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THE STATUS OF SILVERLIP PEARL OYSTER *PINCTADA MAXIMA* (JAMESON) (MOLLUSCA, PTERIDAE) IN THE SOLOMON ISLANDS AFTER A 15-YEAR EXPORT BAN

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ABSTRACT In the Solomon Islands, there have been three periods of commercial exploitation of the silver (gold)-lip pearl oyster *Pinctada maxima*. The most recent ended in 1993, when export of all species of pearl oysters was banned to allow stocks to recover from overexploitation. In 2007, a nationwide survey was undertaken to determine the status of the population. Communities adjacent to former fishing grounds were interviewed about past and current fishing practices, and the abundance, size composition, and quality of *P. maxima* shells were assessed by drift diving. In total, 117 *P. maxima* were recorded, from 33 of 96 transects. When present, the mean density of oysters varied from less than 0.10–1.23 oysters/400-m^2 transect. Size structure was biased toward large individuals, with mean and median shell size for all oysters taken being 219 mm. There appears to have been little or no recovery of *P. maxima* stocks since their export was banned. The existence of small populations of large individuals implies persistent failure of reproduction, spat settlement, and/or recruitment during the past decade. Exploitation may have reduced the *P. maxima* populations to such an extent that their fertilization success has become susceptible to Allee effects. Recent poaching of shell reported by local villagers may have compounded slow or sporadic recruitment. If the stocks do eventually recover, management strategies that protect the recovered population will need to be implemented to prevent a repeat of the overfishing seen in previous harvest cycles.

KEY WORDS: *Pinctada maxima*, pearl oyster, abundance, population size structure, management, Solomon Islands

INTRODUCTION

In the Solomon Islands, small quantities of blacklip (*Pinctada margaritifera*), silver-lip (*Pinctada maxima*), and brown-lip (*Pteria penguin*) pearl oysters have been collected for centuries by free-diving subsistence fishers (Skewes 1990). During the past century, there were 3 phases of commercial exploitation, primarily of *P. maxima* for mother-of-pearl, but also for *P. margaritifera*. The first phase of exploitation took place between 1916 and 1922, and was undertaken by Japanese hard-hat divers based at Aratoba Island near Waghina (Gauld 1975) cited in Colgan (1993)). It is not known how much shell was harvested during that period. A second phase of exploitation began in 1968, in which hard-hat diving was replaced by hookah techniques. Anecdotal evidence indicates that 20 t of *P. maxima* were taken annually during this period, mainly from Hamilton Passage and Nggosele Passage in the Waghina area, and that 22 divers from the area were used at the peak of operations (Colgan 1993). After 4 y, this fishery failed because of declining stocks, increased operational costs, and a decline in mother-of-pearl prices on world markets. A third phase of exploitation for mother-of-pearl commenced in 1987, after a break of 15 y (Colgan 1993). Export figures indicate that between 6 t and 25 t of *P. maxima* shell were harvested annually until 1992 (Richards et al. 1994). By 1993, stocks were so depleted that the export of wild-caught silverlip and blacklip pearl oysters was banned to conserve remaining stocks (Kile 2000). At that time, a survey of the most productive fishing grounds at Waghina and Kia, involving more than 10 h of diving, yielded 12 *P. Maxima*, most of which were had a dorsoventral measurement (DVM) of more than 200 mm (Colgan 1993). It was hoped that the ban would allow the population to recover sufficiently to allow commercial harvesting for mother-of-pearl or to provide young stock to facilitate the development of a pearl culture industry (Richards et al. 1994).

By 2007, renewed interest in the potential for exploitation of pearl oysters in the Solomon Islands and pressure from local marine resource owners raised the question of whether there was sufficient recovery of stocks to allow commercial harvesting. However, no systematic attempts had been made to monitor the size of blacklip or silverlip pearl oyster stocks during the expected recovery period to provide the data on which to make such a decision. The only systematic survey of marine resources in that period was a ‘‘broad-brush’’ assessment of commercially important species, including pearl oysters, undertaken in June 2004 across the Solomon Islands (Ramohia 2006). That survey yielded no silverlip and few blacklip pearl oysters, but did not specifically target pearl oyster habitat, so it left open the possibility that healthy stocks may have been overlooked.

To help to fill this information gap, a survey of eight former *P. maxima* fishing grounds in the Solomon Islands was carried out in 2007. This article presents information on the abundance and size structure based on underwater visual censuses undertaken by teams of hookah divers in April to October 2007.

MATERIALS AND METHODS

Study Area

The Solomon Islands is situated in the southwest Pacific Ocean between latitudes 5–12° S and longitudes 152–170° E. The archipelago is orientated southeast to northwest and consists of 6 major islands, 30 medium-size islands, and 886 smaller islands spread over 600,000 km^2 of ocean (Hughes 2006). The 6 major islands are arranged in a double chain with Choiseul, Isabel, and Malaita to the north, and Makira, Guadalcanal, and New Georgia to the south (Fig. 1).

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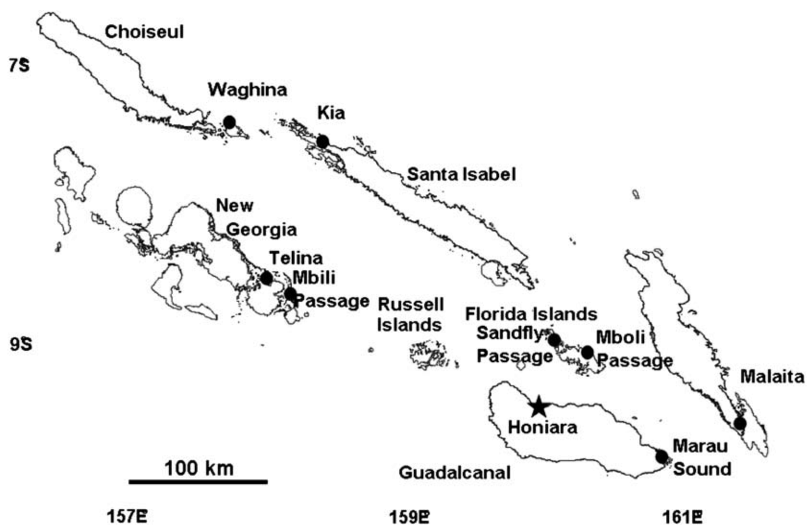

Figure 1. Map showing the relative position of the 8 fishing grounds surveyed in the Solomon Islands.

Interviews with Local Communities

Localities where past exploitation of silverlip pearl oysters has occurred were identified from harvest records held by the Solomon Islands Ministry of Fisheries and Marine Resources. Communities at these localities were visited to seek permission to work in customary waters and to conduct interviews with local fishers regarding historical distribution of pearl oysters, likely current distribution, and occurrence of any recent or ongoing exploitation. At each community, at least five local people who expressed personal experience in pearl oyster fishing were interviewed using a structured questionnaire. The questionnaire was designed to determine how large and important the pearl fishery was in the past and where the most productive grounds were located, and to assess how many oysters were currently present and where they were.

Visual Censuses of Silverlip Pearl Oyster Stocks

Based on historical catch records and interviews with coastal communities, eight fishing grounds that had historically yielded good harvests of *P. maxima* were selected for study (Fig. 1). At each fishing ground, three sites were selected based on fisher interviews that indicated where silverlip pearl oysters were most abundant in the past and most likely to be found in the present. Malaita and Marau Sound were surveyed in April 2007, Mboli Passage in April/May 2007, Sandfly Passage and two grounds in Marovo Lagoon, (Mbili Passage and Telina Island) in May 2007, and Kia and Waghina Island in October 2007.

Sites were surveyed by pairs of hookah divers towed slowly ($\sim$0.5 m/sec) or drifting on prevailing currents in an approximately straight line beneath a small boat. At each site, the divers collected all the pearl oysters they observed along 4 randomly positioned 4-m-wide transects. The geographical coordinates at the beginning and end of each transect, maximum bottom depth, and types of substrata found were also recorded. Position and depth were taken from a Hummingbird 737 (Hummingbird, Eufala, AL) combination GPS/Echo sounder. Transect lengths were derived from straight-line interpolations between start and finish points. The target dive time was 20 min, although at greater depths this had to be adjusted for safety reasons. Because of this, and because current speed varied from site to site, transects varied in length from 69–725 m. The average transect was 305 m long and 27.3 m deep. To accommodate these differences, counts were normalized to a standard area of 400 m^2. Maximum depth varied from 12.4–40.5 m.

All oysters found by the divers were placed in mesh bags and returned to the boat, where the dorso-ventral measurement (DVM) and width of each pearl oyster shell was measured to the nearest millimeter. The quality of the shell exterior was assessed visually as being either high grade, of suspect quality, or low grade. The criteria used in this assessment were related to the Australian standard of B, FAQ, and C, respectively (Hart & Friedman 2004). At each site, haphazardly selected shells were sacrificed to allow the color of the margin and center of the nacreous layer to be assessed using descriptors of white, off-white, and gold. The target number of 10 sacrificial shells per site was not achieved at some sites as a result of low catch numbers.

Statistical Methods

The catches at most grounds were too small to be analyzed statistically. For grounds where pearl oysters were relatively abundant (i.e., Mboli Passage, Kia, and Waghina), ANOVA was used to compare variations in density, length, and width of *P. maxima* among or within the fishing grounds. Variables associated with densities of oysters per standardized 400 m^2 were checked for homogeneity of variance using Cochran's C test prior to analysis, and data were transformed as required. When ANOVA was significant, the Student Newman Keuls test was used to assess the significance of differences in mean density, length, and width between pairs of grounds.

RESULTS

Interviews with Local Communities

Fishers at all locations reported that pearl oysters were regularly observed while fishing for other species, and had no difficulty in identifying three sites where many pearl oysters could be found. The types of environment that fishers reported observing silverlip pearl oysters varied among sites and ranged from fast-flowing, rubble-bottomed channels to relatively quiet, mud-bottomed bays. The fishers at Waghina, Mboli, and Kia indicated that plenty of silverlip oysters were still available in deep and fast-flowing channels with broken coral and gravel substrata, although the respondents from Kia said that silverlip oysters could also be found at shallow depths in embayments, and that they occurred on a variety of substrata, including mud and broken coral. Fishers in Marovo Lagoon (sites at Telina and Mbili) and Sandfly Passage (Ngella) reported that silverlip oysters occurred in slow-flowing and mud-bottomed channels between islands, typically at depths greater than 20 m, and sometimes in good numbers. At Marau and Maramasike, silverlip oysters were reported to be widespread and present in lagoons, passages, and open water.

Respondents indicated that small amounts of shell were still collected at Marau, Mboli Passage, Sandfly Passage, and Maramasike (Malaita), and were used locally for fabrication of jewelry or shell money. They also mentioned that there is a local market for oyster shell at Maramasike (Malaita), and that some divers from Kia have collected and stored shell in the hope that the fishery will be reopened. The respondents at Waghina and Kia mentioned that big harvests of pearl oysters have occasionally been made since the ban and the shell sold to illegal exporters. This was confirmed by the Solomon Island Ministry of Fisheries and Marine Resources, who confiscated a consignment of 3,000 silverlip pearl oyster shells with a median size of 190 mm in 2006 ($n = 98$), and another of 1,000 shells in 2008 (Solomon Islands Ministry of Fisheries and Marine Resources, unpubl.).

Silverlip Pearl Oyster Surveys

Of the eight fishing grounds surveyed, two yielded no *P. maxima*. Of the others, Kia, Waghina, and Mboli were the only grounds where all sites yielded shell. The mean (±SE) density of oysters per 400-m^2 transect ranged from 1.23 ± 0.38 at Waghina, 1.03 ± 0.27 at Kia, and 0.66 ± 0.27 at Mboli Passage to less than 0.1 at Malaita, Marau Sound, and Sandfly Passage (Fig. 2). ANOVA showed no significant differences in density among the three most populous grounds ($P > 0.05$) though differences between sites were significant ($P > 0.05$) at Kia and Waghina (Fig. 3).

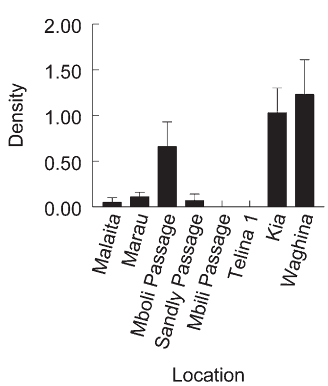

Figure 2. Mean (± SE) densities of silverlip pearl oysters as number per 400-m^2 transect at each fishing ground.

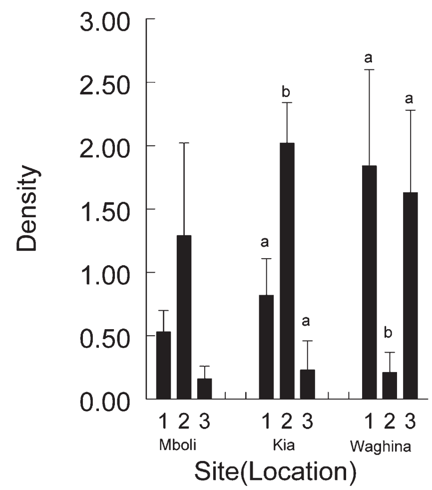

Figure 3. Mean (± SE) densities of silverlip pearl oysters as number per 400-m^2 transect at the sites surveyed at Mboli Passage, Kia, and Waghina. Different symbols above bars indicate that densities differ between sites.

Overall, the oysters varied in DVM from 164–278 mm and in width from 31–69 mm, and had a mean (±SE) DVM and width of 219 ± 2.2 mm and 49 ± 0.8 mm, respectively. More than 80% of oysters were between 191 mm and 240 mm long, and 36–60 mm wide (Fig. 4). The length–frequency distributions of the oysters from Mboli Passage and Waghina were left skewed, whereas that for Kia was right skewed (Fig. 5). The average lengths and widths were not significantly different among the three grounds (Table 1).

The quality of the external shell tended to be good, with 87.3% of the pearl oysters examined receiving a grade of high.

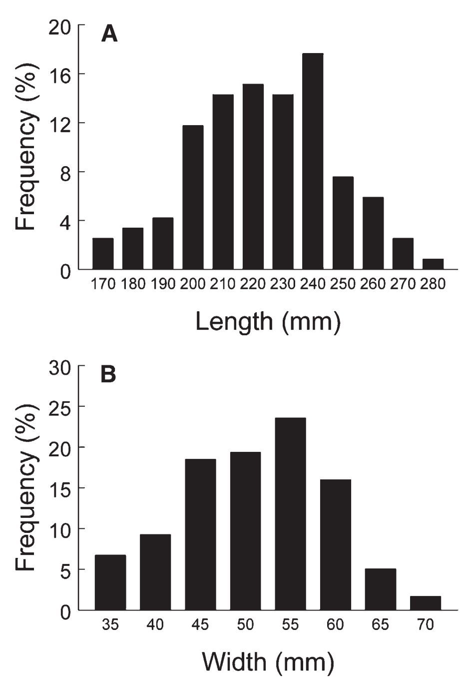

Figure 4. (A, B) Frequency distribution of length (A) and width (B) of the shells of silverlip pearl oysters combined across the 8 fishing grounds ($n = 119$).

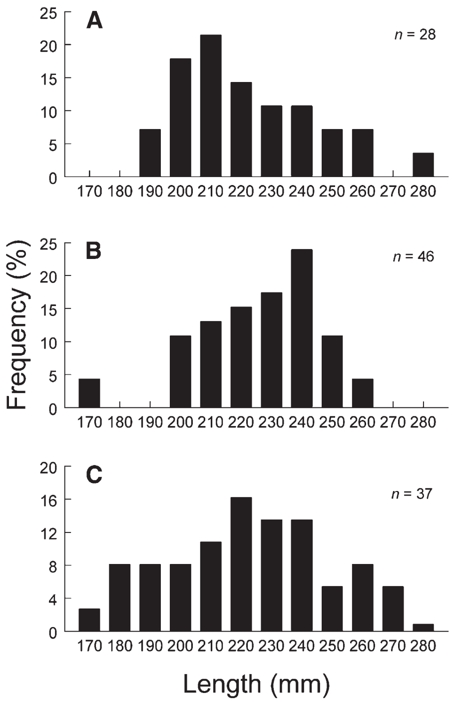

Figure 5. (A–C) Length–frequency distribution of silverlip pearl oysters found at Mboli Passage (A), Kia (B), and Waghina (C).

The shell quality of the remainder was suspect (grade 2). No low-grade shells were encountered. All the shells that were sacrificed to assess quality of the interior shell had white nacre in the middle, but the margins of the nacreous layer varied from white (6%) to off-white (36%) or gold (58%). Oysters with gold margins were more common at Kia, Waghina, and Marau, whereas those with off-white margins were more common at Mboli, and those with a white margin were found only at Kia.

DISCUSSION

Silverlip pearl oysters were found at 6 of the 8 historical fishing grounds surveyed. However, the density of the populations was, in most cases, low. The three sites that yielded the highest densities all had fast-flowing water and coarse, coral rubble/sand substrata, habitats with which *P. maxima* is traditionally associated. Perceptions of local fishers that this species could be found in large numbers in slow-moving, muddy locations proved to be inaccurate.

TABLE 1.

Mean (± SE), median, minimum, and maximum DVM and shell widths of silver-lip oysters collected at Mboli Passage (*n* = 28), Kia (*n* = 46), and Waghina (*n* = 37).

Location	Mean (± S.E.)	Median	Minimum	Maximum
Shell DVM (mm)				
Mboli Passage	218 ± 4	213	185	278
Kia	221 ± 3	225.5	167	255
Waghina	217 ± 4	217	164	268
Shell width (mm)				
Mboli Passage	48 ± 2	46.5	35	69
Kia	50 ± 1	52	31	60
Waghina	50 ± 1	47	31	67

The population size structure was biased toward large individuals, with no individuals below the 160-mm size limit currently considered preferable for round pearl production (Fletcher et al. 2006), and only 4.2% less than 175 mm DVM. The low densities and large sizes of *P. maxima* observed during the current study are consistent with the results of surveys undertaken at Kia and Waghina in the late 1980s and early 1990s (Batty & Kile 1990, Colgan 1993; Nichols, unpubl.). Although quantitative comparisons cannot be made because of different survey methodologies, the current study suggests that little recovery has occurred since then, despite the ban on export of all pearl oyster shells.

The most regionally appropriate, comparable information on the abundance and size structure of a "healthy" (although exploited) wild population of *P. maxima* is probably that from Western Australia, where the commercial importance of the wild stocks has resulted in considerable research and monitoring. Divers there target shell with a size range of 140–180 mm for pearl culture, and catch approximately 30 shells/diver h. In the Solomon survey, we took only one shell in this size range in more than 60 diver h. The paucity of the stocks and unfavorable size of the majority of oysters suggest that exploitation of wild silverlip pearl oysters for pearl culture is currently not an ecologically or economically viable option.

The size distribution of *P. maxima* taken by research drift divers in Western Australia ranges between less than 80 mm to ~250 mm, providing evidence for ongoing recruitment, supported by the presence of 0+ and 1+ y classes (<35 and 40–80 mm, respectively) as epifauna on commercially harvested shell (Hart & Joll 2006). Long-term recruitment data indicate considerable year-on-year variability, and this is consistent with the picture of reproductive success of many marine invertebrates, with a low background level of recruitment being interrupted by occasional very good years (Gaines et al. 1985, Dye 1990, McShane & Smith 1991, Hughes & Tanner 2000). This has also been demonstrated for *P. margaritifera* in the Solomon Islands (Oengpepa et al. 2006). The large size of most Solomon Island *P. maxima*, however, suggests that very few young age classes are present. We found no 0+ or 1+ recruits attached to adult shell, and, if the relationship between shell size and age developed in Western Australia by Hart and Joll (2006) is applicable to the Solomon Island population, the youngest shell found was 6 y old and the median age in our samples was more than 10 y. The apparent absence of young age classes in the Solomon Island populations suggests that there has not been a "good recruitment year" for some time.

The simplest explanation for the presence of small populations of large individuals at all sites, with almost no smaller shell, is persistent failure of recruitment. In addition to natural boom–bust recruitment patterns, two factors related to the historical overfishing may contribute to the poor recruitment in Solomon Island populations: Allee effects and an unfavorable sex ratio. Allee effects occur when population densities are so reduced that the distance between effective male and female broadcast spawners reduces fertilization success, and are significant considerations in the management and recovery of highly exploited benthic invertebrates (Levitan & Sewell 1998, Yund 2000, Gascoigne & Lipcius 2004). *P. maxima* is a protandrous hermaphrodite, with a 50:50 male-to-female ratio at a size of 170 mm in Western Australia (Hart & Joll 2006), but more females than males can be expected to occur at sizes larger than 170 mm. The large average size of the shells surveyed in the Solomon Islands does not preclude males, but does make them less likely, further reducing sperm density during spawning, which modeling studies predict will reduce fertilization efficiency (Lundquist & Bosford 2004).

Other potential contributions to the lack of recovery of stocks include depletion by natural mortality or ongoing fishing. Although natural mortality tends to be low in settled *P. maxima* (Hart & Joll 2006), occasional dramatic reductions in *P. maxima* resulting from natural causes have been reported in the past in the Solomon Islands, with stocks at Ngella having being decimated by disease during the early 1970s, and those at Kia by a red tide in 1971 (Colgan 1993). However, interviews with local villagers did not provide any anecdotal evidence of recent disease. A disease that affects only small shell is also unlikely. Ongoing fishing seems more likely than disease, and our interviews did indicate that small amounts of shell are still being collected at Marau, Mboli Passage, Sandfly Passage, and Malaita, and that large-scale fishing of pearl oysters for mother-of-pearl has taken place recently at both Waghina and Kia. Questionnaire results suggest that these harvests have occurred regularly since the ban whenever the population at Kia and Waghina became large enough to support it. Quantification of this harvesting effect is clearly impossible. The three phases of commercial exploitation of stocks in the Waghina area suggest that some degree of recovery of fished stocks after harvest pressure has been reduced has occurred in the past. The possibility that poaching has contributed to the prevention of this in recent years cannot be dismissed.

If overexploitation, perhaps enhanced by poaching, has caused a marked decline in the number of recruits, recovery of the fished population is likely to fail or be very slow (Jennings et al. 2003). There is evidence that oyster populations can be reduced to points at which recovery is barely possible. Indeed pearl oysters show many of the traits that Roberts and Hawkins (1999) listed as rendering marine species vulnerable to extinction, including longevity, low mortality rate, sex change, poor dispersal as adults, habitat specificity, and sporadic natural recruitment. In some of the atolls in the Cook Islands and French Polynesia, where blacklip pearl oysters were subjected to intense fishing during the late 19th and early 20th centuries, stocks had not recovered from overexploitation by the 1980s (Intes 1984, Sims 1992). Pearl oysters at Suwarrow in the Cook Islands became so depleted during the early 1990s that adults were imported from Penrhyn to assist in their recovery (Dalzell & Adams 1996).

Successful management of commercially exploited benthic marine invertebrate fisheries in developing countries is rare. In the Solomon Islands, in the case of pearl oysters and, more recently, bêche-de-mer, it has taken the form of overexploitation until populations are depleted to levels that are near to commercial extinction, followed by export bans. In countries with limited resources to manage and police fisheries, there are few alternatives available, but this "bottom of the cliff" strategy has not been effective for *P. maxima*. The lack of, or at best, slow recovery of stocks appears to be the result of a combination of poor recruitment, perhaps affected by the wide spacing and biased sex ratio of remaining stocks, coupled with episodic harvests for illegal export from the recovering populations. More robust and effective management options in response to overexploitation than simply a harvest ban are sorely needed, but are hindered by the lack of information on the variables controlling reproductive success in these populations, stock sizes, population dynamics and fishing effort, and the limited local capacity to set and enforce other forms of management. The perception of local fishers that stocks were good in all the surveyed regions is an example of the difference between perception and reality that places additional pressure on management authorities. Our study shows the necessity of quantitative data to ground perceptions and management in reality.

It is possible to design management interventions to facilitate and maintain recovery of pearl oysters in the Solomon Islands. These might include transplanting broodstock into concentrated, policed refuges to alleviate Allee effects and to enhance larval production (Bell et al. 2005), improved local and national monitoring of stocks and policing of harvests and exports, although these all require an enhanced level of resourcing for local authorities. If the silverlip pearl oyster stocks in the Solomon Islands do recover, with or without intervention, new fisheries management strategies will need to be implemented to protect the recovering populations prior to any further form of exploitation, and to prevent another "boom and bust" cycle. The implementation of conventional management strategies, such as quotas, closed seasons, size, and gear limits, is not appropriate for patchily distributed, sessile, broadcast-spawning species that are susceptible to Allee effects (Gascoigne & Lipcius 2004). Such measures can result in the population being reduced to a uniform low density that limits future reproduction and population growth. Instead, measures should focus on facilitating successful spawning. One option for doing this is to establish a network of spawner sanctuaries within defined fishing zones or fully protected, permanent marine reserves (Tegner 1993, Peterson 2002).

Benthic marine invertebrates are important fisheries in many developing Pacific countries, including the Solomon Islands. They allow communities to use their customary natural resources to generate income, but are all too often exploited in ways that maximize short-term monetary gains at the expense of the sustainability of the resource. The characteristics of some of these invertebrates appear to reduce their resilience to such forms of exploitation and thus increase the need for different management approaches. Government authorities are frequently poorly resourced in terms of ecological and baseline population data, as well as enforcement capability to implement effective management. Solving these dilemmas is a major challenge facing Pacific nations, and one that requires new thinking at all levels of engagement in these fisheries.

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LITERATURE CITED

Batty, M. & N. Kile. 1990. Report on the survey of goldlip pearlshell in the Kia area, Ysabel province. Unpublished report of Fisheries Division, Honiara, Solomon Islands. 21 p.

Bell, J. D., P. C. Rothlisberg, J. L. Munro, N. R. Loneragan, W. J. Nash, R. D. Ward & N. L. Andrew. 2005. Restocking and stock enhancement of marine invertebrate fisheries. *Adv. Mar. Biol.* 49:1–374.

Colgan, K. 1993. Survey of *Pinctada maxima,* gold-lip pearl oysters, in the Waghina region, Solomon Islands. FFA report no. 93/46. Honiara, Solomon Islands: South Pacific Forum Fisheries Agency. 24 pp.

Dalzell, P. & T. J. H. Adams. 1996. Sustainability and management of reef fisheries in the Pacific islands. Presented at the 8th International Coral Reef Symposium, Panama City, Panama, June 24–29.

Dye, A. H. 1990. Episodic recruitment of the rock oyster *Saccostrea cucullata* (Born, 1778) on the Transkei coast. *S. Afr. J. Zool.* 25:185–187.

Fletcher, W., K. Friedman, V. Weir, J. McCrea & R. Clark. 2006. Pearl oyster fishery. Ecologically sustainable development report series no. 5. Western Australia: Department of Fisheries. 88 pp.

Gaines, S. D., S. Brown & J. Roughgarden. 1985. Spatial variation in larval concentration as a cause of spatial variation in settlement for the barnacle, *Balanus glandula. Oecologia* 67:267–273.

Gascoigne, J. & R. M. Lipcius. 2004. Allee effects in marine ecosystems. *Mar. Ecol. Prog. Ser.* 269:49–59.

Hart, A. M. & K. J. Friedman. 2004. Mother-of-pearl shell (*Pinctada maxima*): stock evaluation for management and future harvesting in Western Australia. Fisheries Research and Development Corporation project 1998/153. Fisheries research contract report no. 10. Western Australia: Department of Fisheries. 84 pp.

Hart, A. M. & L. M. Joll. 2006. Growth, mortality, recruitment and sex-ratio in wild stocks of silver-lipped pearl oyster *Pinctada maxima* (Jameson) (Mollusca: Pteriidae), in Western Australia. *J. Shellfish Res.* 25:201–210.

Hughes, A. 2006. Benthic communities. In: A. Green, P. Lokani, W. Atu, P. Ramohia, P., Thomas & J. Almany, editors. Solomons Islands marine assessment technical report of survey conducted May 13 to June 17, 2004. Brisane, The Nature Conservancy, Indo-Pacific Resource Centre, Pacific Island Countries report no. 1/06. pp. 157–193.

Hughes, T. P. & J. E. Tanner. 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81:2250–2263.

Intes, A. 1984. L'huitre nacrière et perlière en Polynesie Francaise: mutation de l'exploitation. *Peche Marit.* 1272:161–166.

Jennings, S., M. J. Kaiser & J. D. Reynolds. 2003. Marine fisheries ecology. Victoria, Blackwell Publishing. 417 pp.

Kile, N. 2000. Solomon Islands marine resources overview. *Pac. Econ. Bull.* 15:143–147.

Levitan, D. R. & M. A. Sewell. 1998. Fertilisation success in free-spawning marine invertebrates: review of the evidence and fisheries implications. *Can. Spec. Publ. Fish. Aquat. Sci.* 125:159–164.

Lundquist, C. J., & L. W. Botsford. 2004. Model projections of the fishery implications of the Allee effect in broadcast spawners. *Ecological Applications* 14:929–941.

McShane, P. E. & M. G. Smith. 1991. Recruitment variation in sympatric populations of *Haliotis rubra* (Mollusca: Gastropoda) in southeast Australian waters. *Mar. Ecol. Prog. Ser.* 73:203–210.

Oengpepa, C., I. Hawes, I. Lane, K. R. Friedman & J. Bell. 2006. Long-term variability in spat collections of the blacklip pearl oyster (*Pinctada margaritifera*) in Solomon Islands. *J. Shellfish Res.* 25:955–958.

Peterson, C. H. 2002. Recruitment overfishing in a bivalve mollusc fishery: hard clams (*Mercenaria mercenaria*) in North Carolina. *Can. J. Fish. Aquat. Sci.* 59:96–104.

Ramohia, P. 2006. Fisheries resources: commercially important macro-invertebrates. Solomon Islands marine assessment. In: A. Green, P. Lokani, W. Atu, P. Ramohia, P. Thomas & J. Almany, editors. Solomon Islands marine assessment: technical report of survey conducted May 13 to June 17, 2004. TNC Pacific Island Countries report no 1/06. Brisbane, The Nature Conservancy. pp. 329–400.

Richards, A. H., L. J. Bell & J. D. Bell. 1994. Inshore fisheries resources of Solomon Islands. *Mar. Pollut. Bull.* 29:90–98.

Roberts, C. M. & J. P. Hawkins. 1999. Extinction risk in the sea. *Trends in Ecology and Evolution.* 14:241–246.

Skewes, T. 1990. Marine resource profiles: Solomon Islands. FFA report 90/61. Honiara, Solomon Islands, South Pacific Forum Fisheries Agency. 52 pp.

Sims, N. A. 1992. Abundance and distribution of the black-lip pearl oyster, *Pinctada margaritifera* (L.) (Pteriidae; Bivalvia), in the Cook Islands, South Pacific. *Australian Journal of Marine and Freshwater Research* 43:1409–1421.

Tegner, M. J. 1993. Southern California abalone: can stocks be rebuilt using marine harvest refugia? *Can. J. Fish. Aquat. Sci.* 50:2010–2018.

Yund, P. 2000. How severe is sperm limitation in natural populations of marine invertebrates? *Trends Ecol. Evol.* 15:10–13.