that cost up to $3600 new. Some of the wooden boats are motorized with small engines (e.g. 4-10 hp) that cost up to $1250.

Table 3. Estimated value of the catch and income per fishing trip, at 5 landing sites (Rio Bueno to Salem) on the north coast of Jamaica, July 2000 to July 2001.

	traps	lines	nets	spears	All gears
fishing trips year^{-1}	4900	2370	340	5100	
Catch composition by value (kg)					
quality (US$5.90/kg)	5990	2510	1260	10500	20260
common (US$4.90/kg	21340	3200	870	12310	37720
trash (no value)	2410	130	30	160	2730
Value of the catch (US$)					
total value year^{-1}	$140,000	$30,000	$11,700	$122,000	$303,700
income trip^{-1}	$29	$13	$34	$24	

Other costs of fishing depend on the method involved. For trap fishing, the materials needed include mesh wire, sticks, nails, lacing wire, and rope, and these materials cost about $30 to $50 per trap, depending on the size of the trap and the type of mesh wire used. Most fishers build their own traps, but some hire others to build them. With ongoing repairs, fish traps last about a year before they need to be replaced, though many are lost sooner than that because of storms, careless setting near the reef drop-off, or theft. Trap fishers seem to set their traps very deep and often unmarked, perhaps to avoid theft or poaching by spear fishers. These practices tend to increase the number of lost traps. Motorized boats also need to purchase fuel, which of course varies depending on the size of boat and engine, the condition of the engine, the frequency of fishing trips, the number of traps hauled, and the distance the traps are set away from the beach.

Drop line fishers can expect to spend about $50-$200 for gear per year (fishing line, hooks). Bait is often caught by the fisher himself, or bought at sea from another fisher. Troll fishers may spend money on artificial bait ($5-$10 each) and a great deal on fuel. For this reason, trolling is not commonly practiced, except when moving between fishing grounds to operate other fishing gear. Net fishers, who usually use gill nets of 50 mm (2") to 100 mm (4") mesh size, would spend from $100 to $200 (about 12 kg of net) on average per year.

DISCUSSION

Catch per Unit Area

Our 2000/01 survey yielded an estimated total catch of demersal and neritic pelagic species of 60,770 kg by the five fishing beaches. This included 29,700 kg landed in traps, 5410 kg on lines, 2160 kg in nets and 23,000 kg taken by spearfishers, all taken from a total shelf area of 12 km^2. The harvest is therefore 5 tons/km^2.

These harvests per km^2 are very high by Caribbean standards, but not by those of Pacific coral reef systems (Munro 1984). However, the surveys of 1968, 1996/97 and 2000/01 (Tables 4 and 6), as well as other published surveys in the area (Picou-Gill *et al* 1996, Sary *et al* 1997) have provided consistent estimates of catches and there appear to be no reasons for challenging their accuracy.

Changes in Catch Rates Over Time

There are several data sets that warrant comparison with the current results. These are the 1968 and 1981 surveys of the Jamaican fishery (Nembhard 1970, Sahney 1983) and data collected by the UWI/FIP in 1996 and 1997.

In the 1968 survey, catches were reported by parish and the catches at selected beaches were raised by the total number of operational boats, motorized or non-motorized, operating in the parish. Fortunately, the beaches selected to represent St. Ann were Salem and Swallow Hole and it is therefore possible to make a direct comparison between the 1968 and the 2000/01 data. Table 4 shows the landings by all gears, with catches aggregated to conform with the 1968 survey. Catches have fallen 13% by weight and at least 17% by value, using 2001 prices. However, as there are very few large fish of any species in the catches, our estimates of value in 2000/01 are inflated. Perhaps half of all the "quality " fish are too small to fetch the premium price and the decline in value is therefore probably around 20%.

Table 4. Changes in total catch and value of the catch between 1968 (from Nembhard 1970) and 2000-01, at Swallow Hole, Runaway Bay and Salem fishing beaches, on the north coast of Jamaica.

	Catch		Prices	Value of catch	
	1968	2000/01	2000/01	1968	2000/01
	kg	kg	US$/kg	US$	US$
Kingfish, wahoo	34	260	5.90	202	1534
Tuna, bonito	517	0	4.90	2533	0
Snapper	3648	2778	5.90	21522	16390
Goatfish	1482	776	5.90	8745	4578
Jacks	4719	1704	5.90	27842	10054
Mullet	1196	1	5.90	7058	6
Parrotfish	5563	4340	4.90	27260	21266
Goggle eye	222	471	4.90	1087	2308
Herring, sprat	17	0	4.90	84	0
grouper	3350	1111	5.90	19766	6555
lobster	377	317	5.90	2224	1870
shrimp	90	0	5.90	534	0
Other	6804	12506	4.90	33340	61279
TOTAL	28020	24264		152196	125841
% change		-13.4			-17.3

If catches over the whole study area have declined by the same amount as at Salem and Swallow Hole (-13%), the fishery yield in 1968 from these reefs would have been about 5.7 tons/km^2.

The catches reported by Nembhard (1970) for the parish of Trelawney are based on the beaches of Rio Bueno and Charlotte and are therefore not comparable with our data. In any event, the catch rates reported for this area have a number of anomalies, such as large quantities of parrotfish reported to have been taken on hook and line and of tuna caught in traps and are therefore not considered further.

In the 1981 survey (Sahney 1983), catches from the eastern, northern and western parishes were aggregated and no comparison can be made with the current survey.

Table 5. Changes in the catch and the value of the catch of motorized and unmotorized boats between 1968 (from Nembhard 1970) and 2000-2001, at two landing sites (Swallow Hole in Runaway Bay, and Salem), on the north coast of Jamaica.

	1968		2000/01	
	motorized	non-motorized	motorized	non-motorized
Number of boats	4	43	18	21
Catch year^{-1}	kg	kg	kg	kg
traps	1393	24253	16330	2408
lines	-	1393	570	1879
nets	-	985	1503	36
spears	-	-	223	1315
TOTAL CATCH	1393	26627	18626	5638
Catch boat^{-1}	348	619	1035	268
Value year^{-1}	US$	US$	US$	US$
Total value	7870	144327	96590	29250
Earnings boat^{-1}	1968	3356	5366	1393

Table 5 shows that in 1968, only four motorized craft fished from Salem and Swallow Hole; they seemed to be used irregularly and thus landed very little. The numbers of active motorized craft had risen to about 18 on these two beaches by 2000/01, landing over 1000 kg per year with a value of $5,366. Non-motorized boats fell from 47 to 21 and the catch/boat/year fell from 596 kg to 287 kg. The corresponding value fell from about $3,300 to less than $1,400.

No spear fishers were recorded in St. Ann in 1968. Since then it has become an increasingly important activity. Spear fishing catches remain difficult to estimate because spear fishers move freely along the coast and most do not use established landing sites.

In addition, we have records of catch rates of 43 mm (1 ¼") mesh fish traps for 12 month periods in 1996 and 1997, from the same fishing beaches covered in 2000/01. Changes in the catch rates, by family (in grams trap^{-1} haul^{-1} and in number of fish trap^{-1} haul^{-1}), are shown in Table 6. The catches have been relatively stable over this time period, with the average catch of under 1 kg /haul. Nonetheless, it appears that there has been a very slight increase in the catch rates of fish traps in the fishery, both in weight and number of fish, over the five-year period, but only the increase in the number of fish between 1996 and 2000-01 is likely to be significant. The increase in the catch appears to be due to an increasing number of small fish in the catch, especially small parrotfish. As a result, the average fish size in the catch has actually decreased, especially those of parrotfish, but also other groups such as grunts and groupers.

Table 6. Changes in trap catches: Comparison of catch rates, catch value, and mean fish size in 1.25" mesh traps, between three 12-month periods (in 1996, 1997, and 200-2001) on the north coast of Jamaica.

	1996	1997	00-01	1996	1997	00-01
catches sampled	(110)	(44)	(278)	-	-	-
traps reported	(672)	(279)	(1832)	-	-	-
Catch composition by family						
		g trap^{-1} haul^{-1}			# of fish trap^{-1} haul^{-1}	
Scaridae	244	349	355	2.0	2.7	3.6
Acanthuridae	153	197	153	1.8	2.4	1.7
Holocentridae	50	73	51	0.6	0.8	0.5
Mullidae	18	26	49	0.1	0.2	0.4
Lutjanidae	80	34	48	0.3	0.1	0.2
Haemulidae	56	40	42	0.4	0.3	0.4
Balistidae	30	3	41	0.1	0.03	0.1
Serranidae	39	35	39	0.2	0.2	0.3
Muraenidae	48	28	36	0.03	0.04	0.1
invertebrate	7	11	16	0.01	0.02	0.03
Carangidae	10	25	14	0.1	0.2	0.1
Pomacentridae	14	5	10	0.2	0.1	0.1
Kyphosidae	6	-	10	0.01	-	0.01
others (18 families)	51	47	39	0.21	0.19	0.20
TOTAL	806	873	903	6.0	7.3	7.6
Catch composition by value						
quality	155	96	140	0.7	0.5	0.7
common	559	691	683	4.8	6.4	6.4
trash	92	86	79	0.5	0.4	0.5
Mean fish size (g)	135	120	119	-	-	-
Catch value		US$ trap^{-1} haul^{-1}				
	$ 3.66	$ 3.96	$ 4.17	-	-	-

The value of the catch (in 2001 dollar values) has also increased slightly but it is still only a little more than $4 per trap haul. The total weight of high quality fish has actually decreased since 1996 and there are more lower-valued (common) species in the catch than before. The average fish size in all commercial categories appears to have decreased.

The Costs of Non-Management

Our data show that catches have declined in value since 1968 by 17-20% at 2001 prices. However, we have done an evaluation of management strategies since 1975, when Munro (1975) suggested that an increase from the then prevalent 33 mm maximum aperture mesh (25 mm or 1" between knots) to a mesh size of 66 mm maximum aperture (50 mm or 2" between knots) would increase the value of trap catches by about 30%. An increase to 43 mm (1 ¼") mesh would increase harvest values by 19%. Line catches would also have increased because of the delayed recruitment of all species to the trap fishery. Recruitment rates were also predicted to increase if larger mesh sizes enabled some species to reach maturity before recruitment to the fishery.

Since 1975, the use of 33 mm mesh has declined on the northern coast of Jamaica and, as a result of efforts of the UWI FIP in the Discovery Bay area in the past decade, a substantial proportion of traps have 55 mm (1 ½") mesh. The latter mesh size was calculated by Munro (1975) to produce a very similar relative harvest to the 66 mm mesh, but without the same benefits of delaying recruitment to larger sizes. However, effective fishing intensity has actually increased since 1975, as a result of the increases in numbers of motorized canoes and spear fishers.

Annual catches have declined in value in the survey area by $30,000, mostly as a result of increasing effort, declining recruitment rates and, perhaps, changes in the ecosystem since 1968. If we assume that the decline was linear, the value would have fallen by $6,000 by 1976 (by which time it might have been possible to have management measures in place) instead of increasing by $52,000. If we compound this loss over the next 25 years at 10%/year we arrive at a figure of somewhat over $6.4 million that was lost from this 12 km^2 area of fishing grounds, fished in 1968 by 124 boats. The narrow shelves of the northern, western, and eastern parishes total 699 km^2 (Haughton 1988) and proportionately the compounded total loss would have been about $375 million. If we extend this argument to cover the southern shelf of Jamaica and the proximal oceanic banks (3,471 km^2), all of which are intensively fished with traps, but only assign them half the productivity of the narrow northern shelves, the compounded loss in direct primary production from this shelf and banks is $930 million. Thus, in total, Jamaica has probably lost $1.3 billion over the past 25 years. This figure does not include losses from the vast Pedro Bank and from Morant Bank to the south of Jamaica, that were lightly exploited 25 years ago but which are now reported to have greatly depleted fish stocks.

The foregoing figures might err by a few hundred million dollars. It is undoubtedly difficult to manage small-scale multi-species, multi-gear fisheries. However, the figures suggest that it is surely worth the effort and that management would pay economic, social and political dividends.

ACKNOWLEDGEMENTS

This study was part of the work of the Caribbean Marine Protected Areas Project, funded by the United Kingdom Department for International Development. Nadine Earle and John Samuels collected the vast majority of the data on the fishing beaches, with assistance from several graduate students of the University of the West Indies. Data for 1996-97 were collected by staff of UWI Fisheries Improvement Programme, funded by the Kaiser Jamaica Bauxite Company. We would like to thank the fishers of the area for their assistance in answering all our questions and allowing us to weigh their catches.

REFERENCES

Aiken, K.A. and M.O. Haughton. 1987. Status of the Jamaican reef fishery and proposals for its management. *Proc. Gulf Caribb. Fish. Inst.* 38:469-484.

Haughton, M.O. 1988. An analysis of statistical data from the Jamaican inshore fisheries. Pages 443-454 in: S. Venema, J. Moller-Christensen and D. Pauly. (eds.) *Contributions to Tropical Fisheries Biology. FAO Fish. Rep. 389.*

Hughes, T.P. 1994. Catastrophes, phase-shifts, and large scale degradation of a Caribbean coral reef. *Science* 265: 1547-1552.

Mahon, R. 1989. Fishery management options for the Lesser Antilles. *FAO Field Document* (FI:TCP/RLA/6776) 4. 117 p.

Munro, J.L. 1975. The biology, ecology, exploitation and management of Caribbean reef fishes. Part VI - Assessment of the potential productivity of Jamaican fisheries. *Res. Rept. Zool. Dept., Univ. West Indies* 3(VI): 55 p.

Munro, J.L. (ed.) 1983. *Caribbean Coral Reef Fishery Resources.* ICLARM. Studies and Reviews 7: 258 pp.

Munro, J.L. 1984. Coral reef fisheries and world fish production. *ICLARM Newsletter* 7(4): 3-4.

Munro, J.L. and D.M. Williams. 1985. Assessment and management of coral reef fisheries: Biological, environmental and socio-economic aspects. *Proc. 5th Int. Coral Reef Congress.* 4: 545-581.

Nembhard, B. 1970. The fishing industry of Jamaica: A report on the 1968 sample survey. Agricultural Planning Unit, Ministry of Agriculture and Fisheries, Jamaica.

Picou-Gill, M., J.D. Woodley, M. Miller, Z. Sary, W. Van Barneveld, S. Vatcher and D. Brown. 1996. Catch analysis at Discovery Bay, Jamaica: The status of an artisanal reef fishery. *Proc. Gulf Caribb. Fish. Instit.* 44: 686-693.

Polunin, N.V.C., I.D. Williams, J.G. Carrier, and L.F Robinson. [2000]. Ecological and social impacts in planing Caribbean marine reserves. Department of Marine Sciences, University of Newcastle, 37 pp. Unpubl. MS.

Sahney, A.K. 1983. Sample survey of the fishing industry of Jamaica – 1981. *FAO Fish. Rep.* 278 (Supplement). pp. 255-275.

Sary, Z. 2001. The small scale reef fishery on the central north coast of Jamaica in 2000-01: A biological and socio-economic survey. *ICLARM Caribbean/Eastern Pacific Office Technical Report.* in prep.

Sary, Z., H.A. Oxenford, and J.D. Woodley. 1997. Effects of an increase in trap mesh size on an overexploited coral reef fishery at Discovery Bay, Jamaica. *Marine Ecology Progress Series*, 154: 107–120.

In Press: Proceedings of the 54th Gulf and Caribbean Fisheries Institute. Providenciales, Turks and Caicos Islands. November 12-17, 2001.

THE DISCOVERY BAY FISHERIES RESERVE, JAMAICA[1]

JEREMY WOODLEY[2], ZSOLT SARY[3], PETER GAYLE, WENDY LEE[4],
PETER PARCHMENT[5], LESLIE WALLING[6]
Discovery Bay Marine Laboratory, P.O. Box 35, Discovery Bay, Jamaica
[2] 13 South St., W., Dundas, Ontario L9H 4C3, Canada
*[3] ICLARM Caribbean/Eastern Pacific Office, 158 Inland Messenger, Road Town,
Tortola, British Virgin Islands.*
[4] "Sevenoaks", P.O. Box 212, Runaway Bay, Jamaica
[5] W.I. Social Investment Foundation, Kingston 5, Jamaica W.I
*[6] CPACC Implementation Unit, Lazaretto Complex, Black Rock, St. Michael,
Barbados W.I.*

ABSTRACT

Jamaican north coast coral reef fish stocks have been over-exploited. The Fisheries Improvement Programme (FIP) began in 1988 to help fishers at Discovery Bay to introduce management measures. Social and cultural constraints included poverty and distrust among fishers. FIP initiated: (1) an education programme in reef fisheries and the possibilities of local management; (2) search for alternative occupations for fishers; (3) encouragement of a Discovery Bay Fishermens' Association; in 1994, Association members agreed on a voluntary protected area within Discovery Bay; (4) a Reserve Planning Group, representing all users of the bay; (5) contract with Fishermens' Association: grant funds were transferred to it to employ rangers; (6) marking of the Reserve, and daily patrols, from 1996; (7) legalization of the Reserve: legal protection was sought through government agencies but has not yet been obtained. Within two years of Reserve protection, fishers perceived an increase in fish abundance and asked that the protected area be extended. Studies on fish populations in 1996-98, showed that the Reserve delayed age and size at recruitment to the fisheries and could have enhanced catches in adjacent waters. The failure to gain legal status, and lack of funds for patrolling after 1999, led to decline in compliance with the voluntary restrictions on fishing. Lessons and future prospects are discussed.

---

[1] Contribution Number 000 from the Discovery Bay Marine Laboratory, University of the West Indies.

INTRODUCTION

The Jamaican fin-fishery is largely artisanal, carried out by a fleet of open canoes (each containing 1-5 men), or by swimmers, using traps, hook-and-line, spears and gill-nets (Aiken 1993). Fishermen work on or near the shallow coastal shelves (Fig. 1) and offshore banks, targeting fish in coral reefs and associated habitats. Stocks are over-exploited, especially near shore, and catch rates are very low (Munro 1983, Aiken 1993). Over-fishing is particularly severe along the north coast, where fishermen concentrate their effort on the narrow (<1 km) coastal shelf. As a result of the intense local fishing pressure, Jamaican north coast coral reefs are among the most overfished reefs in the English-speaking Caribbean (Hughes 1994, Roberts 1995). Quality fish such as grouper and snapper are scarce, the catch of other species is dominated by small, young individuals, and the destruction of breeding stock has reduced the possibility of replenishment. A possible secondary effect of this intense level of overfishing is the effect on the reef habitat which supports the fishery. The absence of herbivorous fishes is believed to have been one of the factors facilitating a phase shift in reef composition from a coral to an algal dominated system (Hughes 1994). The infilling of interstices with algal biomass (also promoted by the mass mortality of *Diadema*, Hughes et al. 1987) and associated reduction in complex three dimensional structure (on top of two hurricanes) could have an as yet undocumented effect on the ability of the reef to either sustain itself or act as a suitable habitat for various size classes and species of fishes.

Despite the poor state of the fishery, economic pressures, intensifying in the 1990's, continue to drive men into fishing (Allison 1992; van Barneveld et al. 1996). Some have no alternative, some do a little farming, while others are supplementing income from partial or full-time employment. Since nearshore fish stocks are so accessible, they can be exploited at low economic cost down to levels that give very low economic returns. For example, the average catch in fish traps at Discovery Bay in 1990 was 0.18 kg/trap/day (Picou-Gill et al. 1996). On the north coast, a Jamaican fisher can expect to make on average less than $6 a day (all figures in US$). From this, he must purchase fishing gear, pay for fuel, and support a family of five people. Most people have remained in the fishery either to supplement other incomes, or because they have no alternative. Fishing is given up or reduced when a person has better opportunities elsewhere, and resumed or intensified when times are bad. Multiple occupations are common in the Caribbean, and allow people to increase their economic security. Although a fisher's net income is small, it is in line with other lower income work available in Jamaica. A waiter in a hotel could expect to earn $9 a day, and a scuba-diving guide between $7 to $12 a day. Day laborers can expect to make about $5 to $8 a day. However, other jobs are scarce on the north coast and, in any case, many fishers prefer the independent life-style of fishing.

Improvement of the productivity of an over-exploited fishery depends upon reducing fishing effort. This is always difficult for fishers who are already making very little money. Moreover, in a coral reef fishery, only a few measures are practicable (Munro and Williams, 1985). These include the use of more selective gear, limited entry to the fishery, and protected areas. Marine Protected Areas (MPAs), specifically no-take reserves, are increasingly recommended for the enhancement of depleted coral reef fisheries (eg Bohnsack 1996). Such reserves are often created from the "top, down" and rarely from the "bottom, up", but there are good Caribbean examples of the latter in St. Lucia (Jennings-Clark 1992, Roberts and Hawkins 1997). This paper, which complements that of Woodley and Sary (in press), describes the creation of a no-take MPA at Discovery Bay, Jamaica, by collaboration between a university-based facilitating agency and local fishers. The objective is to enhance local fisheries with a reserve planned from the bottom up, but to be operated within a co-management framework established by government.

METHODS AND BACKGROUND

Study area. Discovery Bay is in the middle of the north coast of Jamaica (Fig. 1). The shallow-water marine environment, both outside and inside the bay (Fig. 1), is dominated by coral reefs and associated habitats (Woodley and Robinson 1977; Gayle and Woodley 1998). The reefs are best developed on the submarine shelf outside the bay. The entrance to the bay has been excavated to make a shipping channel, 12 m deep. In the middle of the bay there is deep water, with shallow sandy lagoons all around, supporting beds of turtle-grass, scattered coral heads and patch reefs. On the steep slopes towards the centre, coral reefs occur down to about 20m, especially at Columbus Park and Red Buoy Reef. All reefs in the area were in good condition until hurricane Allen (1980), the first of a series of impacts (including coral disease, *Diadema* mass mortality, coral bleaching) that, superimposed on chronic over-fishing, led to a catastrophic decline (Hughes 1994). The town of Discovery Bay is at the south-east corner of the bay (Fig. 1). At the south is Port Rhoades, the bauxite loading facility of the Kaiser Jamaica Bauxite Company. Other institutions include a small base for the Jamaica Defence Force Coastguard, a public beach, a small hotel, Columbus Park (which is a historical site for tourists) and the Discovery Bay Marine Laboratory of the University of the West Indies.

Discovery Bay fishing beaches. Fishermen operate from two fishing beaches (registered landing sites) which are quite distinct socially and economically (Fig. 1). Old Folly fishing beach is adjacent to a residential area (and the bauxite loading pier), and is used almost exclusively by local resident fishers; very little other activity (e.g. recreation) takes place on this beach. Top Beach is a much more active place. It is adjacent to high priced beach villas, as well as a growing squatter community, and it is used by a wide variety of people for fishing and recreation, many of whom are visitors from outside the community. There are a number of small shops on the beach, catering to fishers and visitors. The two fishing communities are even separated from each other geographically, by a large tract of rugged, undeveloped land in the middle of Discovery Bay. There is little communication or cooperation between the two fishing beaches, despite the formation of a fishing co-operative, documented in this paper.

The principal target area for Discovery Bay fishers is the shelf outside the bay, which is roughly apportioned between the two beaches: after exiting the ship channel, men from Top Bay generally turn to the East, and those from Old Folly turn

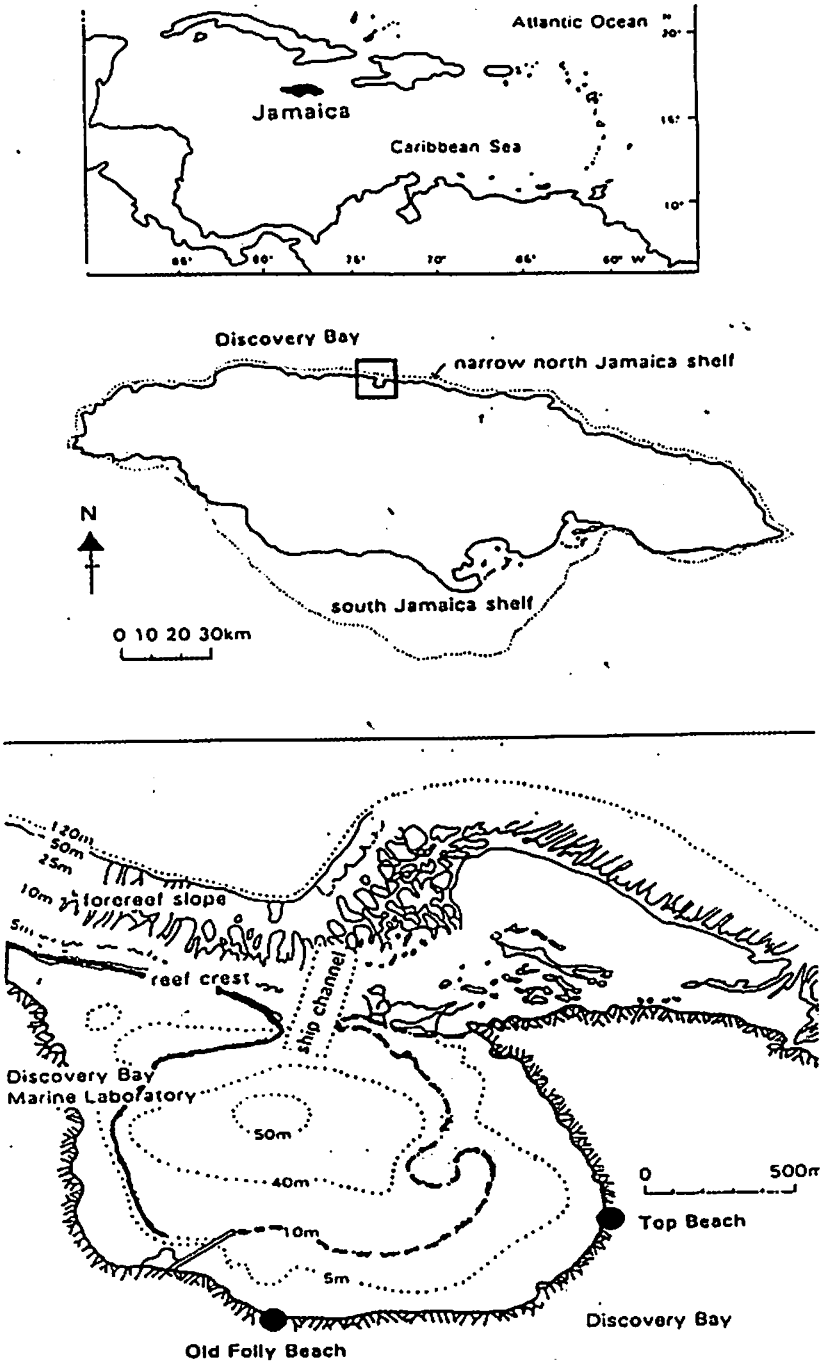


Figure. 1. Map of Jamaica showing the 100 m depth , the location of Discovery Bay and its two fishing beaches and the outline of the Discovery Bay Fisheries Reserve (solid line) and the extension proposed in 1999 (dashed line).

to the West (Allison 1992). The distance that they travel to the East and West is determined by the logistics of travel and the possibility of interference with their gear, which increases with proximity to adjacent communities. Bay fishers may occasionally travel beyond their regular fishing area. Among those who fish within Discovery Bay itself are the young, the old, and other fishers in bad weather.

Fishing effort at Discovery Bay. Approximately 50 active fishers use the two beaches, almost half of them relying on fishing as their sole income earning activity. Generally, each fisher supports another 4 people on their fishing income. Until the mid-1980s, women worked on the beaches as vendors, buying from the fishers (all men) as they returned. Since then, they have been displaced by consumers, who buy up the small catches directly. Over two thirds of fishers own a boat. The majority of these are small, usually unmotorized, wooden canoes about 15 feet in length while the remaining third of the boats are the standard Jamaican 27 foot reinforced fiberglass open canoes, all of which are powered by outboard engines (usually 35 to 65 hp). Many fishers use more than one gear type on each fishing trip. More than half use fishtraps as their primary or secondary gear, owning about 7 traps each. About 45% of fishers use hook and line, and 12% use nets. A tenth of the fishers are full or part time spear fishers, but many other spearfishers have not been enumerated, including a few who fish at night with lamps and SCUBA.

On average, about 6 fishing boats operate every day on the narrow fringing reef in or outside of Discovery Bay. About 4 of these boats are non-motorized. The 6 boats have a total of about 9 people operating from them (captain, share fishers, and crew). In addition, at least 4 spear fishers are fishing in the area. This represents over 2,100 boat trips per year, and over 1,500 spear fishing days per year. Trap fishing boats haul an average of 5 traps per fishing trip. Thus, during the estimated 1,400 trap fishing trips (or boat days) in the area during the year, nearly 7,500 trap hauls are made. Nearly 85% of the trap hauls are of 1.25" mesh traps, and the rest are of 1.5" mesh traps (there appear to be no 1" mesh traps active in the fishery). About 600 boat days are spent hook and line fishing, most of them for drop line fishing; trolling may be done on the way to fishing grounds, but it is rarely the main purpose of a trip. Hook and line fishers target both shallow reef fish stocks and very deep snapper stocks. A small number of fishers use gill nets, setting their nets in shallow reef areas.

The total catch of all fishing in the study area (about 3 km ^{2}) is about 14 tons per year, worth about $88,000. Shared among the approximately 48 active fishers in the area, it represent a yearly income of about $1,850 for the average fisher. The cost of entering and remaining in the fishery is high, except for spear fishing, primarily due to the capital needed to obtain and maintain a boat. Other costs of fishing depend on the method involved: high for trolling, moderately high for traps, less for nets and drop lines, least for spearfishing.

The facilitating agency. The obvious need for management led to the creation, at the Discovery Bay Marine Laboratory (DBML), of the Fisheries Improvement Programme (FIP, Sandeman and Woodley 1994, Woodley and Sary in press). Support from various agencies maintained the program, at levels of staffing ranging from 1 to 5, from 1988 to 2001. Its aims were: to assess the state of the fishery; to discuss the state of the fishery, and possible remediation, with local fishers, while increasing their awareness of the possibilities of coral reef management; to help local fishers introduce fishery management measures; and then to monitor the effects of these measures on fish stocks and catches. An early survey revealed that MPAs were the least unpopular of proposed management measures (with about 30% support), since they would affect people using all gear types equally (Vatcher 1994). FIP worked on other management issues, notably changes in trap mesh size (Sary et al., 1997), but they are not discussed here. Most of the staff were university graduates in biology, while some of the education officers had more training in social sciences (anthropology and environmental education; development studies; agriculture). From 1995, interested people, some of them the children of fisherfolk, were recruited into the Programme from the local community and trained in fish identification and fishery management.

Development of participatory management. Some strategies pursued by FIP on its early days (1988-1993) were general preparation for participatory management; the specific focus on an MPA came later.

Education. The primary contact of FIP staff with the fishing community was through collecting catch-and-effort data when boats returned to the fishing beaches in the mornings. Informal discussion of fishery-related matters was carried out when staff interacted socially with fishers (e.g. while waiting at the beaches for boats that were still at sea). A more formal program of environmental and fishery education was the specific task of designated Education Officers, employed when funds were available. Its initial aims were to increase fishers' knowledge of the fishery resources, to encourage a sustainable approach to fishery management and to promote changes in fishing behaviour expected to result in long-term improvement of fish stocks and catches (Van Barneveld et al. 1996). A varied approach was necessary since the fishermen differed in educational level, fished at diverse times and places, and did not meet as a group. Their knowledge, fishing practices and attitudes to fishery management were assessed by an initial questionnaire (Vatcher 1994), and later re-assessed. At both of the fishing beaches, FIP staff erected notice boards, which were used to display material of local and general interest. These included educational posters, articles from the press, notices from the Fisheries Division of the Ministry of Agriculture, and notices of local meetings. FIP also showed slides and videos, and encouraged visiting scientists to address the fishers about their own work. Increasing numbers of educational videos became available, describing marine ecology and fishery management in other countries, which were well received by fishers. For a while, "video nights" were frequent, combining educational features with more conventional entertainment. In 1991, one of us (W.L.) made a video, with the participation of the Discovery Bay fishing community, entitled "Fish today, Fish tomorrow? Tradition and change in a Jamaican Fishing Community". In 1998, another video was made about the work of FIP, with funding from CFRAMP, entitled "Fishing for a brighter future". In 1997-99, when the Fisheries Reserve was operational, a newsletter, "Fishlinks", was prepared and distributed to fishers, householders on the Bay, and elsewhere in the community.

Alternatives for fishermen. The area from which fishers were displaced by the proposed Reserve was small, and not many men were involved. Nonetheless, as part of the move to reduce reef fishing effort and to explore other sources of income for the fishers, some possible alternative occupations were explored. First was Irish Moss (*Gracilaria*) culture, as developed by CANARI in St. Lucia. Male and female members of the fishing community were taken to demonstrations organized in Jamaica by Dr. Alan Smith, and to a course in St. Lucia. Meanwhile, FIP staff cultured the alga on rafts, following the lead of Macfarlane (1991). Secondly, Dr. R.D. Steele developed floating cage culture of red hybrid *Tilapia* at Discovery Bay with the aim of making the method available to local fishers (Malcolm and Steele in press). Thirdly, funds have been requested to support exploratory offshore fishing, using a new 10 m boat belonging to DBML.

Encouragement of fishers' organizations. It was believed by FIP that the needs of individual fishers would be more effectively articulated by a group organization. In particular, it was felt that a co-operative society might help to develop a community-based approach to fishery problems (Van Barneveld et al. 1996). While wanting to encourage the formation of such a group, we recognized that fishers had been discouraged by the failure of at least two previous attempts to form a fishers' organization at Discovery Bay: one because the treasurer absconded with its money, the other because it had been set up by a well-meaning outsider without any commitment from its members. We took some men to meetings of apparently successful fishing co-operatives on the south coast and to other fishing-related events. In 1991, some men from Old Folly asked for assistance from FIP in establishing a co-operative society. This was no easy task, partly because it was the policy of the Co-operative Department to support larger groups rather than small ones, which were deemed unviable. So the new body became the Alloa Discovery Bay Fishermen's Association (ADBFA), named after the property on which the fishing beach was located.

Formation of the Reserve Planning Group. In 1995, after a Reserve had been proposed (see Results), a Reserve Planning Group (RPG) was formed, and began to meet monthly. Its members were drawn from organizations with an interest in the waters of Discovery Bay, namely: ADBFA, Top Bay fishing beach, Jamaica Defence Force Coastguard, Kaiser Jamaica Bauxite Company and DBML. Two members of FIP acted as Chair and Recording Secretary. ADBFA was represented by four members and the other organizations by one each.

Contract with Fishermens' Association. Running costs for the Reserve, chiefly to hire rangers, had been included in a grant from the Kaiser Jamaica Bauxite Company to the University of the West Indies (UWI) for FIP. In order to foster a sense of stewardship among the fishers, this money, and the responsibility to hire staff, were transferred to them. In 1996, UWI and the ADBFA entered into a contract under which the Association agreed to operate the Reserve, subject to the guidance of the RPG. The Association would employ rangers to patrol the area, in exchange for monthly transfer of funds from UWI, while FIP would certify that the work was done and the money properly accounted for.

Marking of the Reserve, and daily patrols. The ADBFA selected four rangers and a supervisor, who were themselves fishermen or relatives of fishermen. They were trained by the JDF Coastguard and by rangers from the Montego Bay Marine Park. DBML provided large (2 ft diameter) orange buoys, and the new rangers helped to install them around the seaward margins of the Reserve (Fig. 1) in 20 m and 10 m depth. Grant funds were used to purchase a dedicated patrol boat: a small whaler, not suitable for offshore fishing, with the name PATROL painted in bright red letters on its sides. In 1996, daily patrols began, concentrating on early morning hours, when fishermen are generally most active. Since the Reserve was only voluntary, and not yet legal, the role of the rangers was advisory and educational.

Legalization of the Reserve. FIP sought to establish the Reserve as a protected area under the Natural Resources Conservation Act (1991) in 1997. A comprehensive management plan was required, as for a multi-use park, which FIP staff (then reduced) found difficult to compile. Discussion with members of the Fisheries Division in 1999 established that it would be more appropriate, and quicker, to have the Reserve gazetted as a Fish Sanctuary under the Fishing Industry Act (1975). An explanatory document, including a brief management plan with precise co-ordinates of the proposed protected area, was requested.

Research on the fishery. The effectiveness of the Reserve was studied from 1996 to 1999 by an ICLARM project (Munro 1999). One inch mesh traps were used to monitor the size and abundance of reef-fish within the Reserve. In addition, nearly 7,000 fish were caught, marked and released there. Recaptures were sought by continued trapping in the Reserve and from fishers operating elsewhere (Munro 2000). A UWI graduate student has been monitoring reef fish size and abundance by visual census but the work is not yet finished (Black-Clarke, in prep.).

RESULTS

Development of participatory management. Among Jamaican fishers, there are social and cultural constraints on the development of participatory management. Jamaica, like most of the English-speaking Caribbean, has an open-access fishery. Fishers believe that all people have a right to fish in the sea, as long as they do not infringe on the right of others to fish as well. The sea, and fishing, is viewed as a refuge where a person can go and find food when down and out, until he is able to support himself again with other resources or other work. Thus, the sea is significant for many people who do not actually fish, just as family land is significant for the many family members who do not actually live on it. This significance is greater than the sheer economic reward that may come from fishing, which may be only modest. It is an important token of security available to all people. These cultural beliefs and values color fishers' perceptions and practices concerning marine resources. The fact that the fishery is, and is seen to be, free to all, means that there is a general, though variable, resistance to the closure of coastal areas to fishing, such as in the Discovery Bay Fishery Reserve.

Fishers are not a homogeneous group; there are a number of ways fishers differentiate among themselves, a differentiation that affects their attitudes to the Reserve. These differences include the type of fishing gear used, the fishing beach they use, the degree to which fishing is a full-time or part-time occupation, and the perceived wealth of individual fishers.

The difference in type of fishing used has important implications. For example, the effect that the Reserve has on a fisher varies according to the fishing method he uses. Also, fishers tend to be suspicious of those who use other fishing gears. Trap fishers are especially suspicious of spear fishers, as the latter have been known to steal fish from traps. Trap fishers regard this issue extremely seriously. Because of the concern over theft from traps, most fishers who do not themselves use spear guns advocate a ban on spear fishing. Spearfishers respond that fishing with small mesh traps over many decades is the cause of fish stock decline, not spear fishing. There is little constructive dialogue between the groups. Trap fishers also fear theft by other boat operators, and may leave their traps unmarked, despite setting them relatively deep.

Fishers make social distinctions based on geography as well, according to the fishing beach that they use. Fishers from Old Folly tend to regard their Top Beach colleagues as rebellious and uncooperative; while Top Beach fishers seem to have little interest in the activities of the Old Folly community, or in the operation of the fishers' cooperative which is located there. When traps are interfered with, men usually suspect fishers from another beach, or another town.

Although north coast fishers are generally considered to be poor, fishers make economic and social distinctions within the group. Those seen as the richest fishers own their own fiberglass boats, and may have good paying jobs, or have lived overseas for a number of years. These distinctions of wealth and class seem to be very significant among fishers.

The various distinctions fishers make among themselves reduce the potential for co-operation among them. This lack of co-operation, with its associated fragmentation, has of course important consequences for the operation of a Reserve. There is little collective involvement by fishers because crucial elements of social life necessary for that involvement are missing or poorly developed, namely a strong sense of community and community groups willing and able to take on specific responsibilities (White et al. 1994).

Fragmentation and suspicion among fishers make it very difficult to pass information to the fishing community. Men who attend meetings do not generally relay what they have learnt to the other fishers. Moreover, because many fishers cannot read, they will not understand messages on notice-boards, unless colleagues read to them.

There is also little willingness among fishers to make individual sacrifices, such as giving up a particular gear or fishing area for the common good: the sort of sacrifice that a marine protection regime requires. This is hardly surprising, given the low income levels and the economic vulnerability of most fishers. Sacrifice is more likely to be made if fishers perceive a real and immediate personal benefit or, alternatively, if there is some guarantee that others will do the same. This resistance is not absolute, however, and is perhaps more prevalent among the younger men, but all fishers believe that those whose livelihoods are adversely affected by fishing restrictions deserve compensation.

Despite these unpromising social attitudes, there is no doubt that, on the whole, the strategies used for creation and operation of the Reserve worked. What worked and what didn't are described in the following paragraphs.

Education. The education program was most effective when conducted by a staff member with some relevant training, who was dedicated to that role. Other staff could contribute, especially during informal interaction with individuals or small groups, but had to learn some basic rules. First, to show respect to the beliefs and views of fishers, however strange they might seem to be. Education is a two-way process and, despite cultural differences, we can all learn from others. Secondly, not to be too quick to advance one's own recommendations, and not to tell people what they should be doing (unless asked). It was hard not to become promoters of management actions, and staff had to recognize that their role was mainly to provide information to the fishers, so that they could make their own decisions. Especially, we told them what coral reef fishers were doing in other parts of the world, and explained why some of these activities were effective. With respect to fish sanctuaries and other protected areas, material from the Philippines and St Lucia was particularly useful.

Some of the FIP staff were good at interaction with resource users and others were less so, irrespective of their training: personal qualities of empathy, social understanding and sociability are important. Video presentations were popular and reached a wide cross-section of the community. The availability of equipment was crucial: not only VCR and monitor but, for use near the fishing beaches, long extension cords and sometimes a portable generator.

Alternatives for fishermen. Although FIP maintained Irish moss cultures for years, and processed a small amount as a demonstration project, there was little interest among fishermen. Ideally, a culture area would be shallow, sheltered from rough seas, and not much used by others. Discovery Bay is too populous for cultures to be secure from theft, and the adjacent coastline is too rough. The experiments on cage culture of *Tilapia* (Malcolm and Steele in press) worked out how to deal with parasites and other practical problems, but have not yet addressed transfer of the technology to the fishers. One Discovery Bay fisherman stole their thunder by culturing large quantities of *Tilapia* in a small natural sink-hole. FIP members helped some fishers, interested in diving, to find jobs in water-sports.

Encouragement of fishers' organizations. The Fishermen's Association played a crucial role in bringing fishermen together and facilitating collaborative action at Discovery Bay. Its members built a meeting hall at Old Folly beach. Also, with a little help from FIP, it secured two grants: one to build a gear-store and offices, the other to supply large-mesh wire for traps. Their retail gear store now serves many fishers from the north coast, and the ADBFA became a district branch of the Jamaica Co-operative

Union. In 1999, it became the Discovery Bay Fishermen's Cooperative, eight years after the idea was first suggested. Nonetheless, inter-group rivalry is still evident. The ADBFA was established by men from the Old Folly beach and although membership is open to all, few members are from Top Bay beach. Most members are trap- or line-, rather than spearfishers.

Although not every fisherman respected its authority, the ADBFA institutionalized the processes of meeting, and making decisions. After many discussions about possible fish sanctuaries, a meeting of the ADBFA in 1994 decided to "give it a try". The area selected, to be known as the Discovery Bay Fisheries Reserve (DBFR), was in shallow water on the west side of the Bay and covered 27.5 ha (Fig. 1). Not much fishing went on there, but the men were unanimous that the Reserve should not include any of the fore-reef, which is the more productive area.

Formation of the Reserve Planning Group. The RPG has been an effective group, planning the creation and operation of the Reserve, which was to be established by voluntary action of the fishermen before legal protection was sought. The RPG discussed public relations, details of the Reserve boundaries, how they were to be marked, and how restrictions on fishing were to be enforced. Its decisions were reached by consensus, and included adjustment of the boundaries along one section, from 20 m to 10 m, to provide fishermen with an alternative fishing area for use during bad weather. FIP and the ADBFA were represented at every meeting, but attendance from the other entities was irregular. Moreover, although attempts were made to secure representation from the owners of homes on the eastern shore of the Bay (mostly business people based in Kingston), and from the small hotel on the southern shore, no-one came.

Contract with Fishermens' Association. This arrangement worked well, although funds were sometimes late in arriving from Kingston. The ADBFA committee appreciated the 10% overhead paid to the Association for administrative expenses, while UWI appreciated not having to be involved with the temporary employment of staff at long range. When staff performance was unsatisfactory, replacements were quickly hired. However, the quality of the financial accounts maintained by the ADBFA was sometimes poor, and FIP had to provide assistance.

Marking of the Reserve, and daily patrols. It had been proposed that fisher members of the RPG would be present when the marker buoys were installed, but this did not always happen. In consequence, there was some dispute, as to whether the markers had been placed at the correct depth. The large marker buoys were effective advertisement of the Reserve: smaller ones were sometimes stolen. However, large buoys are expensive, and DBML did not put out enough of them.

The rangers and their supervisor(s), never less than two in the patrol boat, carried out their advisory role in a non-threatening way, but pointing out that legal protection would soon be obtained. Most trap fishermen respected the local restrictions. The spearfishers, mostly boys, often did not, although they would say that they were only passing through on the way to the fore-reef. The RPG wanted the rangers to be on patrol at first light, when fishing began, but they were usually late. Also, they probably did not spend enough time in the Reserve, after their initial patrols.

Daily patrols continued, with occasional interruptions, into 1998, when their frequency was reduced due to shortage of funds. Meanwhile, fishermen noticed that fish numbers had increased within the Reserve, and trap fishers began to concentrate immediately outside its outer boundaries. Moreover, men based at Top Bay beach, having seen the benefits of the Reserve on the western side, asked that it be extended all around the Bay. The new boundary details were resolved by discussion among Top Bay fishers, and were accepted by the RPG. The extended Reserve (Fig. 1) covered 108 ha.

Reduced patrols were continued into August 1999, when the last of the rangers were laid off. Patrols were to have been continued on a voluntary basis by the ADBFA and FIP but, for various reasons, only one such patrol was made. In any case, because the Reserve had no legal status, continued protection was hard to maintain. It was threatened by the activities of new fishers, some from outside Discovery Bay, and by other recalcitrant individuals unwilling to comply with voluntary restrictions. By 2000, in the absence of both legal status and active patrolling, even some individuals previously compliant with the restrictions (including two former rangers) were ignoring them.

Legalization of the Reserve. The proposal to establish the DBFR as a fish sanctuary was sent to the Fisheries Division, early in 2000. Unfortunately, by then, Division staff were involved in extensive litigation concerning the conch fishing industry and, up to April 2001, had no time for other work. In 2001, although the Fisheries Division was ready to proceed with formalizing the Reserve's status as a Fish Sanctuary, some uncertainty had arisen about the acceptability of the new boundaries. The issue will be considered at a meeting in November, (the first for two years) of the Reserve Planning Group.

Research on the fishery. Studies on fish populations within the Reserve, in 1996-98, showed that protection in the Reserve delayed age and size at recruitment to the fisheries and therefore enhanced catches in adjacent waters. It was shown to supply some fish (mostly *Sparisoma* spp.) to reefs offshore for several kilometers to the east and west. Species taking up residence in the Reserve had the potential to supplement depleted spawning stock biomasses (Munro 1999, 2000).

DISCUSSION

Development of participatory management. The joint work of the Fisheries Improvement Programme and the fishers of Discovery Bay towards establishing a protected area has had many successes. The most difficult step was the first: for men to agree not to fish in even a small area, and it was preceded by years of discussion. It takes a long time for fishers to change their fishing behavior in response to external advice (A. Alcala, personal communication, 1995; funding agencies please note!). What made it easier was that western Discovery Bay was not a very popular area with trap fishers, and those who did fish there, except for a few old men, also fished outside.

Then, after protection of this area was seen by fishermen to increase the biomass of fish populations, expansion of the reserve was proposed. At that time, in 1998-99, the Reserve was at a peak of effectiveness. Its subsequent decline was due to lack of funds to continue education by patrolling, and the unexpected delay in obtaining legal backing; an event beyond our control. The educational work of the Fisheries Improvement Programme (or any other facilitating organization) is not just about fishery science, but is facilitating local social and economic development. Progress in development often follows an irregular rather than a linear trajectory, and we believe that our strategies, further discussed below, amount to an investment that will yet be rewarded.

Education. A sustained education program was of over-riding importance to the initiation and maintenance of community action. It took many forms and many lessons were learnt, particularly about social interactions between the participants in the management process. Most FIP staff were biologists, and had some training in fishery management. Nonetheless, it had not adequately prepared them all for the tasks of facilitating community action. First, it gave no training in how to work with people. Accustomed to pedagogic teaching, they expected fishermen to readily understand the potential benefits and to want to implement management very soon. They did not realize, when this work began, that for adults to absorb new ideas and change their behavior is a slow process, requiring many years. Secondly, their training encouraged them to believe that they knew what was best for the fishery. It was then difficult not to take an authoritarian approach. Thirdly, because they thought they knew best, some people were slow to appreciate that community education is a two-way process. Biologists could learn from the fishers, both about the natural history of fish and other creatures, and about the social and cultural contexts within which fishing was conducted. Some of these communication errors could have been avoided had the scientists developed more quickly a frame of mind that accepted the fishers as equal co-workers in the process of managing the fishery. Conventional surveys of "knowledge, attitudes and practices" do not always help since they tend to define fishers' experiential and cultural knowledge in terms of "higher" scientific knowledge. Their knowledge is not necessarily wrong, just different. Finally, fishery training caused potential managers to focus on what was thought best for the overall fishery in the long term, and they were not always sensitive to the immediate hardship of the fishers. A reduction in fishing effort generates short-term costs which are usually borne by the fishers. In this context, it can be very helpful if management proposals include some compensation (as in the case of the "two-for-one" mesh exchange; Sary et al. 1997), some alternative activity, or can be phased in slowly.

The interaction with fishers in the course of data collection was itself part of the mutual education process. While FIP staff were gathering useful data, they were developing familiarity with fish species and with the fishers. It was an opportunity to raise interest in fishery data and its value, while staff earned some respect through willingness to get their hands dirty, and demonstration of some knowledge of fishes. There were some negative aspects to the data collection process. First, fears that the information would be given to the tax authorities had to be allayed. More significant, it wasted fishermen's time when customers were clamoring for fish; and not all men wanted to collaborate.

Alternative strategies should be considered, in which data are collected at sea. Most important, not just for education but to show integrity and reliability, scientists must remember to share with fishers the results of data collection.

It was necessary for all participant in the development process to be in continual communication. This was not always easy, because key individuals were distributed between different parts of Discovery Bay and Kingston, 140 km away. The fact that participants moved in different walks of life and social classes did not help. Secondly, but not unrelated, it was essential to build and maintain trust between individuals and thus between the institutions which they represented (Kelleher, in press). Unfortunately, communication and the planning processes have often been disrupted through the departure of FIP staff, either through lack of funding or as expatriates returning home. It has been described as a "revolving door" at DBML for people who take up fishery issues for a while and then leave: not good for a developmental process that may take many years.

Alternatives for fishermen. It is possible that any form of mariculture, which resembles farming more than fishing, and carries continuous responsibilities for maintenance, would be perceived by fishers as imposing a less attractive lifestyle. Moreover the algae, despite their reputation as an aphrodisiac, may be perceived as a less manly product. The few individuals who followed up their interest were women.

Encouragement of fishers' organizations. The manner in which the Fishermen's Association (ADBFA) was formed, well illustrates the point about not telling others what to do. Despite their recent contrary experience, including the failed external imposition, fishers who were exposed to functioning fishers' organizations made their own decision, and asked FIP to help: not the other way round. Subsequently, the fact that the ADBFA was able to attract outside funding was powerful evidence to fishers of the benefits of an organized group. However, the flow of grant money into the ADBFA had some negative effects. Because the funds were managed by a small group, suspicions and further divisions arose. This points to a need for more transparency, and for the involvement of diverse people in any working group.

Formation of the Reserve Planning Group. When fishers from the different beaches were brought together in the RPG, discussing management measures with a wider group, their rivalry was apparent. It is not yet much diminished, but this exposure is a first step towards reducing the differences. In future, the Group must ensure that all users of the bay are represented. This should include the home-owners from the eastern shore; Portside Villas, the small hotel; Puerto Seco, the public beach. In addition, a representative of the Fisheries Division should be invited; under the new Fisheries Act, it is required to chair all such local management committees. Had the RPG kept in closer touch with the Division, the hiatus of 2000/2001 might have been avoided.

Contract with Fishermens' Association. If funds become available again for operation of the Reserve, similar arrangements are recommended.

Marking of the Reserve, and daily patrols. Although the few large orange buoys gave a general impression of the Reserve location more, slightly smaller, but labeled markers would be preferable. Some dispute over the boundaries could have been avoided had fishers always been present when the boundaries were marked.
The patrols could have been more efficient, but they were effective. Some fishermen learned that the Reserve was having a positive effect and adopted the practice of fishing close to its boundaries, as has been reported from Kenya (T.R. McClanahan, personal communication, 1996) and Florida (B. Haskell, personal communication, 1998). Moreover, fishers from Top Bay had sufficient confidence in the Reserve to request its extension. Unfortunately, the perception of more fish in the reserve creates more incentive to poach, making enforcement more difficult.

Legalization of the Reserve. All participants have learned that community action is not enough: legal status for the Reserve is essential. This would have two important effects: first, it would raise the status of the Reserve among the fishers and other citizens of Discovery Bay. Secondly, it would permit enforcement of the DBFR regulations, hitherto voluntary, by concerned fishers or by patrols from the Coastguard base in the Bay. This would be a new situation, and users of the Bay should be allowed a period of education. Moreover, since there is a fear that military personnel might use inappropriately robust methods, they too would benefit from some special training. The RPG should plan a graded suite of responses for enforcement, with legal action a rare last resort.

Outlook for the future: will the DBFR ever succeed? "Will it succeed" includes (a) will it gain legal existence; (b) will it benefit the people of Discovery Bay; and (c) can it be sustained.

(a) The Fisheries Division is now ready and willing to move ahead with legalization of the Reserve, as soon as the Reserve Planning Group gives the go-ahead. A meeting of that Group will be convened shortly, and will review the proposed plan, including the boundaries. Legal declaration of the Protected Area could follow within months.

(b) According to preliminary work by Munro (1999), the Reserve would benefit fish, fishers and the economy. We do not yet know the full extent of those benefits and whether they will outweigh the costs; these, too, are unknown. It is true that only a few trap-fishers and migrant spearfishers will be displaced and running costs could be low, but those calculations should be made as soon as costs and benefits can be quantified. If it is concluded that the Reserve costs more than it is worth, then it could be discontinued.

An increase in the size and abundance of fish within the Reserve would also benefit shore-based recreational line-fishers (permitted in the proposed regulations) and snorkelers, including local residents and a few tourists. It would certainly be of interest to some scientists and students from DBML, particularly if an increase in abundance of fish herbivores had any positive effects on the benthic reef community. However, the great majority of DBML scientists work on the fore-reef, where it is likely that continuing high fishing pressure would prevent there being much noticeable change in fish populations.

A group that would bear some initial cost are the spearfishers who fish in the Bay. Most of these, however, are on their way to or from the fore-reef (except in bad weather) where the catches are better and should be improved by the Reserve. Nonetheless, when stocks improve within the Reserve, spearfishers will be tempted to hunt there, presenting a problem for enforcement. This problem of poaching is also an opportunity to encourage the development of a culture of community responsibility for, and management of, the resource. If it benefits all then it is in their best interests to put some of their differences aside and invest time and effort in securing it against outsiders or against residents who would exploit it to the detriment of other locals willing to make a short term sacrifice for the long term good.

(c) Would the Reserve be sustainable? It was maintained fairly well for three years by advisory patrols who established a degree of voluntary compliance among local fishers. However, it was becoming more difficult when the legal status that had been promised did not materialize. Moreover, the patrols cost about US$15,000 per year, and funding at that level is unlikely to be available. If the Coastguard were able to patrol the Reserve without charge, that would be a huge advantage. Such funds as were obtained could then be used for education and logistic matters.

Education should remain a high priority, to help develop community support for the Reserve. Such support was beginning to develop spontaneously in 1998-99, as the benefits of protection were perceived. If that level of protection is achieved again, the increasing numbers of "believers" might reach a critical mass after which growth would be self-sustaining. It is good that environmental education is now included in Jamaican primary and secondary school curricula. The development of local pride and peer pressure would be the best guarantee of sustainability.

A continuing education program would be run from the Discovery Bay Marine Laboratory, as have others, on and off, for the last 20 years. This has some drawbacks. Fishers may reasonably suspect that DBML has something to gain from a Reserve, perhaps more than the fishers have. This may be reinforced by the perception that Lab staff, sometimes expatriate, gain jobs and degrees while working with the fishers, who seem to gain little from their work. That is partly a consequence of FIP's failure to adequately inform fishers about the results of their research; notably the apparent benefits of the mesh exchange (Sary et al., 1997; Sary et al., 2001) and the Fisheries Reserve (Munro, 1999, 2000).

Operation of the Reserve would be driven by a Management Committee representing all stakeholders, which would be a formal upgrade of the existing Reserve Planning Group. It would still be necessary, at first, for DBML to assist with the material and logistic operation of the Reserve. While the allocation of a contract for patrolling the Reserve to the Alloa Discovery Bay Fishermen's Association undoubtedly focused their minds and effort on the tasks, doubts remain about the ability of local organizations to operate long-term social programs. Some of us despair about contemporary Jamaican society and prevalent negative attitudes, especially in the young, towards anything that requires discipline, sacrifice and perseverance. Perhaps, as in other "Western" societies, this is partly a consequence of the capitalist promotion of individuality and competition. For a community group to function well, one needs a culture of co-operation, trust, avenues for dialogue, respect for democratic decision-making, and the ability to gather and use available information (literacy is a big help). With reference to Jamaican society Espeut (2001) made the point that "discipline does not just happen, it has to be managed - like development.. Where the infrastructure for discipline is in place - including the right values - people often develop orderly habits and a culture of discipline that makes for easy social interaction".If it is not in place, community education is an uphill task, and the establishment of community-run protected areas will take many years.

In any case, it is now widely recognized that it takes a long time for people to change their ways, and the creation of MPAs is no exception. FIP's work in Discovery Bay, like its funding, has been intermittent, with frequent shortage of staff, and this has slowed its progress. In any case, local action alone is not enough: neither top-down nor bottom-up approaches to management can work in isolation. Best is some form of co-management, in which Government provides a framework of education, legislation and enforcement that is supportive of community participation in environmental management. Senior staff at the Centre for Marine Sciences, University of the West Indies, are determined to continue the efforts in support of fish conservation and fishery development, with help from the citizens of Discovery Bay and from the Fisheries Division.

ACKNOWLEDGMENTS

We gratefully acknowledge the participation of other FIP staff, from Trent University, University of the West Indies, Canadian Universities Service Overseas (CUSO) and the United States Peace Corps; and committee members of the Alloa Discovery Bay Fishermens' Association (now Co-operative), led by Patrick Gibson and Shirley Williams. The Fisheries Improvement Programme has been funded, successively, by the Canadian International Development Agency (CIDA), the International Development Research Centre (IDRC), the Kaiser Jamaica Bauxite Company, the Canada Cooperation Fund (Green Fund, Canadian High Commission, Kingston), the CARICOM Fisheries Research and Management Program (CFRAMP), and the International Center for Living Aquatic Resources Management (ICLARM). Recent work by Z.S. on behalf of ICLARM was funded by the United Kingdom Department for International Development. We are very grateful to them all. We also thank Catherine Woodley for her critical comments.

LITERATURE CITED

Aiken, K.A. 1993. Jamaica. In: FAO, ed. Marine fishery resources of the Antilles: Lesser Antilles, Puerto Rico and Hispaniola, Jamaica, Cuba. FAO Fish Tech Pap 326, p 159-180.

Allison, W.R. 1992. The Discovery Bay Fisheries Improvement Project: a status report.

Proceedings, 42nd Gulf & Caribbean Fisheries Institute, Ocho Rios, Jamaica, November1989) p. 331-337.

Bohnsack, J.A. 1996. Maintenance and recovery of reef fishery productivity. In: N.V.C. Polunin and C.M. Roberts, eds. Reef Fisheries. Chapman and Hall, New York, U.S.A., p. 283-313.

Espeut, P. 2001. Article. Daily Gleaner, October 2001.

Gayle, P.M.H. and J.D. Woodley. 1998. Discovery Bay, Jamaica. In: UNESCO. CARICOMP - Caribbean coral reef seagrass and mangrove sites. Coastal region and small islands papers 3, UNESCO, Paris, France, p. 17-33.

Hughes, T.P. 1994. Catastrophes, phase-shifts, and large scale degradation of a Caribbean coral reef. Science 265: 1547-1552.

Hughes, T.P., D.C. Reed & M-J. Boyle. 1987. Herbivory on coral reefs: community structure following mass mortalities of sea-urchins. Journal of Experimental Marine Biology and Ecology. 113: 39-59.

Jennings-Clark, S. 1992. Case Study - Marine resource conflicts and the problems related to the effective management of protected areas along the Souffriere coast, St. Lucia. In: T. van't Hof, ed. Resolving common issues and problems of marine protected areas in the Caribbean, Caribbean Conservation Association, Barbados, p 41-47.

Kelleher, G. In press. The development and establishment of CRMPAs. Proceedings, 9th International Coral Reef Conference, Nusa Dua, Bali, Indonesia, 23-27 October 2000.

Macfarlane, A.H. 1991. The mariculture potential of *Gracilaria* species (Rhodophyta) in Jamaican nitrate-enriched back-reef habitats: growth, nutrient uptake and elemental composition. M.S. thesis. University of Miami, Miami, Florida, U.S.A. 96 p.

Malcolm, L. and R.D. Steele. In press. *Tilapia* mariculture in Jamaica: environmental and economic feasibility. Proceedings, Gulf & Caribbean Fisheries Institute, 54th annual meeting, Providenciales, Turks & Caicos Islands, 12-17 November 2001.

Munro, J.L., ed. 1983. Caribbean coral reef fishery resources ICLARM Studies and Reviews 7, International Centre for Living Aquatic Resources Management, Manila, Luzon, Philippines

Munro, J.L. 1999. Marine Protected areas and the management of coral reef fisheries. Technical Report of ICLARM Caribbean/Eastern Pacific Office, Tortola, British Virgin Islands. 40 p.

Munro, J.L. 2000. Outmigration and movement of tagged coral reef fish in a marine fishery reserve in Jamaica. Proceedings, Gulf & Caribbean Fisheries Institute, 51st annual meeting, St. Croix, U.S. Virgin Islands, November 1998, 557-568.

Munro, J.L. and D.M. Williams. 1985. Assessment and management of coral reef fisheries: biological, environmental and socio-economic aspects. Proceedings 5th International Coral Reef Congress, 1985, 4: 545-581.

Picou-Gill, M., J.D. Woodley, M. Miller, Z. Sary, W. Van Barneveld, S. Vatcher and D. Brown. 1996. Catch analysis at Discovery Bay, Jamaica: the status of an artisanal fishery. Proceedings, Gulf & Caribbean Fisheries Institute, 44th annual meeting, Nassau, Bahamas, November 1991, p. 686-693.

Picou-Gill, M., J.D. Woodley, M. Miller, Z. Sary, W. Van Barneveld, S. Vatcher and D. Brown. 1996. Catch analysis at Discovery Bay, Jamaica: the status of an artisanal fishery. Proceedings, Gulf & Caribbean Fisheries Institute, 44th annual meeting, Nassau, Bahamas, November 1991, p. 686-693.

Roberts, C.M. 1995. Effects of fishing on the ecosystem structure of coral reefs. Conservation Biology 9: 988-995.

Roberts, C.M. and J. P. Hawkins. 1997. How small can a marine reserve be and still be effective? Coral Reefs 16:150.

Sandeman, I.M. and J.D. Woodley. 1994. Jamaica north coast fisheries improvement project: final report to the Canadian International Development Agency. CIDA Report 504/13778, Ottawa, Ontario, Canada.

Sary, Z. The small-scale fishery on the central north coast of Jamaica in 2000-2001: A biological and socio-economic survey. ICLARM Caribbean/Eastern Pacific Office, Technical Report 27 p. plus CD-ROM

Sary, Z., H.A. Oxenford and J.D. Woodley. 1997. Effects of an increase in trap mesh size on an over-exploited coral reef fishery at Discovery Bay, Jamaica. Marine Ecology Progress Series 154:107-120.

Sary, Z., J.L. Munro and J.D. Woodley. In press. Status report on a Jamaican reef fishery: current value and the costs of non-management. Gulf & Caribbean Fisheries Institute, 54th annual meeting, Providenciales, Turks & Caicos Islands, 12-17 November 2001.

Van Barneveld, W., Z. Sary, J.D. Woodley, M. Miller and M. Picou-Gill. 1996. Towards the co-operative management of fishing in Discovery Bay, Jamaica: the role of the Fisheries Improvement Project. Gulf & Caribbean Fisheries Institute, 44th annual meeting, Nassau, Bahamas, November 1991, p. 195-210.

Vatcher S (1994) The Fisheries Improvement Project: Biological and socio-economic findings. Gulf & Caribbean Fisheries Institute, 43rd annual meeting, Nassau, Bahamas, November 1991, p. 17.

White, A.T., L.Z. Hale, Y. Renard and L. Cortes. 1994. Collaborative and Community-based Management of Coral Reefs: Lessons from Experience. Kumarian Press, West Hartford, Connecticut, U.S.A.

Woodley, J.D. and E. Robinson. 1977. Field Guidebook to the Ancient and Modern Reefs of Jamaica. Atlantic Reef Committee, University of Miami, Miami, Florida, U.S.A. 33 p.

Woodley, J.D.and Z. Sary. In press. Development of a locally-managed fisheries reserve at Discovery Bay, Jamaica. Proceedings, 9th International Coral Reef Conference, Nusa Dua, Bali, Indonesia, 23-27 October 2000.

ICLARM
THE WORLD FISH CENTER

THE SMALL SCALE REEF FISHERY ON THE CENTRAL NORTH COAST OF JAMAICA IN 2000-2001: A BIOLOGICAL AND SOCIO-ECONOMIC SURVEY.

by

ZSOLT SARY
ICLARM Caribbean/ Eastern Pacific Office
158 Inland Messenger Service, Road Town, Tortola
British Virgin Islands

Caribbean Marine Protected Areas Project
funded by
United Kingdom Department for International Development

CARIBBEAN/ EASTERN PACIFIC OFFICE TECHNICAL REPORT

November 2001

THE SMALL SCALE REEF FISHERY ON THE CENTRAL NORTH COAST OF JAMAICA:
A BIOLOGICAL AND SOCIO-ECONOMIC SURVEY FROM RIO BUENO (TRELAWNY) TO SALEM (ST. ANN), 2000-2001.

ABSTRACT

This report provides detailed catch and effort information on the reef fishery on the north coast of Jamaica. The study area covered is from Rio Bueno, Trelawny, to Salem, St. Ann, a 22 km long segment of the central north coast. The reef fishery there is typical of the rest of the fishery on this coast, which is believed to be one of the most overfished in the Caribbean. The resource is easily accessible and it is an important source of food and employment, despite its overexploited state.

The estimated current fishing effort in the 12 km^2 study area was over 7000 boat trips per year using traps, lines, or nets. In addition, over 5000 spear fishing trips were made per year. The average income was between US$13 and $29 per trip. The total catch in the study area was about 60 tons per year, worth about $300,000. Despite its overexploited state, the productivity of the reef fishery has remained high, with an estimated yield of 5 tons km^{-2}.

Changes in fish trap catches were examined between 1996 and 2001. The catches remained under 1 kg per trap haul over this time period. There was a slight increase in trap catches and catch value, which increased to a little more than $4 per trap haul. However, the average fish size in the catch decreased and there were more lower valued (common) species in the catch in 2000/01 than before. The average fish size in all commercial categories appeared to drop.

Management measures that could rebuild fish stocks were suggested a quarter of a century ago. However, the central government has not been able to introduce the measures that are necessary to rebuild the fish populations. The University of the West Indies has attempted to introduce a number of management initiatives on a small scale around Discovery Bay, such as a move to larger mesh sizes for fish traps and the establishment of the Discovery Bay Fishery Reserve. Despite some local successes, these management strategies have not been applied on a wider scale.

TABLE OF CONTENT

ACKNOWLEDGEMENTS

This study was part of the work of the Caribbean Marine Protected Areas Project, funded by the United Kingdom Department for International Development. Dr. John L. Munro provided the senior technical direction and overview throughout the study. The report also benefited from the valuable comments of Dr. Jeremy D. Woodley of the Centre for Marine Sciences, University of the West Indies (UWI), Jamaica, as well as from Dr. Ivor D. Williams and Robert M. Power of the ICLARM Caribbean/Eastern Pacific Office (CEPO), BVI. Miss Nadine Earle [Fisheries Improvement Programme (FIP), UWI] and Mr. John Samuels (ICLARM CEPO) collected the vast majority of the data on the fishing beaches, with assistance from several UWI graduate students. Data for 1996-97 were collected by staff of UWI FIP, funded by the Kaiser Jamaica Bauxite Company. I would like to thank the fishers of the area for their assistance in answering all of our questions and allowing us to weigh their catches.

INTRODUCTION

When coral reef researchers or fishery managers look for a case study in Caribbean overfishing, they often think of Jamaica. The reefs on the north coast of the island in particular are recognized as one of the most intensely overfished shallow coralline reef areas in the entire region. This widespread recognition of the problem is largely due to 30 years of research on the reefs of Discovery Bay and the numerous publications reporting the lack of fish there (for example Munro 1983, Aiken and Haughton 1987, Picou-Gill *et al* 1991, Hughes 1994). This paper provides a detailed, updated status report on the fishery on the north coast of Jamaica and it expands on the information presented in Sary *et al* (in press).

Several different fishing methods are commonly used in the Jamaican reef fishery: trap, net (both seine and trammel), drop line, trolling line and spearing. Antillean Z trap is the predominant gear type. The majority of fishing boats on the north coast are small, usually unmotorized wooden canoes, but there are a number of the larger, Jamaican type, 27 foot motorized fiberglass open canoes.

The demand for fish and fish products in Jamaica far exceeds the available local supply. High demand causes the price of fresh fish to be high, despite the fact that most of the local catch is comprised of small species, which would be categorized as trash fish in most other countries. The most common species in the catch are small parrots (e.g. *Sparisoma aurofrenatum*) and surgeonfish (e.g. *Acanthurus bahianus*) (Sary *et al* 1997).

A variety of management tools have been suggested for the management of reef fisheries and there are several reviews of these options (e.g. Munro and Williams 1985; Mahon 1989). Some management measures have been implemented locally, with the assistance of the Discovery Bay Marine Laboratory of the University of the West Indies, on a small scale and in the short term. These included introducing a larger mesh size for fish traps and the establishment of a small fishery reserve, but these strategies have not been applied on a wider scale. Fishers themselves have not taken the initiative to improve the situation, though they all agreed that the fishery is deteriorating. Instead, they have intensified their fishing effort over the years, with greater energy put into catching what is left (Aiken & Haughton 1987).

The study area of Rio Bueno to Salem straddled the Trelawny - St. Ann parish border and it covered approximately 22 km of coastline (Figure 1). The area lies in the centre of the north coast of Jamaica and the reef fishery there is probably very typical of those along the entire coast. The coral reefs lie on a very narrow, accessible submarine shelf. The coral reef fishery is an important source of food and employment, despite its overexploited state. Its open access nature, coupled with high human population growth and intense economic pressures have drawn large numbers of people into the fishery.

The aim of this paper was to quantify the economic importance of the fishery to the local communities. Five separate fishing beaches adjacent to or in Discovery Bay were examined, to assess fishing effort, catches, fishers' incomes, as well as other social and economic indicators.

METHODS

Collection Of Catch And Effort Data

Catch and effort data in the Jamaican north coast artisanal reef fishery was collected from 19 July 2000 to 18 July 2001 at five landing sites in and adjacent to Discovery Bay (Rio Bueno; Old Folly and Top Beach in Discovery Bay; Runaway Bay; and Salem; Figure 1) three or four times a week, on randomized pre-determined days. The survey area covered 26 km of shelf edge at a depth of 100 m and a fishing area of approximately 12 km^2. This excluded the central part of Discovery Bay greater than 30 m deep, which is not fished and is not coralline. To encourage cooperation from fishers, inducements were offered in the form of one ticket in a raffle, held at the end of the survey, for every 10 kg of detailed catch data provided, or one ticket for 25 kg of aggregated catch data.

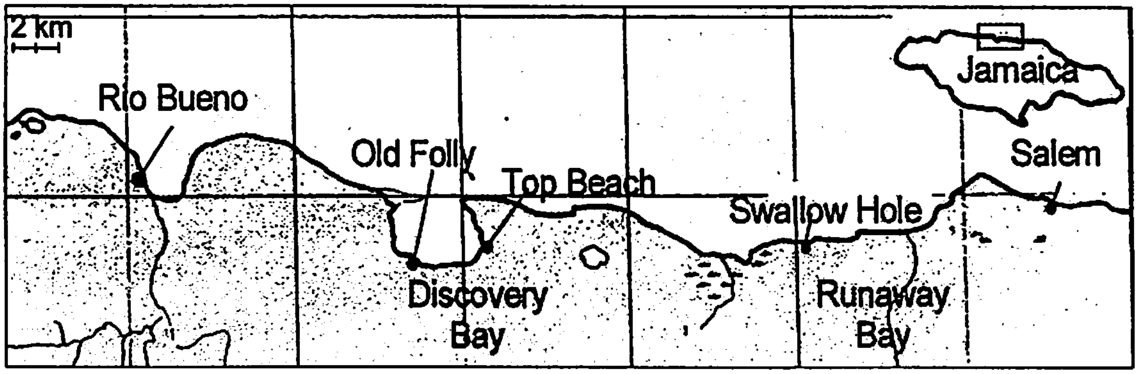


Figure 1. Map of Jamaica, showing study area and the five landing sites.

On each data collection day, the number of active boats (at sea that day), motorized and unmotorized, was enumerated by counting the incoming boats as they were landing on the beach, by counting the empty spaces among the rows of boats and from information from key informants. The number of inactive (seaworthy) boats were also counted at the site. The number of days when fishing was not possible, due to bad weather, was noted.

From the active boats landing at the site, the number of fish and the total weight of each species (to the nearest 0.01 kg) of all catches landed at that site were recorded separately for all consenting fishers (Photograph 1). If sorting of the catch was not possible, an attempt was made to record the total number of fish and total weight of the catch. Fishing effort information (time spent at sea, number of crew members, the number of fish traps hauled, average soak time of gear, mesh size of each fish trap or net, depth fished) was also collected whenever possible. The number of boats missed by the data collectors (due to unusual landing time, too many boats landing at once or uncooperative fishers), was also counted and recorded; the type of fishing gear most likely used by the missed boats was noted.

During the course of the survey, formal interviews were also carried out among the active fishers at the five landing sites using a standard questionnaire to obtain information on the age of the fishers, full/part time status, other occupations of fishers, number of dependents, primary and secondary gear used, the number and size of boats used, number and size of engines used and the number of fish traps of various mesh sizes and other

Photograph 1. Catch and effort data collection at Rio Bueno fishing beach, Trelawny, July 2000. Data collectors are John Samuels, Nadine Earle and Moana Murray, overseen by Dr. John L. Munro.

Photograph 2. Almost 70% of the fishers use Antillean Z-traps as their primary or secondary fishing gear. Salem, St. Ann, November 2000.

gears used in the fishery.

In addition, unpublished catch and effort data, obtained in a similar way to that described above from the same five landing sites, collected by the UWI's Fisheries Improvement Programme (UWI/FIP) from January 1996 to December 1997, was collated and used to examine changes in catch rates in the fishery over the last 5 years. Other sources of data concerning the fishery in the area are the works of Nembhard (1970), Sahney (1983), Munro (1983), Haughton (1988), Picou-Gill et al (1996) Sary et al (1997) and Sary et al (in press).

Data Analysis

Fishing Effort: Fishing effort at each of the five landing sites and overall in the study area, were quantified using the following units of effort: number of active boats (separately for fish trap, net and hook and line fishing), number of share fishers (accompanying the boat captains but keeping their catches separate), number of fish trap hauls (by mesh size) and number of spearfishers (most of them fishing without a boat). In addition, the number of hours spent at sea by each boat (by gear type) and by each spearfisher, as well as the average soak time of traps was also estimated.

The total number of active boats (or boat days) in the fishery per year was estimated for each gear type by calculating the average number of boats that were active on data collection days, multiplied by 365. The total numbers of active share fishers and crew members were estimated in a similar way. Even though fishers may have practiced more than one type of fishing on a fishing trip (e.g. spearfishers often use nets to corral fish; trap fishers often troll a line to and from the fishing grounds), only the primary gear employed on the fishing trip was counted in the effort information.

The total number of trap hauls (separately by mesh size) at each landing site and overall in the study area, was estimated by calculating the average number of trap hauls per active boat in the fishery, multiplied by the total number of boat days within the 12 month period. In addition, the total number of active traps in the fishery was estimated from the fishers' survey.

The total number of active spearfishers (or spear fishing days) was calculated from the number of spearfishers observed in the water from boat cruises within each fishing area multiplied by the estimated proportion of days with fishing activity (with favourable weather).

Boat catch rates: Mean catch rates for fish trap, net and hook and line fishers (in kg boat^{-1} day^{-1}) and for spearfishers (in kg fisher^{-1} day^{-1}) was calculated from sampled catches for the most important species, as well as for each fish family, in the catch. The total catch for the 12 month period, for each landing site (in kg site^{-1} year^{-1}) and for the overall study area (in kg area^{-1} year^{-1}), was estimated by multiplying the mean catch rate per boat (or per spearfisher) by the estimated number of boat days (or spear fishing days) for each species, or fish family, in the catch.

Economic analyses: To estimate the value of the catch in each fishery, fish species were classified into three commercial categories: quality, common and trash, with a corresponding monetary value per unit weight. Based on these three categories, the value of an average catch of each fishing gear was calculated (in US$ fisher^{-1} day^{-1}; rounded to the nearest $1) from the boat catch rates. Then the total value of each fishery at each landing site (in US$ $site^{-1}$ $year^{-1}$) and overall in the study area (in US$ $area^{-1}$ $year^{-1}$; rounded to 3 significant figures) was estimated. This is a somewhat simplified view of the actual situation, where fish are categorized not only by species, but also by size. For example, all snappers were categorized as high quality, although a very small juvenile snapper would be sold as a low quality fish. Therefore, the value of the catch may have been somewhat overestimated if a large proportion of it consisted of small juveniles.

Information on the costs of fishing gears was obtained from the Jamaica Cooperative Union (the main supplier of fishing gear on the island), the Alloa Fishermen's Cooperative (which operates a fishing gear store in Discovery Bay) and from available literature.

Changes in fish trap catch rates: Changes in fish trap catch rates were used as an indicator of changes that may have taken place in the fish stocks that are available to the fishery. The mean catch rates of 1.25" mesh fish traps were calculated (in grams $trap^{-1}$ $haul^{-1}$; and in number of fish $trap^{-1}$ $haul^{-1}$) for three 12-month periods (in 1996, 1997 and 2000-2001) in the study area, for each fish family in the catch. Catch rates of only the 1.25" inch mesh fish traps (the most common mesh size in the fishery), were included, in order to provide a consistent basis for comparison between years in this area and between other studies.

To calculate mean catch rates, first the trap catch rates for each individual sampled catch were calculated (catch divided by the number of fish traps hauled, as reported by the fisher); then the mean trap catch rates among all the sampled catches were calculated. This method of calculating the fish trap catch rates relies on information provided by the fisher (number of traps hauled) which is subject to mis-reporting, but nevertheless it is believed to be relatively accurate. The standard error is shown for each calculation to give an indication whether differences between the years are likely to be significant. Finally, the mean fish size (in grams) is derived for all fish families in the catch, by dividing the calculated mean weight of the catch (grams $trap^{-1}$ $haul^{-1}$) by the calculated number of fish in the catch (number of fish $trap^{-1}$ $haul^{-1}$).

RESULTS

Data Collection

The data collection effort for this study is summarized in Table 1. The total number of data collection days was 174, or approximately 10% of all beach landing days in the one year period (5 sites x 365 days). Each landing site was sampled on average 35 times, although the larger, busier, sites (Rio Bueno, Top Beach and Salem) were sampled more often than the smaller ones (Old Folly and Runaway Bay). On 21% of days, fishing was not possible due to poor weather conditions.

An average of 3.9 active boats were counted per day, 61% of them non-motorized. Data collectors were able to sample the catches in detail (to species level) of 64% of active boats and another 10% were recorded as total weight only; the other 26% of boats were missed. The majority of sampled boats, about 78%, were trap fishing, while 19% were hook and line fishing and 3% were net fishing. Trap fishers were the easiest group to sample; they tended to go to sea at dawn when the sea was calm and they all returned to shore when the morning wind picked up. However, a few trap fishing boats were

Table 1. Data collection: Summary of data collection during a 12 month period at five landing sites on the central north coast of Jamaica; 19 July 2000 to 18 July 2001.

	Rio Bueno		**Discovery Bay**				**Runaway Bay**		**Salem**		**overall**	
			Old Folly		**Top Beach**							
	mean day^{-1}	total site^{-1}	mean day^{-1}	total site^{-1}	mean day^{-1}	total site^{-1}	mean day^{-1}	total site^{-1}	mean day^{-1}	total site^{-1}	mean day^{-1}	total area^{-1}
Data collection days		41		25		42		24		42		174
days with fishing activity		37		18		31		18		33		137
no fishing activity (due to bad weather)		4		7		11		6		9		37
Active boats censused	4.4	182	2.4	60	3.3	140	2.6	62	5.4	226	3.9	670
Non-motorized	2.8	115	2.1	53	2.0	85	1.3	32	3.0	126	2.4	411
Motorized	1.6	67	0.3	7	1.3	55	1.3	30	2.4	100	1.5	259
Boat captain catches												
Recorded in detail	3.2	131	1.8	46	1.9	80	2.0	47	3.0	124	2.5	428
Trap	2.7	111	1.4	36	1.7	70	1.7	40	1.8	77	1.9	334
Hook and line	0.5	20	0.4	10	0.2	8	0.3	7	0.9	36	0.5	81
Net	-	0	-	0	0.05	2	-	0	0.3	11	0.1	13
Total weight recorded only	0.5	20	-	0	0.4	16	0.3	8	0.6	26	0.4	70
Trap	0.5	19	-	0	0.3	14	0.3	8	0.5	19	0.3	60
Hook and line	-	0	-	0	0.02	1	-	0	0.1	5	0.03	6
Net	0.02	1	-	0	0.02	1	-	0	0.05	2	0.02	4
No data recorded	0.8	31	0.6	14	1.0	44	0.3	7	1.8	77	1.0	178
Share fishers catches (in addition to boat captain's catch)												
Recorded in detail	0.1	3	0.1	2	0.2	9	0.1	3	0.3	14	0.2	30
Trap	0.05	2	0.04	1	0.2	9	0.1	2	0.3	14	0.2	28
Hook and line	0.02	1	0.04	1	-	0	0.04	1	-	0	0.02	3
Total weight recorded only (Trap)	0.02	1	-	0	-	0	0.04	1	0.02	1	0.02	3
Spear fishers catches												
Recorded in detail	-	0	-	0	0.1	5	-	0	0.5	20	0.1	25
Total weight only	-	0	-	0	0.1	3	-	0	0.1	3	0.03	6

missed when a large number of boats landed at the same time. The majority of the boats missed were hook and line fishing; these boats often operated at night (targeting nocturnal reef fish and deep-slope snappers), or in the afternoon (fishing for parrotfish; a small, little known part of the fishery). About 10% of the active boat captains refused to provide data when approached by data collectors.

The spear fishers were heavily under-sampled. Of the estimated 15 spear fishers that operated in the area on average each day, data collectors were able to sample less than 1%. Therefore, estimates of the spear fishing catch are based on a very small sample size.

The Fishers, The Fishing Gear and Fishing Effort

Key characteristics of the fishing community and the fishing gear they use are summarized in Table 2. The estimated fishing effort in the fishery, by gear type, is shown in Table 3.

There were approximately 130 active fishers in the area, almost 60% of them relying on fishing as their only income earning activity. On average, each fisher supported another 4 people on their fishing income. The average age of fishers was 49 years.

Almost 70% of the fishers used fish traps as their primary or secondary gear (Photograph 2). Three mesh sizes were used in wire mesh traps. The most common had 43 mm maximum aperture (32 mm or 1 ¼" between knots) and about 71% of the traps in the fishery were made of this mesh size. Traps with larger 55 mm mesh (38 mm or 1 ½" between knots) were less often used (26% of traps) and traps with 33 mm mesh (25 mm or 1" between knots) were uncommon (3%). The average trap fisher owned about 10 traps. Therefore, there were as many as 900 fish traps in the fishery, about 230 of them made of 1.5" mesh size. However, a significant number of these traps were not actively fishing at any one time, as traps were often brought ashore for repairs or storage (Photograph 3).

About 50% of fishers used hook and line. Hook and line fishers targeted both shallow reef fish stocks and very deep snapper stocks. A small number of fishers used gill nets, about 1 boat per day, setting their nets in shallow reef areas. Net and line fishing boats appeared to spend nearly twice as much time at sea per trip as trap fishing boats.

About 32 fishers were full- or part-time spear fishers. Their enumeration was difficult because they did not usually operate from boats. They tended to not use established landing sites and, instead, entered and left the water anywhere along the shore. A limited set of visual surveys along the coast provided the estimates of fishing effort. Their catch was also difficult to estimate because spearfishers sold their catch at various locations in the communities and many were unwilling to cooperate with data collectors.

Almost two thirds of fishers owned a boat. There were approximately 85 boats (not including derelict boats or boats under repair/construction) that were based at the five landing sites. The average boat size was 6.5 m (20 feet). Over 60% of the boats were small, usually unmotorized wooden canoes about 3 m in length (Photograph 4), while the remaining third of the boats were the standard Jamaican 8 m reinforced fiberglass open canoes, which were powered by outboard engines (usually 35 to 65 hp). The actual number of functioning boats at each site fluctuated somewhat, as some fishers move from

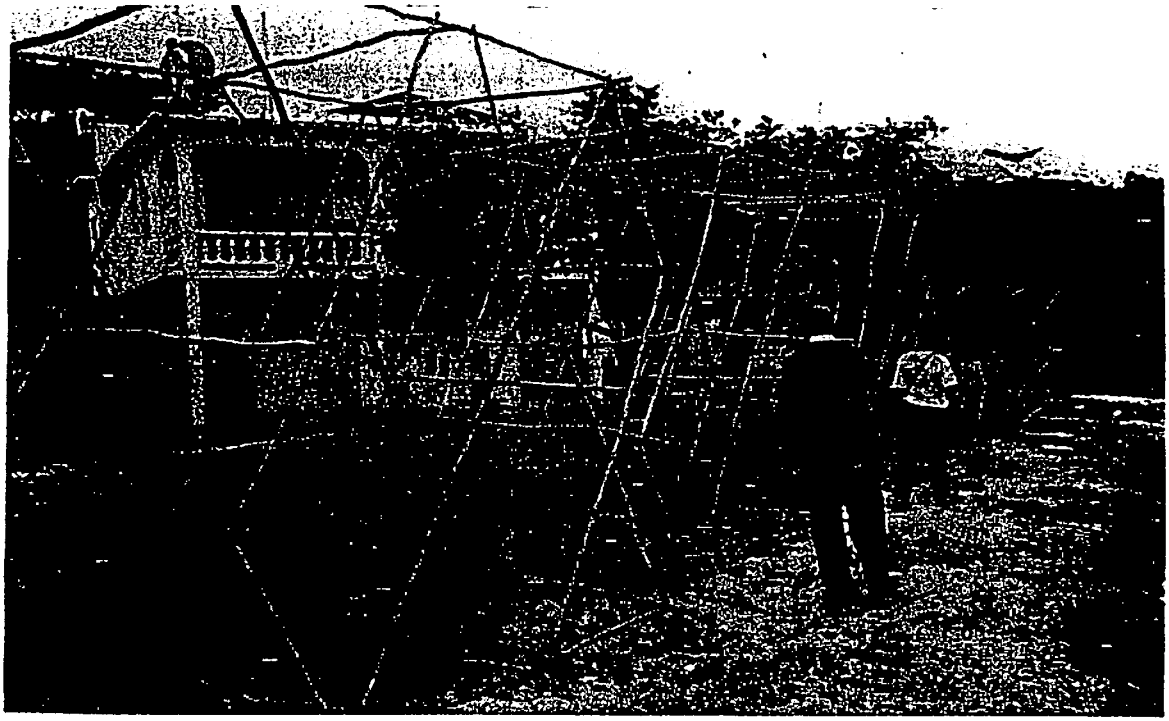
Table 2. The Fishers: Survey of active fishers at five landing sites on the north coast of Jamaica, July 2000 to July 2001.

	Rio Bueno	**Old Folly**	**Top Beach**	**Runaway Bay**	**Salem**	**Overall**
(Number in survey)	(19)	(13)	(24)	(10)	(33)	(99)
Estimated number of active fishers	30	18	30	15	37	130
Female fishers	1	0	0	1	0	2
Average age	46	52	54	52	45	49
Full time fishers	58%	46%	52%	50%	73%	59%
Boat owners	69%	68%	65%	45%	69%	63%
Average boat length (m)	6.9	5.4	6.4	7.9	6.4	6.5
Boats motorized	36%	36%	33%	80%	61%	47%
Average motor size (hp)	36	8	30	35	29	28
Share fishers (use other fishers' boats)	14%	10%	17%	35%	11%	17%
Does not use boat	17%	22%	18%	20%	20%	19%
Primary fishing gear						
Trap	70%	39%	70%	60%	59%	62%
Line	10%	39%	3%	20%	14%	15%
Net	3%	0%	7%	0%	5%	4%
Spear	17%	22%	20%	20%	22%	20%
Secondary fishing gear						
Trap	5%	8%	8%	20%	3%	7%
Line	42%	15%	42%	40%	33%	35%
Net	0%	15%	4%	0%	9%	6%
Spear	5%	0%	13%	0%	3%	5%
Average number of traps owned by trap fishers	11.9	6.4	7.2	10.9	10.7	9.7
1" mesh traps	0.5	0	0	0	0.5	0.2
1.25" mesh traps	10.9	4.3	4.6	8.6	6.3	7.0
1.5" mesh traps	0.9	2.1	2.6	2.3	3.9	2.5
Estimated total number of active traps in fishery	250	60	170	120	300	900
1" mesh traps	10	0	0	0	20	30
1.25" mesh traps	220	40	110	90	180	640
1.5" mesh traps	20	20	60	30	100	230
Average number of dependent adults per fisher	0.9	1.6	0.7	2.0	1.1	1.1
Average number of dependent children per fisher	2.2	4.3	1.8	3.4	3.6	3.0

Table 3. Fishing effort: Estimated fishing effort at five landing sites on the north coast of Jamaica, July 2000 to July 2001.

	Rio Bueno		**Old Folly**		**Top Beach**		**Runaway Bay**		**Salem**		**overall**	
	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total area^{-1} year^{-1}
Functional boats (sea worthy)	15.1		13.7		17.2		13.4		25.7		95	
range	*12 - 18*		*9 - 15*		*15 - 18*		*12 - 15*		*22 - 27*		*85-105*	
Active boats (at sea)	4.4	1620	2.4	880	3.3	1220	2.6	940	5.4	1960	20	7300
upper range	*9*		*5*		*8*		*6*		*14*		*46*	
Active motorized boats	1.6	600	0.3	100	1.3	480	1.3	460	2.4	870	7.6	2800
Share fishers (catch separate from boat captains)	0.1	40	0.1	30	0.2	70	0.1	50	0.4	130	0.9	300
Crew (no separate catch)	2.9	1040	0.8	280	0.8	290	1.7	640	1.1	380	8.0	2900
Trap fishing												
Active boats	3.4	1240	1.6	590	2.3	840	2.1	760	2.7	970	13	4900
Mean time spent at sea (hours/fisher)	3.7		3.0		2.9		3.5		3.1		3.3	
Number of trap hauls	8.1	10,000	4.8	2800	5.4	4600	7.4	5600	8.3	8000	38	34300
1" mesh traps	0.1	120	0	0	0	0	0	0	0.1	100	0.2	200
1.25" mesh traps	7.8	9700	3.8	2200	4.7	4000	5.9	4500	7.0	6800	32	30100
1.5" mesh traps	0.2	250	0.9	500	0.7	600	1.5	1100	1.2	1200	5.0	4000
Mean soak time (days), 1.25" mesh traps	1.7		3.4		1.9		5.3		2.2		2.8	
Mean soak time (days), 1.5" mesh traps	unknown		4.0		6.8		6.2		4.7		5.2	
Mean depth (m)	27		20		23		33		27		27	
Drop line fishing												
Active boats - drop line fishing	0.9	340	0.8	290	0.8	310	0.5	170	2.1	760	6	2100
Active boats - trolling*	0.2	55	0.04	15	0.1	25	0.1	30	0.3	120	0.7	270
Mean time spent at sea (hours/fisher)	5.7		7.4		4.4		5.9		4.1		5.1	
Mean depth fished (m) - drop line	129		60		93		104		61		82	
Net fishing												
Active boats	0.02	10	0.01	5	0.2	60	0	0	0.6	230	1	340
Mean time spent at sea (hours/fisher)	unknown		unknown		5.7		0		4.4		4.5	
Mean depth fished (m)	unknown		unknown		23		0		14		15	
Spear fishing												
Active spearfishers (no boat used)	5.0	1830	1.5	550	2.5	910	2.0	730	3.0	1100	14	5000
Mean time spent at sea (hours/fisher)	unknown		unknown		2.7		unknown		3.0		2.9	
Mean depth fished (m)	unknown		unknown		24		unknown		20		22	

* troll line fishing is generally carried out to and from fishing grounds, therefore it is often practiced in addition to other fishing methods.



Photograph 3. Very large "jack" traps are stored on shore awaiting the summer fish season. Rio Bueno fishing beach, Trelawny. June 2001.

Photograph 4. Typical wooden fishing boat, Old Folly fishing beach, Discovery Bay, St. Ann. July 2001.

one site to another, some new boats were brought onto the sites, some old ones were removed, etc. The average number of boats at each site throughout the sampling period, as well as the range, is shown in Table 3.

There were approximately another 10 boats operated in the fishing area but were not based at these landing sites and were based at isolated locations along the coastline. The catches of these boats were not sampled, but they were assumed to operate in a similar fashion as boats at the main landing sites and they were factored in the estimates of total catches.

On an average day, there were about 20 boats fishing on the narrow fringing reef along this 22 km coast line, about 12 of them non-motorized. The 20 boats had approximately 29 people operating from them (captain, share fishers and crew). In addition, about 15 spear fishers were also fishing in the area. This represented over 7000 boat days and over 5000 spear fishing days per year. As mentioned before, many fishers operated more than one gear on each fishing trip.

Trap fishing boats hauled an average of seven traps per fishing trip. Thus, during the estimated 5000 trap fishing trips (or boat days) in the area during the year, nearly 35,000 trap hauls were made. Nearly 90% of the trap hauls were of 1.25" mesh traps and nearly all the rest of the hauls were of 1.5" mesh trap hauls. Small mesh traps were hauled almost twice as often as the larger mesh traps. On average, trap fishers set their traps 27 m deep.

Catch Rates

The catch rates of trap fishing boats are shown in Table 4a and 4b. Table 4a shows the species composition of the boat catches, as well as the value of the catch and Table 4b shows the family composition of the catch.

The average catch of a trap fishing boat (Photograph 5) was 6.1 kg per trip and the average income was $29 a day (all figures in US$; 2001 exchange rate = US$1:J$45); this was shared between the boat captain and his crew. The eastern part of the fishing area appeared to be the most productive, with the largest average catches recorded in Runaway Bay and in Salem. The most important fish species in the catch were *Sparisoma aurofrenatum* and *Acanthurus bahianus*, which together made up 30% of the catch. No other species comprised more than 5% of the catch. A few large groupers, such as *Mycteroperca venenosa*, were still occasionally caught and made up about 1% of the catch (Photograph 6). About 8% of the catch consisted of unmarketable trash fish. The total catch over the entire area by fish traps was just under 30 tons per year, with a value of $140,000.

The catch rates of hook and line fishing is shown in Table 5a and 5b, of net fishing in Table 6a and 6b and of spear fishing in Table 7a and 7b.

The most important species for hook and line fishing was *Selar crumenophthalmus*, which made up 26% of the drop line catches and *Sphyraena barracuda* which comprised 74% of the trolling catches. For net fishing, the top species was *Caranx ruber* (21% of the catch) and for spear fishing it was *Sphyraena barracuda* (31%).

The most lucrative fishing activity appeared to be net fishing, with an average income of $34 per boat trip, but the success of this activity was seasonal when jacks were

Table 4a. Trap fishing: Mean daily catch and estimated total catch (by species), at 5 landing sites on the north coast of Jamaica, July 2000 to July 2001.

	Rio Bueno		Old Folly		Top Beach		Runaway Bay		Salem		OVERALL		
	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}		total area^{-1} year^{-1}
Active boats (Sample size)	3.4	1240 (107)	1.6	590 (34)	2.3	840 (69)	2.1	760 (38)	2.7	970 (80)	13		4900 (328)
<u>Catch composition by species</u>	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	% of total	kg area^{-1} year^{-1}
Sparisoma aurofrenatum	1.34	1660	0.75	440	1.18	990	0.93	710	1.06	1030	1.13	19%	5540
Acanthurus bahianus	0.81	1000	0.38	220	0.47	400	0.62	470	0.72	700	0.65	11%	3190
Sparisoma chrysopterum	0.32	390	0.39	230	0.18	150	0.53	400	0.36	350	0.33	5%	1620
Ocyurus chrysurus	0.14	180	0.00	0	0.06	50	0.40	300	0.64	620	0.26	4%	1280
Sparisoma rubripinne	0.09	120	0.10	60	0.10	90	0.16	120	0.81	780	0.28	5%	1360
Scarus taeniopterus	0.30	380	0.13	80	0.41	340	0.17	130	0.21	200	0.27	4%	1320
Sparisoma viride	0.10	120	0.17	100	0.18	150	0.25	190	0.41	400	0.22	4%	1060
Acanthurus coeruleus	0.15	190	0.20	120	0.18	150	0.40	300	0.22	210	0.21	3%	1020
Holocentrus rufus	0.22	270	0.07	40	0.14	120	0.24	180	0.26	250	0.20	3%	980
Haemulon flavolineatum	0.22	270	0.06	30	0.09	80	0.21	160	0.18	180	0.17	3%	810
Lutjanus apodus	0.11	143	0.03	15	0.05	46	0.13	100	0.23	220	0.12	2%	600
Gymnothorax moringa	0.11	130	0.09	52	0.03	20	0.25	190	0.27	260	0.14	2%	700
Caranx ruber	0.11	140	0.05	28	0.03	30	0.49	373	0.10	94	0.13	2%	640
Balistes vetula	0.08	96	0.00	0	0.03	22	0.20	152	0.16	153	0.09	2%	450
Mulloidichthys martinicus	0.09	109	0.06	40	0.09	70	0.23	177	0.17	162	0.12	2%	590
Pseudopeneus maculatus	0.06	80	0.02	10	0.10	86	0.22	160	0.20	198	0.12	2%	580
Epinephelus fulvus	0.10	130	0.03	20	0.12	104	0.12	90	0.15	147	0.11	2%	560
Acanthurus chirurgus	0.11	140	0.10	61	0.07	56	0.16	130	0.13	120	0.11	2%	540
Epinephelus cruentatus	0.10	127	0.03	20	0.07	56	0.16	124	0.15	145	0.11	2%	520
Scarus iserti	0.06	75	0.07	41	0.12	100	0.16	120	0.12	120	0.10	2%	490
Mycteroperca venenosa	0.08	100	0.00	2	0.00	0	0.19	148	0.01	10	0.05	1%	250
Lutjanus analis	0.08	96	0.02	10	0.13	112	0.22	170	0.01	9	0.08	1%	410
Myripristes jacobus	0.07	91	0.03	17	0.04	35	0.15	110	0.12	115	0.08	1%	400
Haemulon plumieri	0.05	60	0.12	70	0.04	40	0.14	107	0.08	80	0.07	1%	360
Gymnothorax funebris	0.03	34	0.07	42	0.00	0	0.12	91	0.16	158	0.07	1%	340
Panulirus argus	0.09	114	0.00	0	0.04	34	0.21	157	0.04	34	0.07	1%	350
Mithrax spinosissimus	0.00	6	0.08	45	0.01	9	0.23	178	0.00	0	0.04	0.6%	190
others (80 species)	0.70	872	0.82	484	0.41	343	1.47	1118	0.66	638	0.73	12%	3580
total catch	5.74	7100	3.86	2300	4.38	3700	8.78	6700	7.62	7400	6.07	100%	29700
<u>Catch value</u>													
quality fish (US\$5.90/kg)	0.95	1180	0.55	320	0.66	560	2.80	2130	1.61	1560	1.22	20%	5990
common fish (US\$4.90/kg)	4.44	5500	2.70	1590	3.55	2980	5.12	3890	5.28	5120	4.35	72%	21340
trash fish (no monetary value)	0.35	440	0.61	360	0.17	140	0.86	650	0.73	710	0.49	8%	2410
	\$ boat^{-1} day^{-1}	\$ site^{-1} year^{-1}	\$ boat^{-1} day^{-1}	\$ site^{-1} year^{-1}	\$ boat^{-1} day^{-1}	\$ site^{-1} year^{-1}	\$ boat^{-1} day^{-1}	\$ site^{-1} year^{-1}	\$ boat^{-1} day^{-1}	\$ site^{-1} year^{-1}	\$ boat^{-1} day^{-1}		\$ area^{-1} year^{-1}
total income (US\$)	\$ 27	\$ 33,900	\$ 16	\$ 9,700	\$ 21	\$ 17,900	\$ 42	\$ 31,600	\$ 35	\$ 34,300	\$ 29		\$ 140,000

Table 4b. Trap fishing: Mean daily catch and estimated total catch (by fish family), at 5 landing sites on the north coast of Jamaica, July 2000 to July 2001.

	Rio Bueno		Old Folly		Top Beach		Runaway Bay		Salem		OVERALL		
Catch composition by family	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	% of total	kg area^{-1} year^{-1}
Scaridae	2.26	2800	1.60	940	2.18	1830	2.21	1680	2.98	2890	2.34	39%	11500
Acanthuridae	1.07	1330	0.69	410	0.72	600	1.19	900	1.07	1040	0.97	16%	4750
Lutjanidae	0.40	500	0.08	50	0.26	210	0.98	740	0.92	890	0.53	9%	2600
Holocentridae	0.36	450	0.14	80	0.22	180	0.54	410	0.45	430	0.35	6%	1710
Haemulidae	0.31	390	0.21	120	0.17	140	0.49	370	0.31	300	0.29	5%	1430
Serranidae	0.29	360	0.07	40	0.20	170	0.48	370	0.32	310	0.28	5%	1360
Mullidae	0.15	190	0.08	50	0.19	160	0.45	340	0.37	360	0.24	4%	1180
Muraenidae	0.15	190	0.19	110	0.03	20	0.41	310	0.43	420	0.23	4%	1110
Carangidae	0.15	190	0.09	50	0.08	70	0.51	390	0.16	160	0.17	3%	850
invertebrate	0.10	130	0.08	50	0.07	60	0.61	460	0.13	120	0.16	3%	780
Balistidae	0.09	110	0.02	9	0.10	90	0.25	190	0.18	180	0.13	2%	620
Labridae	0.08	100	0.01	7	0.04	30	0.08	63	0.05	50	0.06	0.9%	280
Kyphosidae	0.15	185	0.00	0	0.00	0	0.03	25	0.00	0	0.05	0.9%	260
Diodontidae	0.00	0	0.29	170	0.04	35	0.02	10	0.02	20	0.05	0.8%	220
Pomacentridae	0.03	40	0.07	40	0.01	5	0.11	80	0.06	59	0.045	0.7%	220
Priacanthidae	0.05	60	0.00	3	0.01	5	0.14	110	0.02	20	0.038	0.6%	190
Sparidae	0.01	16	0.00	0	0.02	16	0.04	30	0.05	51	0.026	0.4%	130
Gerridae	0.00	4	0.14	80	0.01	7	0.00	0	0.02	20	0.022	0.4%	110
Monacanthidae	0.01	13	0.00	0	0.01	9	0.05	40	0.03	30	0.019	0.3%	91
Scorpaenidae	0.01	15	0.01	7	0.02	13	0.05	40	0.01	14	0.018	0.3%	87
Ostraciidae	0.01	10	0.01	5	0.01	5	0.03	20	0.02	18	0.013	0.2%	63
Pomacanthidae	0.02	19	0.01	9	0.00	3	0.03	20	0.00	2	0.011	0.2%	53
Grammistidae	0.01	20	0.00	0	0.00	0	0.03	20	0.01	10	0.010	0.2%	47
Sphyraenidae	0.00	0	0.07	42	0.00	0	0.00	0	0.00	0	0.007	0.1%	36
Ephippidae	0.00	0	0.00	0	0.00	0	0.05	40	0.00	0	0.006	0.1%	30
Chaetodontidae	0.00	3	0.01	4	0.00	1	0.00	0	0.01	6	0.003	0.05%	16
Bothidae	0.00	2	0.00	0	0.00	3	0.00	0	0.00	3	0.002	0.03%	10
Aulostomidae	0.01	8	0.00	0	0.00	0	0.00	0	0.00	0	0.002	0.03%	10
Sciaenidae	0.00	0	0.00	2	0.00	2	0.01	8	0.00	0	0.002	0.03%	10
Synodontidae	0.00	5	0.00	2	0.00	0	0.00	0	0.00	0	0.002	0.03%	8
Malacanthidae	0.00	5	0.00	0	0.00	0	0.00	0	0.00	0	0.001	0.02%	7
Mugilidae	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	>0.001	0.01%	2
TOTAL CATCH	5.74	7100	3.86	2300	4.38	3700	8.78	6700	7.62	7400	6.07		29700

Photograph 5. A typical catch from a trap fishing trip. Rio Bueno fishing beach, Trelawny. June 2001.

Photograph 6. A few large groupers, such as these *Mycteroperca venenosa*, are still caught on occasions, and make up 1% of the total trap catch. Swallow Hole fishing beach, Runaway Bay, St. Ann. June 2001.

Table 5a. Hook and line fishing: Mean daily catch and estimated total catch (by species), at 5 landing sites on the north coast of Jamaica, July 2000 to July 2001.

	Rio Bueno		Old Folly		Top Beach		Runaway Bay		Salem		OVERALL		
	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}		total area^{-1} year^{-1}
Active boats - drop line	0.9	340	0.8	290	0.8	310	0.5	170	2.1	760	5.7		2100
(Sample size)		(22)		(12)		(15)		(5)		(29)			(83)
Active boats - troll line	0.15	55	0.04	15	0.07	25	0.08	30	0.33	120	0.74		270
(Sample size)		(6)		(1)		(3)		(2)		(14)			(26)
Catch composition - drop line	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	% of total	kg area^{-1} year^{-1}
Selar crumenophthalmus	0.60	210	0.11	30	0.15	50	0.34	60	1.06	800	0.59	26%	1240
Cephalopholis cruentata	0.32	110	0.14	40	0.23	70	0.55	90	0.38	290	0.31	14%	660
Lutjanus vivanus	0.17	60	0.00	0	0.75	230	0.11	20	0.03	30	0.20	9%	410
Sphyraena barracuda	0.25	90	0.00	0	0.14	40	0.00	0	0.19	140	0.16	7%	330
Holocentrus rufus	0.05	20	0.09	25	0.06	20	0.52	89	0.17	130	0.13	6%	270
Cephalopholis fulva	0.05	18	0.12	30	0.25	78	0.00	0	0.10	80	0.11	5%	240
Tylosurus crocodilus	0.00	0	0.08	20	0.00	0	0.00	0	0.25	191	0.10	4%	210
Etelis oculatus	0.25	80	0.00	0	0.09	29	0.00	0	0.01	7	0.09	4%	180
Sparisoma aurofrenatum	0.01	2	0.53	152	0.00	0	0.00	0	0.00	0	0.08	3%	160
Scomberomorus cavalla	0.23	78	0.00	0	0.00	0	0.00	0	0.00	0	0.06	3%	130
Holocentrus ascensionis	0.01	5	0.05	14	0.01	3	0.00	0	0.12	88	0.05	2%	110
Malacanthus plumieri	0.01	3	0.02	6	0.00	0	0.03	5	0.10	74	0.04	2%	87
Scomberomorus regalis	0.15	53	0.00	0	0.00	0	0.00	0	0.00	0	0.04	2%	86
Caranx lugubris	0.00	0	0.00	0	0.00	0	0.63	107	0.00	0	0.04	2%	80
Haemulon plumieri	0.01	3	0.15	42	0.03	8	0.00	0	0.01	4	0.03	1%	62
others (41 species)	0.16	56	0.63	182	0.17	51	0.39	66	0.12	90	0.23	10%	480
TOTAL drop line catch	**2.28**	**770**	**1.90**	**550**	**1.87**	**580**	**2.57**	**440**	**2.53**	**1920**	**2.26**	**100%**	**4700**
Catch composition - troll line													
Sphyraena barracuda	4.09	220	6.30	90	2.90	70	2.08	60	2.53	300	3.04	74%	820
Scomberomorus cavalla	0.00	0	0.00	0	0.00	0	6.25	190	0.00	0	0.48	12%	130
Tylosurus crocodilus	0.00	0	0.00	0	0.32	10	0.00	0	0.69	80	0.41	10%	110
Thunnus atlanticus	0.00	0	0.00	0	0.00	0	0.00	0	0.29	30	0.16	4%	42
Scomberomorus regalis	0.14	8	0.00	0	0.00	0	0.00	0	0.00	0	0.03	0.8%	9
Cetropomus undecimalis	0.00	0	0.00	0	0.00	0	0.00	0	0.03	3	0.01	0.3%	4
TOTAL trolling catch	**4.23**	**230**	**6.30**	**90**	**3.22**	**80**	**8.33**	**250**	**3.53**	**420**	**4.11**	**100%**	**1110**
TOTAL LINE CATCH (mean)	**2.53**	**1000**	**2.10**	**640**	**1.97**	**660**	**3.45**	**690**	**2.66**	**2340**	**2.45**		**5810**
Catch composition by value													
quality fish (US$5.90/kg)	1.55	612	0.85	258	1.23	412	2.00	400	0.61	534	1.06	43%	2510
common fish (US$4.90/kg)	0.94	371	1.16	352	0.71	238	1.34	268	2.04	1797	1.35	55%	3200
trash fish (no monetary value)	0.04	17	0.10	30	0.03	10	0.11	22	0.05	43	0.05	2%	130
	$ boat^{-1} day^{-1}	$ site^{-1} year^{-1}	$ boat^{-1} day^{-1}	$ site^{-1} year^{-1}	$ boat^{-1} day^{-1}	$ site^{-1} year^{-1}	$ boat^{-1} day^{-1}	$ site^{-1} year^{-1}	$ boat^{-1} day^{-1}	$ site^{-1} year^{-1}	$ boat^{-1} day^{-1}		$ area^{-1} year^{-1}
TOTAL VALUE (US$)	**$ 14**	**$ 5,400**	**$ 11**	**$ 3,200**	**$ 11**	**$ 3,600**	**$ 18**	**$ 3,700**	**$ 14**	**$ 12,000**	**$ 13**		**$ 30,000**

Table 5b. Hook and line fishing: Mean daily catch and estimated total catch (by fish family), at 5 landing sites on the north coast of Jamaica, July 2000 to July 2001.

	Rio Bueno		**Old Folly**		**Top Beach**		**Runaway Bay**		**Salem**		**OVERALL**		
Catch composition - drop line	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	% of total	kg area^{-1} year^{-1}
Carangidae	0.62	210	0.22	60	0.23	70	0.97	160	1.06	800	**0.67**	**30%**	**1400**
Serranidae	0.38	130	0.28	80	0.49	150	0.57	100	0.51	390	**0.44**	**20%**	**920**
Lutjanidae	0.46	160	0.30	90	0.89	280	0.24	40	0.06	40	**0.36**	**16%**	**760**
Holocentridae	0.10	30	0.16	50	0.08	30	0.52	90	0.30	230	**0.20**	**9%**	**420**
Sphyraenidae	0.25	90	0.00	0	0.14	40	0.00	0	0.19	140	**0.16**	**7%**	**330**
Scombridae	0.38	131	0.00	0	0.00	0	0.00	0	0.00	0	**0.10**	**5%**	**210**
Belonidae	0.00	0	0.08	20	0.00	0	0.00	0	0.25	191	**0.10**	**4%**	**210**
Scaridae	0.01	0	0.56	163	0.00	0	0.00	0	0.00	2	**0.08**	**4%**	**180**
Malacanthidae	0.01	3	0.02	6	0.00	0	0.03	5	0.10	70	**0.04**	**2%**	**87**
Haemulidae	0.02	7	0.15	44	0.03	11	0.08	14	0.01	6	**0.04**	**2%**	**87**
Labridae	0.02	5	0.06	16	0.02	5	0.03	4	0.02	12	**0.02**	**1%**	**46**
others (10 families)	0.03	9	0.08	22	0.00	0	0.13	22	0.05	38	**0.04**	**2%**	**91**
total drop line catch	**2.28**	**770**	**1.90**	**550**	**1.87**	**580**	**2.57**	**440**	**2.53**	**1920**	**2.26**	**100%**	**4700**
Catch composition - troll line													
Sphyraenidae	4.09	220	6.30	90	2.90	70	2.08	60	2.53	300	**3.04**	**74%**	**820**
Scombridae	0.14	10	0.00	0	0.00	0	6.25	190	0.29	30	**0.67**	**16%**	**180**
Belonidae	0.00	0	0.00	0	0.32	10	0.00	0	0.69	80	**0.41**	**10%**	**110**
Centropomidae	0.00	0	0.00	0	0.00	0	0.00	0	0.03	0	**0.01**	**0.3%**	**4**
total trolling catch	**4.23**	**230**	**6.30**	**90**	**3.22**	**80**	**8.33**	**250**	**3.53**	**420**	**4.11**	**100%**	**1110**
TOTAL LINE CATCH (mean)	2.53	1000	2.10	640	1.97	660	3.45	690	2.66	2340	2.45		5810

Table 6a. Net fishing: Mean daily catch and estimated total catch (by species), at 5 landing sites on the north coast of Jamaica, July 2000 to July 2001.

	Rio Bueno		**Old Folly**		**Top Beach**		**Runaway Bay**		**Salem**		**OVERALL**		
	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}		total area^{-1} year^{-1}
Active boats	0.02	9	0.01	5	0.2	64	0.0	0	0.6	230	0.9		340
(Sample size)		(0)		(0)		(2)		(0)		(11)			(13)
Catch composition by species	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	% of total	kg area^{-1} year^{-1}
Caranx ruber		(12)		(7)	1.10	71		(0)	1.37	310	1.32	21%	450
Albula vulpes		(6)		(3)	0.00	0		(0)	0.74	170	0.63	10%	210
Haemulon plumieri		(4)		(2)	0.58	37		(0)	0.46	110	0.48	8%	160
Priacanthus cruentatus		(4)		(2)	0.00	0		(0)	0.55	130	0.46	7%	160
Haemulon sciurus		(3)		(2)	0.33	21		(0)	0.30	69	0.31	5%	104
Gerres cinereus		(3)		(1)	0.00	0		(0)	0.34	78	0.29	5%	98
Caranx bartholomei		(3)		(1)	0.00	0		(0)	0.34	77	0.28	4%	97
Sparisoma chrysopterum		(2)		(1)	0.35	23		(0)	0.24	54	0.25	4%	86
Priacanthus arenatus		(2)		(1)	0.00	0		(0)	0.25	58	0.21	3%	72
Scorpaena plumieri		(2)		(1)	0.00	0		(0)	0.24	56	0.21	3%	70
Calamus bajonado		(2)		(1)	0.98	63		(0)	0.03	8	0.18	3%	60
Selar crumenophthalmus		(2)		(1)	0.65	41		(0)	0.09	21	0.18	3%	60
Sphyraena barracuda		(1)		(1)	0.00	0		(0)	0.18	42	0.15	2%	52
Lutjanus mahogoni		(1)		(1)	0.13	8		(0)	0.14	32	0.14	2%	47
Tylosurus crocodilus		(1)		(1)	0.00	0		(0)	0.14	31	0.12	2%	39
Sparisoma rubripinne		(1)		(1)	0.23	14		(0)	0.09	21	0.11	2%	38
Lutjanus synagris		(1)		(1)	0.00	0		(0)	0.13	29	0.11	2%	37
Acanthurus bahianus		(1)		(1)	0.00	0		(0)	0.12	28	0.10	2%	35
Sparisoma viride		(1)		(1)	0.00	0		(0)	0.12	27	0.10	2%	34
Mulloidichthys martinicus		(1)		(0)	0.15	10		(0)	0.07	17	0.09	1%	29
Haemulon parrai		(1)		(0)	0.00	0		(0)	0.09	20	0.07	1%	25
Rypticus saponaceus		(1)		(0)	0.00	0		(0)	0.08	19	0.07	1%	24
Lutjanus apodus		(1)		(0)	0.00	0		(0)	0.09	22	0.08	1%	26
Ocyurus chrysurus		(0)		(0)	0.00	0		(0)	0.08	18	0.05	1%	18
others (17 species)		(3)		(2)	0.38	24		(0)	0.37	84	0.37	6%	125
TOTAL CATCH		(56)		(32)	4.85	310		(0)	6.65	1530	6.34	100%	2160
Catch composition by value													
quality fish (US\$5.90/kg)		(33)		(19)	2.28	150		(0)	4.02	920	3.72	59%	1260
common fish (US\$4.90/kg)		(23)		(13)	2.57	170		(0)	2.54	590	2.55	40%	870
trash fish (no monetary value)		(1)		(0)	0.00	0		(0)	0.09	20	0.08	1%	30
	\$ boat day^{-1}	\$ site year^{-1}	\$ boat day^{-1}	\$ site year^{-1}	\$ boat day^{-1}	\$ site year^{-1}	\$ boat day^{-1}	\$ site year^{-1}	\$ boat day^{-1}	\$ site year^{-1}	\$ boat day^{-1}		\$ area year^{-1}
TOTAL VALUE (US\$)	\$ -	\$ 310	\$ -	\$ 170	\$ 26	\$ 1,700	\$ -	\$ -	\$ 36	\$ 8,300	\$ 34		\$ 11,700

Table 6b. Net fishing: Mean daily catch and estimated total catch (by fish family), at 5 landing sites on the north coast of Jamaica, July 2000 to July 2001.

	Rio Bueno		Old Folly		Top Beach		Runaway Bay		Salem		OVERALL		
Catch composition by family	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	kg site^{-1} year^{-1}	kg boat^{-1} day^{-1}	% of total	kg area^{-1} year^{-1}
Carangidae		(16)		(9)	1.75	110		(0)	1.81	420	1.79	28%	610
Haemulidae		(8)		(4)	0.90	60		(0)	0.88	200	0.88	14%	300
Priacanthidae		(6)		(3)	0.00	0		(0)	0.80	180	0.68	11%	230
Albulidae		(6)		(3)	0.00	0		(0)	0.74	170	0.63	10%	210
Scaridae		(5)		(3)	0.73	50		(0)	0.53	120	0.56	9%	190
Lutjanidae		(4)		(2)	0.13	10		(0)	0.51	120	0.43	7%	150
Gerridae		(3)		(1)	0.00	0		(0)	0.34	80	0.29	5%	100
Scorpaenidae		(2)		(1)	0.00	0		(0)	0.24	60	0.21	3%	70
Sparidae		(2)		(1)	0.98	60		(0)	0.03	10	0.18	3%	60
Acanthuridae		(1)		(1)	0.18	10		(0)	0.16	40	0.16	3%	55
Sphyraenidae		(1)		(1)	0.00	0		(0)	0.18	40	0.15	2%	52
Belonidae		(1)		(1)	0.00	0		(0)	0.14	30	0.12	2%	39
Mullidae		(1)		(0)	0.15	10		(0)	0.08	20	0.09	1%	32
Grammistidae		(1)		(0)	0.00	0		(0)	0.08	20	0.07	1%	24
Serranidae		(1)		(0)	0.00	0		(0)	0.07	20	0.06	1%	21
Scombridae		(0)		(0)	0.00	0		(0)	0.03	10	0.03	0.4%	9
Exocoetidae		(0)		(0)	0.00	0		(0)	0.02	0	0.01	0.2%	5
Holocentridae		(0)		(0)	0.00	0		(0)	0.01	0	0.01	0.2%	4
Pomacanthidae		(0)		(0)	0.05	0		(0)	0.00	0	0.01	0.1%	3
TOTAL CATCH		(56)		(32)	4.85	300		(0)	6.65	1500	6.34	100%	2160

Table 7a. Spear fishing: Mean daily catch and estimated total catch (by species), at 5 landing sites on the north coast of Jamaica, July 2000 to July 2001.

	Rio Bueno		Old Folly		Top Beach		Runaway Bay		Salem		OVERALL		
	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}	total site^{-1} year^{-1}	day^{-1}		total area^{-1} year^{-1}
Active fishers	5	1830	1.50	550	2.5	910	2	730	3	1100	14		5100
(Sample size)		(0)		(0)		(5)		(0)		(19)			(24)
Catch composition by species		kg site^{-1} year^{-1}		kg site^{-1} year^{-1}	kg fisher^{-1} day^{-1}	kg site^{-1} year^{-1}		kg site^{-1} year^{-1}	kg fisher^{-1} day^{-1}	kg site^{-1} year^{-1}	kg fisher^{-1} day^{-1}	% of total	kg area^{-1} year^{-1}
Sphyraena barracuda		(2600)		(770)	0.00	0		(1020)	1.78	1960	1.40	31%	7100
Sparisoma viride		(990)		(300)	0.13	120		(400)	0.65	720	0.54	12%	2800
Sparisoma rubripinne		(630)		(190)	0.38	350		(250)	0.34	370	0.35	8%	1800
Priacanthus cruentatus		(460)		(140)	0.30	270		(180)	0.24	260	0.25	6%	1300
Sparisoma chrysopterum		(370)		(110)	0.43	390		(150)	0.14	160	0.20	5%	1040
Pseudopeneus maculatus		(370)		(110)	0.35	320		(150)	0.16	180	0.20	4%	1020
Cephalopholis cruentata		(360)		(110)	0.30	270		(150)	0.17	190	0.20	4%	1020
Acanthurus coeruleus		(360)		(110)	0.21	190		(140)	0.19	210	0.19	4%	990
Sparisoma aurofrenatum		(300)		(91)	0.20	180		(120)	0.16	170	0.17	4%	850
Panulirus argus		(250)		(74)	0.09	82		(100)	0.15	160	0.14	3%	690
Cephalopholis fulva		(200)		(61)	0.31	280		(81)	0.06	64	0.11	2%	570
Scarus taeniopterus		(190)		(58)	0.51	460		(78)	0.00	0	0.11	2%	540
Haemulon sciurus		(150)		(45)	0.32	290		(59)	0.02	20	0.08	2%	410
Lutjanus apodus		(140)		(43)	0.00	0		(57)	0.10	110	0.08	2%	400
Haemulon carbonarium		(120)		(36)	0.12	110		(48)	0.05	57	0.07	1%	340
Caranx ruber		(110)		(33)	0.00	0		(43)	0.08	83	0.06	1%	300
others (20 species)		(670)		(200)	0.51	470		(270)	0.33	360	0.37	8%	1900
TOTAL CATCH		(8200)		(2500)	4.17	3800		(3300)	4.61	5100	4.50	100%	23000
Catch composition by value													
quality fish (US$5.90/kg)		(3770)		(1130)	0.92	840		(1500)	2.37	2610	2.06	46%	10500
common fish (US$4.90/kg)		(4420)		(1330)	3.19	2900		(1760)	2.21	2430	2.41	54%	12310
trash fish (no monetary value)		(60)		(20)	0.06	50		(20)	0.02	20	0.03	1%	160
		$ site^{-1} year^{-1}		$ site^{-1} year^{-1}	$ fisher^{-1} day^{-1}	$ site^{-1} year^{-1}		$ site^{-1} year^{-1}	$ fisher^{-1} day^{-1}	$ site^{-1} year^{-1}	$ fisher^{-1} day^{-1}		$ area^{-1} year^{-1}
TOTAL VALUE (US$)		$ 44,000		$ 13,000	$ 21	$ 19,200		$ 17,000	$ 25	$ 27,300	$ 24		$ 122,000

Table 7b. Spear fishing: Mean daily catch and estimated total catch (by fish family), at 5 landing sites on the north coast of Jamaica, July 2000 to July 2001.

	Rio Bueno	**Old Folly**	**Top Beach**		**Runaway Bay**	**Salem**		**OVERALL**		
Catch composition by family	kg site^{-1} year^{-1}	kg site^{-1} year^{-1}	kg fisher^{-1} day^{-1}	kg site^{-1} year^{-1}	kg site^{-1} year^{-1}	kg fisher^{-1} day^{-1}	kg site^{-1} year^{-1}	kg fisher^{-1} day^{-1}	% of total	kg area^{-1} year^{-1}
Sphyraenidae	(2549)	(765)	0.00	0	(1020)	1.78	1960	1.40	31%	7140
Scaridae	(2516)	(755)	1.65	1510	(1006)	1.31	1440	1.38	31%	7050
Serranidae	(566)	(170)	0.61	560	(226)	0.23	250	0.31	7%	1580
Priacanthidae	(455)	(137)	0.30	270	(182)	0.24	260	0.25	6%	1280
Mullidae	(422)	(127)	0.46	420	(169)	0.17	190	0.23	5%	1180
Acanthuridae	(419)	(126)	0.25	230	(168)	0.22	250	0.23	5%	1170
Haemulidae	(325)	(98)	0.47	430	(130)	0.10	110	0.18	4%	910
invertebrate	(300)	(90)	0.23	210	(120)	0.15	160	0.16	4%	840
Lutjanidae	(217)	(65)	0.00	0	(87)	0.15	170	0.12	3%	610
Holocentridae	(116)	(35)	0.16	150	(46)	0.04	42	0.06	1%	320
Carangidae	(109)	(33)	0.00	0	(43)	0.08	83	0.06	1%	300
Labridae	(65)	(19)	0.00	0	(26)	0.04	49	0.04	0.8%	180
Scorpaenidae	(34)	(10)	0.00	0	(14)	0.02	26	0.02	0.4%	96
Synodontidae	(34)	(10)	0.00	0	(14)	0.02	26	0.02	0.4%	96
Ephippidae	(30)	(9)	0.00	0	(12)	0.02	23	0.02	0.4%	85
Gerridae	(27)	(8)	0.03	27	(11)	0.01	12	0.01	0.3%	75
Monacanthidae	(21)	(6)	0.00	0	(9)	0.01	16	0.01	0.3%	60
Pomacanthidae	(11)	(3)	0.00	0	(5)	0.01	9	0.01	0.1%	32
TOTAL CATCH	(8200)	(2500)	4.17	3800	(3300)	4.61	5100	4.50	100%	23000

more common in the fishing area. Also, several net fishers were, in fact, spear fishers using nets and boats; when they operated their nets, they swam around herding fish into it and spearing any fish too large to be gilled in the net (drive netting). This activity was very labour intensive and required physical endurance. Nonetheless, given the relatively high catch rates per boat, it was not clear why more fishers did not take up net fishing.

Line fishing was the least rewarding fishing activity with fishers making less than $15 per trip, though this type of fishing was still popular since it was the least gear- and labour-intensive of all the fishing practices. The estimated catch of all drop line fishers was about 4.7 tons per year, with a value of $25,600. Troll lines yielded a total of 1.1 tons, valued at $5,600. Net fishing yielded 2.2 tons per year, with a value of $11,700. Spear fishers were estimated to land 23 tons, with a value of $122,000.

Economic Analyses

The total catch of all fishing in the study area was about 60 tons per year, worth about $300,000. Shared among the approximately 130 active fishers in the area, it represented a yearly income of less than $2400 per year for the average fisher.

The value of the total catch was relatively high because of the high demand for fish in Jamaica. During the study period, fish were sold on the fishing beaches directly to the consumers and occasionally to vendors, in two categories. The "quality" fish were sold for $5.90/kg (J$120/lb) and usually included groupers, snappers, goatfish, jacks, large grunts, most pelagic predators (such as Spanish mackerel and wahoo) and lobsters. In fact, almost any large fish was rated as "quality" and small "quality" fish were downgraded to "common". "Common" fish included most of the other reef species, such as parrotfish, surgeonfish, angelfish, small grunt and crabs, which were sold for $4.90/kg (J$100/lb). Unmarketable "trash" fish included moray eels, scorpion fish, file fish and very small fish. These were generally kept by the fisher for home consumption or given away to indigent persons or to people who helped pull the boats up on shore.

The cost of entering and remaining in the fishery was high, except for spear fishing, primarily due to the capital needed to obtain and maintain a boat. The initial costs ranged from $800 to $8000, depending on whether a new or second hand boat and engine were bought. Plywood boats were the least expensive at about $400 to $900, while fiberglass boats cost over $4000 new. Dugout canoes were rare due to the scarcity of large accessible cottonwood trees. Large fiberglass boats needed large engines (35 to 65 hp) which cost up to $3600 new. Some of the wooden boats were motorized with small engines (e.g. 4 to 10 hp, cost up to $1250) but most were not.

Other costs of fishing depend on the method involved. For trap fishing, the materials needed are mesh wire, sticks, nails, lacing wire and rope and these materials cost about $30 to $50 per trap, depending on the size of the trap and the type of mesh wire used. Most fishers built their own traps, but some hired others to build them. With ongoing repairs, fish traps could last about a year before they needed to be replaced, though many were lost at sea sooner than that because of storms, careless setting near the reef drop-off, or theft. Trap fishers seemed to set their traps very deep and often unmarked, perhaps to avoid theft or poaching by spear fishers. These practices tended to increase the number of lost traps. Owners of motorized boats also needed to purchase fuel, which of course varied depending on the size of the boat and engine, the condition of the engine, the frequency of fishing trips, the number of traps hauled and the distance the traps were set away from the beach.

Drop line fishers could expect to spend about $50-$200 for gear per year (fishing line, hooks). Bait was often caught by the fisher himself or bought at sea from another fisher. Troll fishers may have spent money on artificial bait ($5-$10 each) and a great deal on fuel. For this reason, trolling was not commonly practiced, except when moving between fishing grounds to operate other fishing gear. Net fishers, who usually used gill nets of 50 mm (2") to 100 mm (4") mesh size, would spend between $100 to $200 (about 12 kg of net) on average per year.

Changes In Catch Rates Over Time

Changes in the catch rates of 1.25" mesh fish traps between three 12-month periods in 1996, 1997 and 2000/01 are shown in Table 8. The catches were relatively stable over this time period, with the average catch of under 1 kg per trap haul. Mean soak time also remained stable at just under 3 days between hauls for the 1.25" mesh traps.

There did appear to be a very slight increase in fish trap catch rates, both in weight and number of fish, over the five year period, but only the increase in the number of fish between 1996 and 2000-2001 was likely significant. The increase in the catch appeared to be due to an increasing number of small fish in the catch, especially small parrotfish. As a result, the average fish size in the catch actually decreased over the time period, especially those of parrotfish, but also other groups such as grunts and groupers.

The value of the catch (in 2001 dollar values) also increased slightly but it was still only a little more than $4 per trap haul. The total weight of high quality fish actually decreased from 1996 to 2000/01 and there were more lower valued (common) species in the catch than earlier. The average fish size in all commercial categories also decreased.

DISCUSSION

This survey yielded an estimated total catch of demersal and neritic pelagic species of 60,770 kg by the five fishing beaches. This included 29,700 kg landed in traps, 5410 kg on lines, 2160 kg in nets and 23,000 kg taken by spearfishers, all taken from a total shelf area of 12 km$^{2.}$ The harvest was therefore estimated to be 5 tons/km^2.

These harvests per km^2 are very high by Caribbean standards, but not by those of Pacific coral reef systems (Munro 1984). However, the numerous surveys of the fishery, from 1968, 1990/94, 1996/97 and 2000/01, have provided consistent estimates of catches and there appear to be no reasons for challenging their accuracy.

The Jamaican north coast reefs are known to be one of the most overfished reefs in the Caribbean. This study confirmed that the fishing pressure on these reefs is enormous. Each and every day, on average, over 40 fishers scoured the narrow fringing reef along this 22 kms of coastline; almost 30 people pulling fish traps, nets and fishing lines from boats, another 15 people in the water using spear guns. This amounted to over sixteen thousand fishing trips over the course of the year, all in search of fish within this 12 km^2 fishing area. This figure included only active fishers known to operate regularly in the fishery and did not include an unknown number of recreational fishers who may have cast a line from the rocky shores along the coastline. Jamaica's north coast reefs have been enduring intense fishing pressure like this for decades.

Table 8. Comparison of catch rates, fish sizes and catch values in 1.25" mesh traps in 1996, 1997 and 2000-01 in the study area on the north coast of Jamaica.

	Weight per trap			Number of fish per trap			mean fish size		
	1996	1997	00-01	1996	1997	00-01	1996	1997	00-01
number of catches sampled	(110)	(44)	(278)						
number of traps reported	(672)	(279)	(1832)						
Catch composition by family	grams trap^{-1} haul^{-1}			fish trap^{-1} haul^{-1}			grams		
Scaridae	244	349	355	2.0	2.7	3.6	123	128	99
Acanthuridae	153	197	153	1.8	2.4	1.7	87	82	89
Holocentridae	50	73	51	0.6	0.8	0.5	84	90	94
Mullidae	18	26	49	0.1	0.2	0.4	142	162	127
Lutjanidae	80	34	48	0.3	0.1	0.2	245	352	295
Haemulidae	58	40	42	0.4	0.3	0.4	144	119	116
Balistidae	30	3	41	0.1	0.03	0.1	537	118	627
Serranidae	39	35	39	0.2	0.2	0.3	193	150	137
Muraenidae	48	28	36	0.03	0.04	0.1	1511	635	709
invertebrate	7	11	16	0.01	0.02	0.03	494	655	536
Carangidae	10	25	14	0.1	0.2	0.1	178	146	202
Pomacentridae	14	5	10	0.2	0.1	0.1	69	85	74
Kyphosidae	6	-	10	0.01	-	0.01	460	-	706
Labridae	1	5	8	0.01	0.04	0.1	120	120	123
Diodontidae	9	29	6	0.01	0.03	0.01	728	1087	1060
Scorpaenidae	7	3	5	0.02	0.01	0.01	353	423	529
Priacanthidae	5	2	4	0.04	0.01	0.04	130	130	100
Sparidae	8	-	4	0.01	-	<0.01	850	-	1105
Ostraciidae	3	1	3	0.01	0.01	0.01	239	225	243
Gerridae	7	2	2	0.03	0.01	0.01	240	175	232
Monacanthidae	2	-	2	0.02	-	0.01	155	-	285
Pomacanthidae	5	2	2	0.03	0.02	0.02	157	84	78
Grammistidae	1	-	1	<0.01	-	<0.01	257	-	235
Chaetodontidae	0.5	3	1	0.01	0.1	0.01	49	55	57
Aulostomidae	0.2	-	0.2	<0.01	-	<0.01	250	-	650
Sciaenidae	0.2	-	0.2	<0.01	-	<0.01	80	-	109
Bothidae	-	-	0.1	-	-	<0.01	-	-	225
Synodontidae	1	-	0.1	0.01	-	<0.01	150	-	400
Malacanthidae	-	0.3	0.1	-	<0.01	<0.01	-	100	450
Mugilidae	-	-	<0.1	-	-	<0.01	-	-	110
Dactylopteridae	-	0.4		-	<0.01	-	-	150	-
total	**806**	**873**	**903**	**6.0**	**7.3**	**7.6**	**135**	**120**	**119**
standard error	(96)	(109)	(46)	(0.6)	(0.8)	(0.4)	-	-	-
Catch composition by value									
quality	155	96	140	0.7	0.5	0.7	217	205	197
common	559	691	683	4.8	6.4	6.4	117	108	106
trash	92	86	79	0.5	0.4	0.5	201	201	173
Catch value	US$ trap^{-1} haul^{-1}								
	$ 3.66	$ 3.96	$ 4.17	-	-	-	-	-	-

Predictably, the rewards for this huge effort are very small. On the north coast in 2000/01, a Jamaican fisher could expect to make on average little more than $200 a month (equals a daily average of $6 including non-fishing days). From this, he had to purchase fishing gear, pay for fuel and support a family of (on average) five people. Most people nonetheless remain in the fishery to either supplement other incomes or simply because they have no other alternative. Fishing is given up or reduced when a person had better opportunities elsewhere and resumed or intensified when times are bad. As a result, the number of fishers using an area can fluctuate substantially over time. Multiple occupations are common in the Caribbean and allow people to increase their economic security (Polunin *et al* 2000).

Although a fisher's net income is low, it is not much lower than the income of those working in other industries, such as tourism. A waiter in a hotel can expect to earn $15 a day and a scuba-diving guide makes $12-20 a day. Day labourers can make about $8-15 a day (Polunin *et al* 2000, P. Gayle *pers comm*). However, other jobs are scarce in the area and, in any case, many fishers do not wish to work in other industries as other jobs do not allow the same independence in working as does fishing.

A number of non-fishers earned money on the fishing beaches, for example, by scaling and cleaning fish (which earned about $0.50 per pound of fish cleaned) and fish vending (purchasing fish on the beach and taking it to markets or buyers' houses to sell at a profit, again about $0.50 per pound). Moreover, at all beaches there were small businesses - shops, bars and restaurants - that relied on the presence of people on the fishing beaches. Most of these businesses bought fish from local fishers and served it to their customers, ensuring a small but steady market for the catch. They also sold other food and drink to fishers and to those people visiting the beaches to purchase fish, or to swim.

Even though Jamaica has an open access fishery, it has been argued that in practice, fishing is not necessarily free for all (Berkes 1987). Fishing beaches are said to act as a kind of territorial system, where fishers must set their traps close to their beach or risk losing them and a person wishing to fish from a beach must first be acceptable to the community of fishers who use it. At the same time, many fishers spent little time on their fishing beach beyond what was necessary to set off for and return from their fishing and hence had little social interaction with other fishers. Social cohesion on the fishing beaches appeared to be weak and there was little evidence of it limiting fishing effort in any substantial way. Because the entire area is heavily fished, there appeared to be little incentive to travel many kilometres from their home beaches.

A much more powerful force limiting fishing effort was the financial costs of entering fishing. These costs were high for all fishing types, except spear fishing, because of the capital needed to obtain a boat, either new or second hand. Most fishers would have liked to own a 27' fiberglass boat because it could last over 20 years and could increase the fisher's status among his peers. However, wooden boats were much more common because they were cheaper to buy and they could be rowed around without the need for an engine. The initial cost of entering the fishery was 40-360% of the annual average income of a fisher.

Owing to the high cost of owning a boat and to locally high unemployment rates, many young men have entered the fishery in recent years as spear fishers. Spear fishing was almost non-existent in the 1960's (Nembhard 1970, J.D. Woodley *pers comm*), yet by 2000/01, spear fishers landed an estimated 40% of the total catch in the area. The continually increasing number of spear fishers on the fishing grounds and their apparent ability to land a higher proportion of quality fish that other less selective gear types in the fishery, had led to escalating distrust, tension and conflict between spear fishers and the rest of the fishing community.

The Discovery Bay area fishery was the target of numerous management attempts during the 1990's, with the aim of improving fishers' livelihood, restoring the coral reef fish communities and addressing the ecosystem collapse that the reefs experienced on this coast. The University of the West Indies had attempted to address some of these problems, with backing from various local, industrial and international donors (Woodley and Sary in press, Woodley *et al* in press). However, progress had been difficult due to the huge problems facing would-be fishery managers, such as the high levels of distrust and conflict among fishers, widespread illiteracy and unemployment in the communities and lack of a traditional culture of community-based resource management in the country.

Nevertheless, there appeared to be a small increase in the catch rates in the fishery between 1996 and 2000/01. One possible cause of these observed changes may have been the management measures which were implemented in this fishery over the previous years. The Discovery Bay Fishery Reserve was established in 1996 and may have had a positive impact on local catches by delaying the size and age of recruitment to the fishery of certain fish groups that use the Reserve as a nursery area (Munro 2000).

The trap catch rates might have also benefited from the move to larger mesh sizes for the traps, encouraged by UWI with mesh exchange programs in 1991 (in Discovery Bay) and 1996/97 (in Rio Bueno, Runaway Bay and Salem). The proportion of large mesh traps (26%) in 2000/01 was much higher then when the mesh exchange began at Discovery Bay (6%), while the total number of traps in use has not increased and may have declined. The decrease in the number of small mesh fish traps after the mesh change may have reduced fishing mortality on small round bodied species, which would have benefited most from such a change in gear (Sary *et al* 1997). Unfortunately, the fishers gradually moved back to using small mesh traps and in 2000/01 appeared to be harvesting the increased number of small individuals which may have recruited to the fishery.

In any case, it is very difficult to pinpoint causes for changes in the catch rates; the differences over time may not be statistically significant because of the high variability normally observed in trap catches. Also, the fish stocks are exploited by numerous other gear types and the fluctuations in their catch were not examined. There are numerous other biological and human factors that may have impacted the reef ecosystem as well, such as the gradual return of the sea urchin ,*Diadema antillarum*, to the reef and signs of coral recovery in the area (Edmunds and Carpenter 2001, Cho and Woodley in press).

Despite the very high fishing effort, the reefs on this coast have remained surprisingly productive. The estimated total catch of 60 metric tones in the study area represents about 5 tons/km^2 of reef, which was near the high end of production estimates for Caribbean reefs (e.g. Munro 1983). The fishery directly supported at least 600 people and the fish caught continued to provide a valuable food source for a growing population in the area. However, if the fishery were meaningfully managed, i.e. fishing effort were somehow reduced, it could produce a larger and much better quality catch and offer an improved livelihood to those remaining in it. Escape gaps for traps may offer one feasible management option for overexploited trap fisheries in the Caribbean (Munro *et al* in press). Given the escalating economic and political problems facing Jamaica, however, fishing will likely continue to be the employment of last resort for Jamaica's poor.

REFERENCES

Aiken, K.A. and M.O. Haughton. 1987. Status of the Jamaican reef fishery and proposals for its management. Proc. Gulf Caribb. Fish. Inst. 38:469-484.

Berkes, F. 1987. The common property resource problem and the fisheries of Barbados and Jamaica. Environmental Management 11:225-235.

Cho, L. and J.D. Woodley. *In press*. Recovery of reefs at Discovery Bay, Jamaica and the role of *Diadema antillarum*. Proc. Int. Coral Reef Symp. 9:

Edmunds, P.J and R.C. Carpenter. 2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. PNAS 98(9):5067–5071.

Haughton, M.O. 1988. An analysis of statistical data from the Jamaican inshore fisheries. Pages 443-454 in: S. Venema, J. Moller-Christensen and D. Pauly. (eds.) Contributions to Tropical Fisheries Biology. FAO Fish. Rep. 389.

Hughes, T.P. 1994. Catastrophes, phase-shifts and large scale degradation of a Caribbean coral reef. Science 265:1547-1552.

Mahon, R. 1989. Fishery management options for the Lesser Antilles. FAO Field Document (FI:TCP/RLA/6776) 4:117 p.

Munro, J.L. (ed.) 1983. Caribbean Coral Reef Fishery Resources. ICLARM Studies and Reviews 7:258 p.

Munro, J.L. 1984. Coral reef fisheries and world fish production. ICLARM Newsletter 7(4):3-4.

Munro, J.L. 2000. Outmigration and movement of tagged coral reef fish in a marine fishery reserve in Jamaica. Proc. Gulf Caribb. Fish. Inst. 51: 557-568.

Munro, J.L. and D.M. Williams. 1985. Assessment and management of coral reef fisheries: Biological, environmental and socio-economic aspects. Proc. 5th Int. Coral Reef Congress. 4:545-581.

Munro, J.L ., Z. Sary and F.R. Gill. *In press*. Escape gaps: An option for the management of Caribbean trap fisheries. Proc. Gulf Caribb. Fish. Inst. 54:

Nembhard, B. 1970. The fishing industry of Jamaica: A report on the 1968 sample survey. Agricultural Planning Unit, Ministry of Agriculture and Fisheries, Jamaica.

Picou-Gill, M., J.D. Woodley, M. Miller, Z. Sary, W. Van Barneveld, S. Vatcher and D. Brown. 1996. Catch analysis at Discovery Bay, Jamaica: The status of an artisanal reef fishery. Proc. Gulf Caribb. Fish. Inst. 44:686-693.

Polunin, N.V.C., I.D. Williams, J.G. Carrier and L.F Robinson. 2000. Ecological and social impacts in planning Caribbean marine reserves. Department of Marine Sciences, University of Newcastle, 37 pp. Unpubl. MS.

Sahney, A.K. 1983. Sample survey of the fishing industry of Jamaica – 1981. FAO Fish. Rep. 278 (Supplement):255-275.

Sary, Z., J.L. Munro and J.D. Woodley. *In press*. Status report on a Jamaican reef fishery: Current value and the costs of non-management. Proc. Gulf Caribb. Fish. Inst. 54:

Sary, Z., H.A. Oxenford and J.D. Woodley. 1997. Effects of an increase in trap mesh size on an overexploited coral reef fishery at Discovery Bay, Jamaica. Marine Ecology Progress Series, 154:107–120.

Woodley, J.D. and Z. Sary. *In press*. Development of a locally-managed fisheries reserve at Discovery Bay, Jamaica. Proc. Int. Coral Reef Symp. 9:

Woodley. J.D., Z. Sary, P. Gayle, W. Lee, P. Parchment and L. Walling. *In press*. The Discovery Bay Fishery Reserve. Proc. Gulf Caribb. Fish: Inst. 54: