Some Advances and Developments in Coral Reef Fisheries Research: 1973-1982[1]

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ABSTRACT

Scientific progress in the study of coral reef fisheries in the past decade stems mostly from technical innovations such as the method for estimating ages from daily rings in otoliths, the development of length-structured stock assessment techniques combined with the availability of relatively inexpensive programable calculators and micro-computers and the wide availability of SCUBA facilities.

The development of techniques for extraction of the maximum amount of information from length-frequency data offers the possibility of re-analyzing existing data sets and deriving estimates of growth and mortality estimates. Substantial advances have been made towards an understanding of reproduction and recruitment in coral reef fisheries. Arising from the accumulated knowledge of reef fish reproduction it is suggested that, as a general rule, reef fish populations are recruitment limited.

Visual-census techniques have become more quantitative and methods of estimating the area fished by stationary gears, such as traps, have been developed, thus leading to the possibility of improved estimates of the abundance and density of reef fish stocks. A number of multi-species models have been developed which could be applied to reef fish stocks but parameter estimation remains a major obstacle.

The maximum potential sustainable fish harvest from coral reefs remains unknown, but it is clear that harvests of demersal and neritic pelagic fishes of 4-6 mt $km^{-2} \times yr^{-1}$ are taken from many tropical coralline shelves and that very much greater harvests of fishes per unit area are attainable in areas which have a dense cover of actively-growing corals.

The objective of this paper is to identify and discuss areas in which significant progress has been made in the last 10 years towards an understanding of the fundamental processes governing the productivity of coral reef fisheries, and to highlight the areas where considerable doubt or even controversy exists. The number of recent papers which refer to fishes of coral reefs is enormous and although few relate directly to reef fisheries, they have in many cases contributed to our understanding of reef fish productivity.

The early part of the past decade saw the completion of major Caribbean reef resource surveys and studies in Jamaican waters (Munro, 1977), in the Bahamas (Thompson, 1978) and the completion of the FAO/UNDP Caribbean Reel Fishery Development Project (Kawaguchi, 1974, Wolf and Chislett, 1974) and the, perhaps belated, recognition that coral reef fishery resources are capable of supplying a significant part of the world's fish supply (S.V. Smith, 1978; Carpenter, 1977).

Additionally, the presumptive causative organism responsible for ciguatera fish poisoning, *Gambierdiscus toxicus,* was isolated and identified (Yasumoto et al., 1977) giving new impetus to further investigations of this problem (Randall, 1980; De Sylva and Higman, 1980).

On taxonomic matters, the publication of the FAO Species Identification Sheets for Fishery Purposes covering the Caribbean and Indo-Pacific (Fischer, 1978; Fischer and Whitehead, 1974) should have reduced the major taxonomic confusions and led to some degree of uniformity on nomenclatoral matters for the exploited species. The publication of semi-popular manuals (Nagelkerken, 1981) will also lead to a greater degree of assurance in dealing with fishermen.

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TECHNICAL ADVANCES

Several significant technical developments have paved the way for advances in coral reef fisheries research. Perhaps the most significant of these was the recognition of Panella (1974; 1971) that certain micro-structures in otoliths were, in fact, daily rings. It is now clearly established that at least the younger stages of many coral reef fishes can be aged by this technique (Brothers, 1980; 1982; Brothers and McFarland, 1981; Ralston 1977; 1980; Ralston and Miyamoto 1982).

Secondly, the now common availability of air compressors and other SCUBA facilities, even in remote locations, has extended the range of possible observations on coral reefs and their frequency and duration, leading to a better overall understanding of reef phenomena.

Thirdly, and perhaps most important of all, has been the development of length-frequency based methods of fish stock assessment. These methods have their origin in the equation developed by Beverton and Holt (1956) which states that

$$Z = K\,(L_\infty - \bar{L}) \,/\, (\bar{L} - L')$$

in which Z is the coefficient of mortality, K is the coefficient of growth, L_∞ is the asymptotic length, L' is the smallest length of fish which is fully represented in the catch and $\bar{L}$ is the average length of all fishes lying between L' and L_∞. However, with few exceptions, the usefulness of the method, whereby mortality rates can be estimated from catch length-frequency distribution data and growth rate estimates, was not generally recognized and it remained virtually unused for many years (Munro, 1980b).

However, Green (1970), Ebert (1973), van Sickle (1977) and Powell (1979) subsequently produced a succession of papers demonstrating the estimation of growth and/or mortality rates from size distributions. Ssentengo and Larkin (1973) produced an equation similar to that of Beverton and Holt (1956) and Saila and Lough

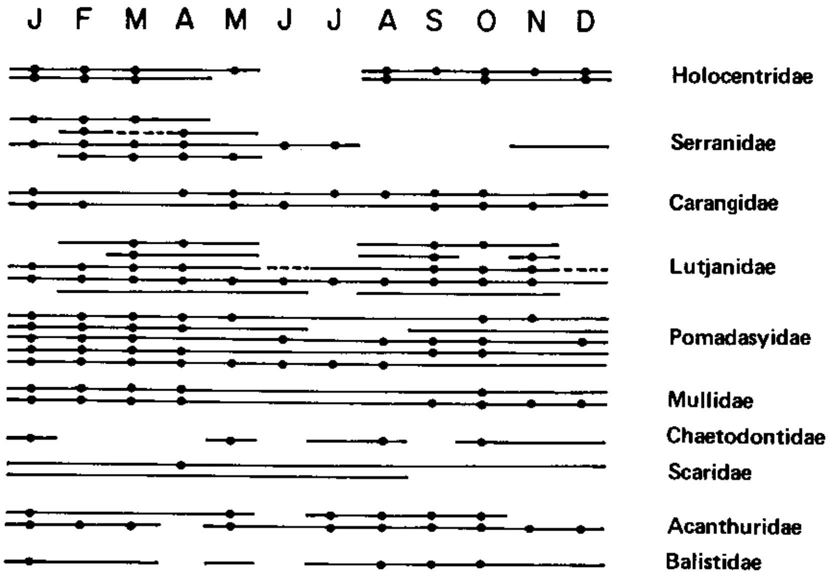

Figure 1. Synopsis of data on spawning seasons of 26 commercially important species of coral reef fishes in Jamaican waters (from Wyatt 1976; Thompson and Munro 1974a, b, c; Billings and Munro 1974; Munro 1974c; Aikin 1975a, b; Reeson 1975a, b). Horizontal bars indicate months in which ripe or spent fishes were obtained. Dots indicate months in which more than 20% of the fishes in the sample had ripe or spent gonads. Broken lines indicate months for which there are no data.

(1981) a synthesis of the above-mentioned works. Jones (1981) developed the techniques of length cohort analysis (which requires catch statistics in addition to length-frequency data) and Pauly (1982) has developed a method for deriving a catch curve from length-frequency data and growth parameters.

Additionally, a method for processing length-frequency data on micro-computers which removes the subjectivity of modal progression analyses and derives a best possible fit to any set of data has been developed by Pauly and David (1981). Micro-computer based methods for comprehensive stock assessments based almost exclusively on length-frequency distributions have been developed by Pope, Pauly and co-workers and will soon be published.

What these developments mean, in essence, is that existing sets of length-frequency data can be reappraised and first, or improved, estimates of growth and mortality rates obtained. One question that has not yet been solved is the problem of assessing what represents an adequate sample size for a length-frequency distribution and, as in any fishery, obtaining an unbiased sample of fishes.

Finally, Pauly (1980a, b) has demonstrated that the inter-relationships which exist between temperature, growth parameters and natural mortality rates are sufficiently close that a useful degree of predictability of, say, natural mortality rates is possible given estimates of growth parameters and mean environmental temperatures.

Although new methodologies have emerged, there are still relatively few sets of data pertaining to coral reef fishes to which these methods can be applied.

SCIENTIFIC ADVANCES

Reproduction and Recruitment

The question of the seasonality of spawning and periodicity of recruitment (which are not necessarily the same things) has received attention. In Jamaican waters, it was found that there were two main spawning periods for most of the larger species of reef fishes with maxima around March-April and September-October (Munro, 1974a). Figures 1 and 2 show a synopsis of the Jamaican data.

Watson and Leis (1974) noted that spring and fall spawning peaks around Hawaii coincided with periods of weakened currents and Johannes (1978) found that 13 of 18 spawning peaks listed in the literature coincided with periods when prevailing winds were weakest and suggested that reproductive strategies of tropical marine fishes have evolved in part to maximize recruitment of offshore larvae to nearby inshore habitats. Data for Kenyan waters (Nzioka, 1979) and for the Great Barrier Reef (Russel et al., 1977) appear to add further weight to this hypothesis. However, data for the spawning periods of the large species of serranids (Goeden, 1978; Chen et al., 1980; Nagelkerken, 1979; Olsen and La Place, 1979 and Thompson and Munro, 1974a) do not appear to fit with any known pattern and our understanding of these phenomena is far from complete. It appears that the spring and fall peaks (Fig. 2), which seem to be confirmed for the Caribbean (Munro, 1974a; Luckhurst and Luckhurst, 1977; Powles, 1975), might converge in more northern waters and be replaced by a single summer peak (Grimes and Huntsman, 1980; Bradley and Bryon, 1974; Futch and Bruger, 1976).

Additionally, it is clear that some spawning occurs throughout the year for most tropical species (Colin, 1978; 1982; Erdman, 1977; Boardman and Weiler, 1980) and that periodic peaks merely reflect the times of increased activity within the tropical zone. Johannes (1978) has collected ample evidence that a lunar periodicity of spawning is also most often superimposed upon whatever seasonal patterns exist.

One of the principal features of research on coral reef fishes (as opposed to fisheries), in the last decade, has been the enormous proliferation of ethological studies and the controversy which arose, and is perhaps not yet resolved, over whether reef

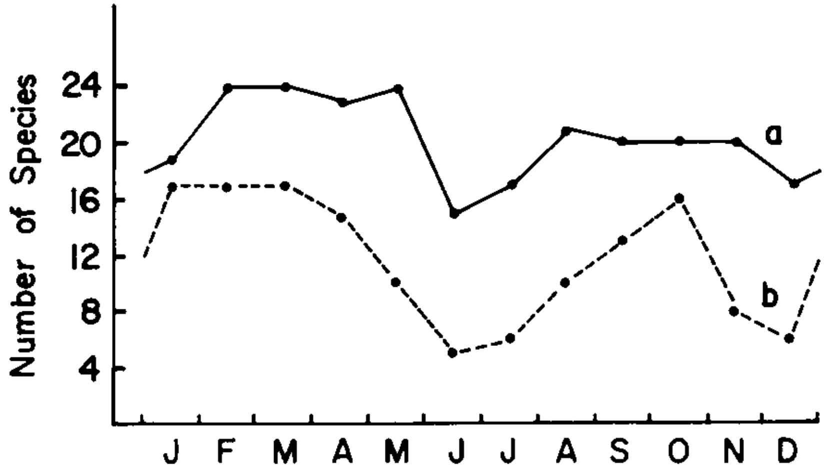

Figure 2. Numbers of species in Jamaican waters, of a total of 26, in which (a) some ripe fishes were found in a given month and (b) in which more than 20% of fishes in the sample had ripe or spent gonads.

fishes partition the resources of the reef in some fashion or simply indulge in a scramble for space (or other resources) by adding new recruits to the system at the greatest possible rate. This argument appears to have been sparked off by the work of Russell et al. (1974) who, on the basis of observations on the Great Barrier Reef, suggested that colonization is essentially a random process. This was amplified by Sale (1976) and other investigators soon made contributions (Sale, 1978; Luckhurst and Luckhurst, 1977; Dale, 1978; C.L. Smith, 1978).

Helfman (1978a) summarized the then existing situation, by which time various proponents had agreed that space on reefs is limiting and that recruitment from the plankton is a random process, but disagreed on whether reef fishes partition the resources. The case against any sort of resource partitioning and in favor of a random colonization process seems to have been made by Bohnsack and Talbot (1980) who found no differences in the number of species, number of females and mean number of individuals per reef for isolated model reefs in Florida and Great Barrier Reef waters. Also, Talbot et al. (1978) and Brock et al. (1979) concluded that, at least, over small areas of reef, long-term stability of the reef fish community composition was unlikely because of the combination of high predation rates and a random process of colonization of vacant space by new recruits.

A summary of and comments on the recruitment phenomena are given by Sale (1982) and by McFarland (1982). The latter concludes "that recruitment to inshore reefs is dependent on several factors — the individual species' capacity to prolong larval life, the effect of currents on the dispersion and settlement of recruits, the constancy or periodicity in the production of eggs and larvae through reproductive drive and the nature of the settlement site," which is as succinct a synopsis as can be found. Johannes et al. (1981) have suggested that, notwithstanding occasional long distance dispersal of larvae, post-larvae and/or juveniles, a high degree of reef fish recruitment might be derived from local spawning, that genetic interchange might be limited and discrete stocks of reef fish species might exist.

One particular feature of the reef fish debate appears to have been the tacit assumption that space on reefs is a factor which limits the population size of virtually all reef fish. However, as suggested recently by Doherty (1981), and previously by Munro et al. (1973) in a somewhat different context, there is no evidence whatever that planktonic dispersal of the larvae of reef fishes regularly provides more recruitment than most populations can absorb. Munro et al. (1973) observed that catch rates from virgin reef fish stocks at Pedro Bank in the west-central Caribbean were markedly less than at Rosalind Bank, which is proximal to the Nicaragua-Honduras shelf and suggested that the absence of any shallow waters upstream of Pedro Bank combined with the apparent absence of any significant mechanisms for retaining larvae such as gyres, accounted for these differences.

It is here suggested that all reef dwelling fishes (and perhaps also many other demersal reef organisms) with pelagic larvae are normally recruitment limited. That is, that the population densities of those organisms in which the young need to settle from the plankton onto a suitable substratum is limited by the larval survival rates in the plankton, by the abundance of predators on and around the settling substratum and by the likelihood of current systems depositing the young near suitable settlement sites.

Certainly, in the case of coral reef fishes, if not other organisms, the limiting factors all work to reduce recruitment. The characteristic spawning aggregations (Colin, 1982; Randall, 1961; Randall and Randall, 1963) are attended by abundant egg-eating planktivores (Colin, 1978) and any eggs that are not wafted away from the reefs are preyed upon by a great variety of organisms (Hobson and Chess, 1978; Leis, 1981). Once into the oceanic plankton, the larvae and post-larvae are also prey to a host of pelagic fishes including tuna, and are then largely dependent upon some chance current system returning them to a safe substratum. Johannes (1978), Powles (1975) and Leis and Miller (1976) have all suggested that gyres are important in retaining larvae around islands and indeed, if this were not so, islands such as Barbados, Pitcairn and Easter Island would be devoid of all neritic fishes with pelagic larvae. Instead, these islands have substantial fish populations and it would be interesting to investigate whether such communities are composed predominantly of forms having short larval lives (perhaps Lutjanids).

However, there is no evidence that the reproductive strategies proposed by Johannes (1978), which consist of spawning as far seaward as possible, preferably in the late afternoon (as predation on eggs is reduced at night: Hobson and Chess 1978) on a strongly ebbing spring tide, combined with gyre systems at the calmest periods of the year, regularly succeed in *saturating* the reef environment with newly-metamorphosed post-larvae.

Rather, it now appears that the strategy of most reef dwelling fishes is to spawn over extended periods with some concentration of activity into certain favorable periods (summer or spring and fall, coinciding with calm periods with low current velocities) in the "hope" that the requisite "environmental window" [analogous to the "survival window" proposed by G. Sharp (see Bakun et al., 1982)] of biotic and abiotic factors will be open and will permit significant numbers of larvae to pass through and survive to settlement. Periodic opening of the environmental window will result in episodic recruitment. It also seems likely that the conjunction to a greater or lesser degree of all factors necessary for survival which results in the opening of the window might well be a local phenomenon, with only a basic relationship to the seasons or to lunar rhythms. From the time of settlement onwards, the system will be predator-controlled, with vacant territories constantly created on the reef for those species which require a defendable territory, and heavy predation upon all small elements of the fauna.

There seems to be little doubt that very wide dispersal of larvae is achieved by those reef fishes and invertebrates which have long-lived larvae and post-larvae. In many cases, favourable currents, eddy systems or geographical locations probably cause particular areas to regularly receive abundant recruits and thus support large populations of certain species, whereas different areas might be chronically short of recruits because of unfavorable geographic circumstances. Pedro Bank which lies 1500 km downstream from the islands of the Eastern Caribbean seems a likely example of the latter condition, whereas much of the Bahamas, Florida and the East Coast of the USA which lie downstream of other Caribbean reef systems might be much more favorably placed to receive recruits. It is suggested that reef fisheries of most island systems which do not lie within a massive gyre or precisely at an optimum distance downstream of another reef system are chronically recruitment limited and that even under the most favorable circumstances, there are few instances of saturation of the habitat by juveniles (Kami and Ikehara, 1976).

A final point concerning reproduction which has emerged in the last decade is that many families of coral reef fishes, including members of the Serranidae (Nagelkerken, 1979; Jones, 1980; Goeden, 1978), Lethrinidae (Lebeau and Cueff, 1975), Scaridae, Sparidae, Labridae, Pomacanthinae (Smith, 1975) and Amphiprioninae (Moyer and Nakazono, 1978), are sequential hermaphrodites, and in some groups, also diandric or digynous (Smith, 1982). We require a far better understanding of the factors triggering sex change if we are to make any rational steps towards management strategies for such species, failing which recruitment from exploited stocks might become drastically limited, if not extinguished (Smith, 1982).

Parameter Estimation

Despite the methodological advances mentioned previously, there is still no consensus on the general order of magnitude of growth rates attained by coral reef fishes and of natural mortality rates which might prevail. None of the detailed studies of recruitment of small reef fishes which have been conducted appear to have been accompanied by estimates of subsequent growth and mortality, such that turnover rates in the reef community could be estimated.

There are still few published accounts of attempts to age commercially important coral reef fishes on the basis of daily rings in otoliths, the exceptions being the works of Ralston (1977; 1980; 1981) and Moffitt (1980) on various Hawaiian reef fishes and of McFarland (1980) who found that juvenile *Haemulon flavolineatum* could be aged at least up to 700 days, by which time they attained lengths of up to 12 cm, but that best results were for the first 100 days of life.

Pauly and Ingles (1981) have analyzed a number of data sets for reef fishes using the ELEFAN I micro-computer program (Pauly and David, 1981), which also can accommodate temperature-induced seasonal growth oscillations. I have reanalyzed length-frequency data collected in Jamaica using the ELEFAN I program to test whether any better interpretations of the data are obtainable and have also applied the ELEFAN I programs to published length-frequency data for reef fishes from the west coast of Florida (Salomon et al., 1981).

All of the above-mentioned estimates plus others culled from the literature are summarized in Table 1 from which it is apparent that some success has attended analyses of annular marks on scales and otoliths in areas near the edge of the tropics. It is also obvious that if growth checks cause discernible marks on hard parts, overall growth rates in such regions might be expected to be lower than in equatorial regions. The analysis of Pauly (1981) suggests that for a given species, larger asymptotic sizes (L_∞) and lower growth coefficients (K) would be attained in cooler regions.

Pauly (1982) has also devised a micro-computer based method (ELEFAN II), which converts length-frequency distributions into catch curves, given inputs of the growth coefficient K, and the asymptotic length, L_∞. The slope of the right-hand descending limb of the catch curve is an estimate of total mortality. Also, Pauly

Table 1. Estimates of the coefficient of growth, K, and the asymptotic length L_∞, of various coral reef fishes. Values marked with an asterisk (*) have been recalculated from the original data and are given in cm, TL, FL or SL. Asymptotic lengths given in brackets are assumed values based upon the largest specimens in the sample

Species	Source	Locality	Method	K	L_∞ (cm)
SERRANIDAE					
Mycteroperca venenosa	Thompson and Munro, 1974a	Jamaica	Otoliths	0.17	(86) TL
Mycteroperca microlepis	Salomon et al., 1981	Florida	ELEFAN 1	0.155	*129.7TL
	Manooch & Haimovica, 1978	E. coast, USA	Otoliths	0.121	129.0TL
Plectropomus leopardus	Pauly and Ingles, 1981	Great Barrier Reef	ELEFAN 1	0.25	64.7TL
Epinephelus striatus	Olsen & La Place, 1979	Virgin Islands	Probit analysis	0.185	97.4TL
Epinephelus morio	Moe, 1969	E. Gulf Mexico	Otoliths	0.18	80.0TL
	Melo, 1976	Campeche	Otoliths	0.11	92.8TL
Epinephelus guttatus	Thompson & Munro, 1974a	Jamaica	Modal progress	0.24	52 TL
		Jamaica	ELEFAN 1	0.22	*54.5TL
Epinephelus fulva	Burnett-Herkes, 1975	Bermuda		0.18	
	Thompson & Munro, 1974a	Jamaica	Modal progress	0.63	34 TL
			ELEFAN 1	0.56	*35.5TL
Epinephelus cruentatum	Thompson & Munro, 1974a	Jamaica	Modal progress	0.34	34 TL
Epinephelus sexfasciatus	Pauly and Ingles, 1981	Philippines	ELEFAN 1	0.51	30.9SL
LUTJANIDAE					
Lutjanus campechanus	Futch & Bruger, 1976	Florida	Otoliths	0.35	*(60)TL
	Nelson & Manooch, 1982	Florida	Scales & Otoliths	0.155	97 TL
Lutjanus bohar	Salomon et al., 1981	Florida	ELEFAN 1	0.225	*95.4TL
	Talbot, 1960	Kenya	Scales	0.27	*(66)TL
	Wheeler & Ommaney,	Seychelles & Amirantes	Peterson method	0.33	*(66)TL
Pristipomoides filamentosus	Ralston,* 1980	Hawaiian Is.	Otolith daily rings	0.164	80.5FL
Rhomboplites aurorubens	Grimes, 1978	N & S Carolina	Scales	0.198	62.7FL
Ocyurus chrysurus	Thompson & Munro, 1974c	Jamaica	Modal progress	0.25	60 FL
POMADASYIDAE (Haemulidae)					
Haemulon album	Billings & Munro, 1974	Jamaica	Peterson method	0.20	65 FL
Haemulon plumieri	Manooch, 1976	N & S Carolina	Scales	0.11	64 TL
	Billings & Munro, 1974	Jamaica	Modal progress	0.35	42 FL
		Jamaica	ELEFAN 1	0.275	*39.8FL
Haemulon sciurus	Billings & Munro, 1974	Jamaica	Modal progress	0.26	40 FL
			ELEFAN 1	0.24	*40.2FL
Haemulon aurolineatum	Manooch & Barans, 1982	N & S Carolina	Scales	0.22	31 TL
LETHRINIDAE					
Lethrinus nebulosus	Loubens, 1978	New Caledonia	Otoliths	0.21	(71) SL
Lethrinus enigmaticus	Lebeau & Cueff, 1975	Saya de Malha	Scales	0.13	*(55) TL
CARANGIDAE					
Caranx ruber	Thompson * Munro, 1974b	Jamaica	Modal progress	0.24	52 FL
			ELEFAN 1	0.24	*56 FL
POMACENTRIDAE					
Eupomacentrus planifrons	Pauly & Ingles, 1981	Jamaica	ELEFAN 1	0.58	11.6SL
	Males & Females			0.33	11.6SL
CHAETODONTIDAE					
Chaetodon miliaris	Ralston, 1977	Hawaii	Otoloth daily rings	1.13	12.7SL
BALISTIDAE					
Balistes vetula	Aiken, 1975b	Jamaica	Modal progress	0.57	45 FL
			ELEFAN 1	0.53	*47 FL

Refer also to the paper by G. Loubens, Biologie de quèlques espèces de poisson du lagon Néo-Caledonien III Croissance. Cahiers de l'Indo-Pacifique 2(2): 101-153 (1980) which gives estimates of growth parameters for 28 species of fishes, mostly reef inhabiting.

(1980a) has derived an empirical equation which states that $\log_{10}M = -0.0066 - 0.279 \log_{10}L_\infty + 0.6543 \log_{10}K + 0.4634 \log_{10}T$ in which M is the calculated coefficient of natural mortality, K is the coefficient of growth, L_∞ is the asymptotic length and T is the mean water temperature.

Length-frequency distributions of catches of various species of fishes taken at unexploited parts of Pedro Bank in the Caribbean by myself and co-workers (Munro, 1974a) were previously used to estimate natural mortality rates using the formulation of Beverton and Holt (1956) and these data have been reanalyzed using the ELEFAN II program. The results of these analyses will be published in detail elsewhere, but it can be noted here that the estimates obtained from the length-converted catch curves and those derived from the Beverton and Holt (1956) equation are generally similar but that those derived from the empirical equation of Pauly (1980a) are substantially lower.

The length-converted catch curves permit the detection of changes in catchability or mortality with increasing age or size and are of principal importance in this respect.

All methods based on length-frequency distributions assume that there have been no systematic changes in recruitment, that catchability is not size-related once fishes are fully retainable by the fishing gear and that the samples are therefore reasonable representations of the entire recruited stock. Hartsuijker (1982) has suggested that the catchabilities of reef fishes in traps change with increasing size. Most of the species so far tested show reasonably linear descending arms of the catch curves. The exceptions are *Epinephelus guttatus* and *E. fulva* in which there appear to be systematic decreases in the catchabilities of larger fishes or progressive increases in mortality with increasing size.

It is concluded that length-converted catch curves offer an excellent means for deriving estimates of mortality rates from length-frequency data and for deriving information on such matters as the effects of exploitation of the community upon natural mortality rates (Munro, 1974a; 1980b; Jones, 1979).

Stock Assessments

The perfection of SCUBA diving equipment has led to the development of highly sophisticated visual censusing techniques (Craik, 1981; Brock, 1982; Sale and Douglas, 1981), giving considerable confidence in density estimates of diurnally active species when surveys are properly executed. However, with very few exceptions, such techniques have not been applied to commercially-exploited species.

Additionally, Eggers et al. (1982) have presented a method whereby it is possible to estimate the average area from which a trap or other stationary fishing gear draws its catch of a particular species. The method has not yet been applied to coral reef fisheries but it appears that this, combined with the visual-census techniques and further advances in our understanding of how traps actually function (Stevenson and Stuart-Sharkey, 1980; Olsen et al., 1978; Craig, 1976; Munro, 1974b; Munro et al., 1971) gives promise of population estimation based on trapping. If a set of definitive experiments are conducted, it might be possible to convert the results of previous trap fishery investigations (Wolf and Chislett, 1974; Munro, 1980a; Hartsuijker, 1982) to estimates of population densities.

Although as demonstrated by Munro (1975; 1977), it is possible to merely sum the results of conventional single species assessments in a multispecies coral reef fishery, the degree of uncertainty attached to the input parameters and most especially the unknown extent to which parameters are influenced by species interactions, limits the usefulness of this approach (Munro, 1980b).

Making assessments using total biomass—fishing intensity surplus yield curves in which the fishing intensities per unit area are regressed against catch-per-unit of effort from different, but ecologically similar areas (Munro and Thompson, 1973) has found some usefulness in making assessments in other coral reef areas (Gulland, 1979), but application to coral reef fisheries remains limited by the acute non-availability of appropriate statistics. The work of Bazigos (1974) offers some hope of correcting this situation.

A number of multi-species models have been proposed in recent years (Andersen and Ursin, 1977; Pope, 1979; Saila, 1982; Powers and Crow, 1982) but all remain bedevilled by the problems of parameter estimation. A promising approach arising from a simplification of ecosystem models, such as that of Laevastu and Favorite (1978) has been developed by Polovina and Tagami (1980) for the French Frigate Shoals, in which an ecosystem model is simply based upon estimates of biomass, production and consumption at different trophic levels. A similar approach has been developed by Larkin and Gazey (1982). Given the availability of good census techniques combined with a much improved knowledge of food and feeding of reef fishes (Talbot and Goldman, 1972; Ogden, 1976; Ogden and Lobel, 1978; Hobson and Chess, 1978; Parrish et al., 1980; Randall, 1980; Hay, 1981) it would appear that such models have the greatest potential for giving an insight into the complex reactions wrought on a community by exploitation, which is almost invariably selective.

At a more immediate level, multispecies analyses by Stevenson (1978) of the Puerto Rican trap fishery and by Ralston (1980) demonstrate that useful results can still be generated by using fairly conventional techniques. There is clearly scope for further conventional stock assessments, particularly if length composition data (Jones, 1981) are effectively utilized to conduct virtual population analysis (VPA) and cohort analysis.

Potential Harvests from Coral Reef Areas

This particular topic has generated considerable interest (Smith, 1978) and an equal amount of confusion in recent years. Most available data have been summarized by Marshall (1980) and recapitulated by Marten and Polovina (1982). Basically, it appears from the available evidence that harvests of fish of 4-6 mt km^{-2} yr^{-1} are attainable from *coralline shelves* (Munro, 1977; Wijkstrom, 1974; Carpenter, 1977; Murdy and Ferraris, 1980; Bayliss-Smith, in press). Such shelves, extending from the shore to an arbitrary 200-m isobath encompass seagrass beds, sand flats, submerged reefs and emergent reefs, and all other habitats (Marshall, 1980). The fishes included in the statistics have usually comprised all neritic species.

More recent evidence from fisheries based on reef flats and almost pure stands of coral has shown that harvests of reef fish and invertebrates per unit area of actively growing coral are far in excess of those mentioned above. Hill (1978) and Wass (1982), respectively estimated average yields of fish of 8 mt km^{-2} yr^{-1} and 18 km^{-2} yr^{-1} for the shoreline fishery of American Samoa, plus very large catches of invertebrates when harvests from depths of only 0-8 m are considered. In the Central Philippines, Alcala (1981) and Alcala and Luchavez (1981) have estimated harvests of 13 mt km^{-2} yr^{-1} at Apo Island and a range of 9.7-23.7 (mean 16.5) mt km^{-2} yr^{-1} over a 5-year period at Sumilon Island. In both cases, only reef fish are considered and invertebrates and transient pelagics were excluded from the estimation. The harvests in the above-mentioned instances are from depths down to 60 m and the intervening depths are substantially covered with living corals. Both island shelves have been subjected to exploitation for many years.

It is clear that questions of potential productivity of coralline shelves relate closely to the depths involved, to the areas of living coral cover and to the productivity of adjacent habitats, and a recent workshop (Saila and Roedel, 1980) has recommended that the possibility of relating coral reef fishing potential to a morphoedaphic index be pursued. This has been further explored by Marshall (1981), but these questions require additional field work, backed up by a solid statistical base, before they can be resolved.

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