Coral reef fishing and coral-algal phase shifts: implications for global reef status

John W. McManus, Lambert A. B. Meñez,
Kathleen N. Kesner-Reyes, Sheila G. Vergara, and
M. C. Ablan

McManus, J. W., Meñez, L. A. B., Kesner-Reyes, K. N., Vergara, S. G., and Ablan,
M. C. 2000. Coral reef fishing and coral-algal phase shifts: implications for global reef
status. – ICES Journal of Marine Science, 57: 572–578.

Coral reef fisheries support tens of millions of people, mostly in developing countries.
Fishing on reefs can be classified into three stages: manageable, ecosystem-overfished,
and Malthusian-overfished. Fishing with blasting devices and poisons is often associ-
ated with the third stage. Reductions in herbivory caused by overfishing may enhance
the likelihood of organic pollution causing a coral–algal phase shift following major
disturbances. However, cage studies indicate that reduction in herbivory can lead to
the proliferation of algae even in the absence of eutrophication. A major concern with
the widespread coral bleaching associated with the 1997–1998 El Niño event is the
likelihood that reefs already stressed by overfishing and organic pollution may not
return to coral dominance after severe bleaching. Clues to levels of fishing and to the
potential to recover from disturbances include changes in the de-vegetated "haloes"
around coral stands on reef flats and the differing spectral signatures of live coral,
recently dead coral, and coral covered with red encrusting, green filamentous, or
brown frondose algae. These clues may facilitate broad area assessments of shallow
reef areas via aircraft, space shuttles, or satellites.

© 2000 International Council for the Exploration of the Sea

Key words: coral reef fisheries, remote sensing, coral-algal phase shifts, destructive
fishing, Randall zones.

*J. W. McManus (corresponding author), L. Meñez, K. N. Kesner-Reyes, S. Vergara, and
M. C. Ablan: International Center for Living Aquatic Resources Management
(ICLARM), MCPO Box 2631-0718, Makati City, Philippines [fax: +1 632 816 3183,
e-mail: jmcmanus@cgiar.org]*

Introduction

Coral reef fisheries provide food and livelihood to tens
of millions of people throughout tropical and subtropi-
cal seas. A large proportion of these dependants survive
on marginal incomes because of declining catches result-
ing from overfishing. A rapidly growing body of infor-
mation on the fisheries and on ecological linkages within
coral reef systems relevant to fisheries has been sum-
marized in three recent volumes – Sale (1991), Polunin
and Roberts (1996), and Birkeland (1997). Miller (1998)
reviewed coral–algal relationships. McManus (1997)
provided a general overview of potential fishery impacts.
McManus and Vergara (1998) give additional infor-
mation on the extent of destructive fishing. We synthe-
size the available information to produce a framework
for understanding the effects of fishing with respect to
coral–algal phase shifts. We classify levels of fishing into
three stages and then illustrate the major linkages

between fishing and the abundance of coral and algae on
the reef. Finally, we discuss the implications of heavy
fishing for the recovery of reefs from disturbances,
including the recent global bleaching event.

Definitions

We refer to a disturbance as a short-term force that acts
on a time frame of a few hours to several months and
reduces the abundance of major reef species. Examples
would include an outbreak of corallivorous starfish, a
storm, or a period of warm seawater causing a coral
bleaching event. A stress is a longer-term factor that
results in a departure from the biophysical conditions
under which the biota developed over previous decades.
Common stresses include constant pollution or fishing
pressure over periods of years. A phase shift is a
long-term (potentially decadal) change in community

Table 1. Characteristics of coral reef fishing according to three main stages (I. Manageable stage; II. Ecosystem-overfishing; III. Malthusian-overfishing). Not all fisheries may exhibit all features simultaneously.

	Stage I	Stage II	Stage III
Characteristic parrotfish, market spp. siganids	Snappers, groupers, immature parrotfish, sharks, moray eels, wrasses, siganids giant clams, conchs		Mature wrasses, butterflyfishes
Median sizes	>100 cm	25–100 cm	8–25 cm
Hooks, traps, mesh	Frequent	Moderate	Rare
Blasting, poisoning	Occasional	Common	Frequent
c.p.u.e. (legal methods)		High	Moderate Low
Value per fish	High	Moderate	Low
De-vegetated haloes	Moderate	Large	Small
Algae on dead coral	Calcareous	Calcareous/green filamentous	
Examples	Australia	Kenya	Philippines, Jamaica

structure. In this case, we refer specifically to a shift from dominance of reef-building coral (referred to as "coral" here as opposed to "soft coral", etc.) to one by fleshy algae (non-calcareous macroalgae). By dominant, we mean the most abundant macro-organism in terms of bottom cover in broad groupings (coral, macroalgae, calcareous algae, turf algae, microalgae, soft coral, sponge, etc.).

Stages of overfishing

There are hundreds of types of coral reef fisheries, and various combinations of methods and effort levels affect reefs in complex ways. However, it is possible to roughly classify the status of many reef fisheries into three stages (Table 1).

- Stage I: Relatively unstressed coral reefs support large species that are easy to harvest. Because these species are generally high-valued, it is desirable to maintain their populations and to ensure that large individuals are perpetually available for harvesting. This is the strategy of fisheries management systems, such as that of the Great Barrier Reef Marine Park Authority in Australia, which aims to maintain fisheries for mature groupers, snappers, and a limited number of other species. By ensuring that target species are maintained above some minimum level, the Authority also helps to ensure income from tourists coming to view the dense fish communities and associated benthos. Many species common on near-pristine reefs, such as giant clams, conchs, and sharks, are easily depleted and must be carefully managed.
- Stage II: In more heavily fished reef systems, large, high-valued predatory fish such as groupers and snappers become uncommon, and there is a tendency to fish for lower-valued species, such as parrotfish,

wrasses, and siganids (rabbitfish). Initially, the fishery concentrates on larger adult or subadult fish. The shift from high-valued to lower-valued species, both within the ecosystem and on the market, indicates a case of ecosystem overfishing (Pauly, 1979). Recent global volunteer surveys of the Reef Check Program have noted that many of the world's reefs assumed to be pristine were unusually depopulated of large groupers and wrasses (Hodgson, in press), a finding attributed in part to the live-fish trade (Johannes and Riepen, 1995). The widespread depletion of sharks on reefs has been noted by Stevens *et al.* (in press). Around certain islands of the Central Pacific, a variety of fish species has been harvested for decades, and parrotfish, wrasses, and siganids have been harvested along with groupers and snappers. Thus, the rarity of fish such as adult groupers and snappers on the reefs, but also on the local markets, may be the best indicator of a Stage II fishery.
- Stage III: Under intense coastal crowding, open access to fisheries and the absence of alternative livelihoods, coastal fisheries tend to fill with participants until the average fisher receives little or no net income. This condition has been described as Malthusian-overfishing (Pauly *et al.*, 1989; Pauly, 1990), and often involves the use of gear which is harmful to the environment (e.g. blasting, poisoning) or to the fishers themselves (e.g. make-shift hookah devices) as discussed elsewhere (McManus *et al.*, 1992, 1995; McManus, 1996). Blast fishing has been reported from 42 countries, poison fishing from 17 countries, and the two methods co-occur in at least 15 countries (McManus and Vergara, 1998). Two important indicators of Stage III fisheries may be identifiable through aerial photography and/or the use of multispectral scanners on airplanes, space

shuttles, and satellites. "Haloes" or "Randall zones" are areas around coral patches that are kept clear of vegetation by herbivorous fish or invertebrates such as sea urchins (Randall, 1965; Pennings, 1998). They are particularly visible on reef flats, where seagrass predominates and where interspersed patches of coral may be subject to coral–algal phase shifts. Fishing of piscivorous fish is expected to result in larger haloes, as herbivorous fish range farther from coral shelter and/or become more abundant (Miller and Hay, 1995). However, very intense fishing, including harvests of herbivorous fish and/or invertebrates, may lead to the disappearance of the haloes as vegetation closes in on the coral patches. This is particularly evident on the heavily fished Bolinao reef flat in the Philippines, in which aerial photographs clearly show former halos filled in with various densities of seagrass (McManus *et al.*, 1992). A second indicator may be the type of algae that characteristically settles on dead coral. On near-pristine reefs, dead coral generally becomes covered with calcareous encrusting algae, which appear to encourage coral settlement and growth (Yap and Gomez, 1988). However, in the absence of herbivorous fishes, green filamentous algae (e.g., Enteromorpha) tend to proliferate on dead coral. This process may be followed by the settlement of brown frondose algae (McClanahan, 1997). The spectral signatures for zooxanthellae in living coral, recently dead coral, encrusting red calcareous algae, green algae, and brown algae are markedly different, and can be detected by multispectral scanners able to discriminate at the 10 nm bandwidth (McManus, 1989; Hardy *et al.*, 1996; McManus and Noordeloos, 1998). As with Randall zones, it may be possible to identify heavily overfished reefs with remote imagery.

Examples of each stage may be found in each major coral reef region of the world. Most Pacific islands and of Australasia would be in stage I, although overfishing may occur for instance in parts of Fiji. Measures of overfishing increase as one moves from the Caribbean to East Africa, South Asia, and South-east Asia.

Coral–algal competition

A major concern in assessments of global coral reef status is the shift from coral to algal dominance on reefs (Jameson *et al.*, 1995; Eakin *et al.*, 1997; Maragos *et al.*, 1996; Bryant *et al.*, 1998; Wilkinson, 1998). This phase shift (Done, 1992) could be a result of chronic pressures which favour fleshy algae over hard coral, such as constant fishing for herbivores or organic pollution. Alternatively, it may involve a more permanent shift in state in which the algae, once dominant, inhibit coral settlement and/or the establishment of herbivores. In

both cases, the stress (usually due to fishing and/or pollution) may not be the immediate cause of the shift but rather reduces the capacity of the reef to recover from a disturbance, such as a storm. The difference is that a permanent shift may persist also after elimination of the stress factor. "Permanent" in this context means at least until a major disturbance disrupted the dominance by algae in favour of the corals, given that the stress had been abated.

An example of a phase shift to an alternative, apparently stable, state is given by Hatcher (1984) and discussed in Knowlton (1992) and Miller (1998). On an Australian reef, the red alga (*Asparagopsis taxiformis*) was kept under control by grazing fish feeding incidentally on germlings. After a ship grounding, the fish were dispersed and the alga overgrew much of the coral. Upon the return of the grazers, the red alga remained dominant because the larger fronds were unpalatable. Thus, only another disturbance that reduces the cover would permit a return to coral dominance. However, algae in general tend to be more resilient to disturbances than corals, and it is difficult to imagine one that would reduce algal cover without also driving away herbivorous fish. Therefore, the algal state may be more stable than the coral state.

Because crustose coralline algae may enhance coral settlement (Yap and Gomez, 1988; Morse *et al.*, 1988; Morse and Morse, 1993; Richmond, 1997), and fleshy algae generally reduce the area available for encrusting algae, some inhibition of coral settlement is possible if fleshy algae become dominant. Fishing for herbivores may improve the capacity for, and favour, fleshy algae to avail of increased nutrients (Littler and Littler, 1984). Thus, the two sources of stress, reduced herbivory and increased organics might be synergistic. However, cage experiments tend to emphasize the role of herbivory over eutrophication in the maintenance of coral dominance (Sammarco, 1982; Lewis, 1986; Carpenter, 1986). Fleshy algae often proliferate upon the exclusion of herbivores even in the absence of increased nutrient levels (Miller and Hay, 1998; Miller, 1998). Hatcher and Larkum (1983) found experimentally, using cages and nitrogen additions, that the addition of nutrients tended to increase algal production, but the standing stock only increased when grazers were excluded.

The best-documented case of a coral–algal phase shift refers to the northern coast of Jamaica. Hughes (1994) demonstrated, based on permanent quadrant monitoring, that coral cover dropped from over 50% to less than 5% on reef slopes over a period from the mid-1970s to the early 1990s (see also Liddell and Ohlhorst, 1986). The major elements in the explanation were as follows:

- fishing reduced herbivory
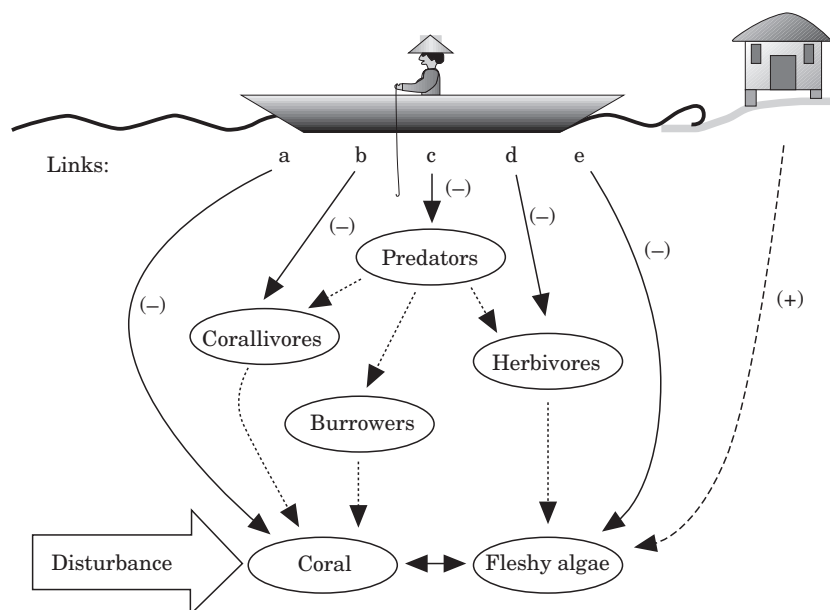- the herbivorous sea urchin (*Diadema antellarum*) became abundant (cf. Hay, 1984)

Figure 1. Diagram showing major potential effects of fishing with respect to coral–algal competition. Solid arrows are negative effects, dashed arrow is a positive effect, and dotted arrows are negative effects that might be lessened by fishing. Disturbances include large storms, bleaching events, sudden outbreaks of corallivores, or diseases and other factors causing widespread coral death from which an unstressed reef is likely to recover. Letters a–f refer to discussion in the text.

- Hurricane Allen damaged corals extensively in 1980
- *Diadema* was reduced by a mass mortality in 1983 (cause unknown)
- fleshy algae became widespread
- bleaching events further reduced coral cover in 1987, 1989, and 1990
- intense cover of fleshy algae related to a lack of recovery of herbivory now inhibits the settlement of corals.

Apparently a combination of factors has resulted in persistently low coral cover. Others have commented that effluents from the heavily developed coastlines of Jamaica could also have been an additional factor (Hodgson, 1994; CARICOMP and Ogden, 1994; Lapointe, 1997; but see Hughes *et al.*, in press). However, the example does illustrate the importance of understanding the interrelationships between fishing and other stress factors.

Direct and indirect effects of fishing

Many field observations and experiments on the control of benthic dominance of coral reefs have been published. Although few studies have been conducted at time and space scales typically relevant to the management of whole reef systems (Hughes, 1997), they do provide clues as to specific mechanisms of interaction of explanatory value.

The major components of the conceptual model of the impacts of fishing on coral–algal dominance (Fig. 1) are

the fishers, the coastal community to which they belong, predators which may have a regulating effect on the populations and/or activities of various components, corallivores, burrowers that degrade the substrate on which corals can develop, and herbivores feeding on algae that would otherwise either grow over living coral or settle after disturbances to the exclusion of settling coral. Damselfish (*Stegastes* spp.) that modify the environment to raise algae on dead coral have been omitted here because it is not clear whether the activity inhibits or enhances coral settlement (Sammarco and Carleton, 1981). Information pertaining to each of the links to fishing activities (letters correspond to Fig. 1) includes:

(a) Harvesting of specific coral and the ancillary damage to neighbouring corals has been a concern (McManus, 1980; Wells and Alcala, 1987), although the volume is, with few exceptions, considered too low to cause major reef degradation. Various fishing gears cause direct damage to corals, including blasting devices (Saila *et al.*, 1993; McManus *et al.*, 1995), poisons (Barber and Pratt, 1997; Johannes and Reipen, 1995; Eldredge, 1987), and trawling gear or devices used to clear trawling grounds (McManus, 1997).

(b) A variety of corallivorous fish feed on corals (Neudecker, 1979; Reese, 1994; Miller and Hay, 1998). A noticeable example is the large parrotfish (*Bulbometapon muricatus*) of the Indo-Pacific, which

characteristically swims in schools, pausing to feed by breaking off chunks of live coral (Randall, 1974). Schools of large adults are becoming increasingly rare because of spearfishing, as the fish are particularly easy targets. Stocks of several species of parrotfish may be depleted in Stage II or III fisheries. Butterflyfish are collected for the aquarium trade and, particularly in Stage III fisheries, also for food. They generally eat small amounts of coral polyps from several colonies each day, thereby minimizing effects on particular corals. It is conceivable that, in a Stage I fishery, reduction of predation could actually favour corallivorous fish. Most other corallivores (e.g., echinoderms and gastropods) have little commercial value and are not widely harvested. Volunteer divers are frequently enlisted to harvest the starfish (*Acanthaster planci*). However, starfish populations inevitably decline within weeks or months after an outburst, and it has been difficult to demonstrate that harvesting has accelerated these declines (Yamaguchi, 1986).

(c) Secondary effects of prey removal by predators have been difficult to demonstrate (Jennings and Polunin, 1997). There is reasonable evidence that the primary cause of recent outbreaks of *Acanthaster* on the Great Barrier Reef has been the removal by fishing of a suite of lethrinid-like fishes which normally feed on young starfish (Bradbury and Seymour, 1997). Evidence that removing predators of herbivorous fish leads to increases in populations of the latter has been weak at best, although it has been suggested that it has locally led to extensions of the Randall zones (Jennings and Polunin, 1997). There is reasonable evidence that removal of triggerfish by fishers may be linked to increases in the burrowing sea urchin (*Echinometra*), leading to extensive bioerosion in reefs in Kenya (McClanahan and Muthiga, 1988; McClanahan *et al.*, 1996).

(d) The best-established case in which fishing for herbivorous fish has been implicated as a cause of a coral–algal phase shift is the Jamaica example discussed above. Glovers Reef in Belize, where fishing for herbivores is considered an important factor in the reduction of coral by 75% and the increase in macroalgae by 315% over a 25-year period provides a similar case (McClanahan and Muthiga, 1998). The problem of corals becoming replaced by fleshy macroalgae is worldwide, but it remains difficult to distinguish the effects of reduced herbivory from those of increased organic nutrients.

(e) Although harvesting of naturally growing coral reef seaweeds is widespread, the species involved (e.g., *Caulerpa* spp.) are rarely implicated in overgrowing or otherwise replacing corals on large scales.

(f) Run-off associated with coastal villages may include untreated sewage, nutrients from detergents, and

fertilizers. Heavily fished reefs are generally associated with heavily settled coasts as well. A well-documented case of organic enrichment causing a shift to algal dominance is that of Kaneohe Bay (Kinsey, 1988), where the removal of a sewage source was followed by reversion to coral dominance in many parts of the Bay. However, other factors, including fishing, may have played a substantial role (Hunter and Evans, 1994; Stimson *et al.*, 1996).

Enhancing direct harvest of fleshy algae

As the range of products obtainable from seaweeds increases, it may be possible to develop industries to encourage fishers to reduce fishing time in favour of harvesting problematic macroalgal species. For example, the slope of a long fringing reef in southern portions of Bolinao (western Luzon, Philippines) is dominated by *Sargassum* spp. The plants scour the substrate, preventing the settlement of corals. Historical records are lacking, but the situation is supposedly relatively recent and may be related to agricultural run-off. The seaweed could be easily processed to make liquid fertilizer. More generally, hundreds of products have been developed from reef algae (e.g. *Eucheuma* and *Kapaphycus*) by investors engaged in their large-scale cultivation (McManus *et al.*, 1992). The development of an industry for exploitation of wild algae may not only reduce fishing pressure in the area, but could possibly enhance coral growth (McManus *et al.*, 1992). Thus, the weak link between the fisher and the fleshy algae has the potential to be strengthened.

The 1997 to 1999 global bleaching event

The greatest concern with fishing is the possibility that the recoverability of reefs to disturbances is reduced. Most reefs are subjected to major disturbances on a sporadic basis. Such events would provide an opportunity to test whether reefs subject to intense fishing for herbivores are more likely to undergo a phase shift. During the unusually strong El Niño event from 1997 to 1998, extending into La Niña of late 1998 to 1999, sea surface temperatures were unusually high for variable periods across a large percentage of the world's coral-supporting waters. Reports of massive coral mortality cover most of these areas (Wilkinson, 1998). This could provide the ultimate test for our hypothesis.

Fortunately, not all reefs within areas of anomalously high water temperatures were subjected to bleaching. Factors such as local upwelling and long-term adaptation of some corals to periodic contact with entrained heated water masses appear to have limited the effects and the full extent of the damage has yet to be quantified. More significantly, however, efforts are needed to

determine over the next few years which, if any, of these damaged reefs has undergone a coral–algal phase shift.

We predict that those reefs that have supported intensive fisheries will be those least likely to recover from the bleaching event. Ultimately, these reefs are also of greatest concern, because their degradation will have the most serious consequences for the human populations they support.

Acknowledgements

References

Barber, C. V., and Pratt, V. R. 1997. Sullied seas. Strategies for combating cyanide fishing in Southeast Asia and beyond. World Resources Institute, Washington, D.C.

Birkeland, C. (ed.) 1997. Life and Death of Coral Reefs. Chapman and Hall, NY.

Bradbury, R., and Seymour, R. 1997. Waiting for COTS. Proceedings of the 8th International Coral Reef Symposium, Panama, 2: 1357–1362.

Bryant, D., Burke, L., McManus, J., and Spalding, M. 1998. Reefs at Risk: a Map-Based Indicator of Threats to the World's Coral Reefs. World Resources Institute, New York. 56 pp.

CARICOMP, and Ogden, J. C. 1994. Letter. Science, 266: 1931.

Carpenter, R. C. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecological Monograph, 56: 345–365.

Done, T. J. 1992. Phase shifts in coral reef communities and their ecological significance. Hydrobiologia, 247: 121–132.

Eakin, C. M., McManus, J. W., Spalding, M. D., and Jameson, S. C. 1998. Global coral reef status: where do we go from here? Proceedings of the 8th International Coral Reef Symposium, Panama, 1: 277–282.

Eldredge, L. G. 1987. Poisons for fishing on coral reefs. *In* Human Impacts on Coral Reefs: Facts and Recommendations, pp. 61–66. Ed. by B. Salvat. Antenne Museum EPHE, French Polynesia.

Glenn, C., McManus, J., Talaue, L., and Banzon, V. 1981. Distributions of live foraminifers on a portion of Apo Reef, Mindoro, Philippines. Proceedings of the 4th International Coral Reef Symposium, Manila, 2: 775–781.

Hardy, J. T., Dustan, P., and Mazel, C. H. 1996. Bio-optics of reef organisms in relation to remote sensing. Proceedings of the 8th International Coral Reef Symposium, Panama (Abstracts) p. 82.

Hatcher, B. G. 1984. A maritime accident provides evidence for alternate stable states in benthic communities on coral reefs. Coral Reefs, 3: 199–204.

Hatcher, B. G., and Larkum, A. W. D. 1983. An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. Journal of Experimental Marine Biology and Ecology, 69: 61–84.

Hay, M. E. 1984. Patterns of fish and urchin grazing: are previous results typical? Ecology, 65: 446–454.

Hodgson, G. 1994. Letter. Science, 266: 1930–1931.

Hodgson, G. In press. A global assessment of human effects on coral reefs. Marine Pollution Bulletin.

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

Hughes, T. 1997. Symposium on the Effects of Climate Change on Coral Reefs.

Hughes, T. P., Szmant, A. M., Steneck, R., Carpenter, R. C., and Miller, S. L. In press. Algal blooms on coral reefs: what are the causes? Limnology and Oceanography.

Hunter, C. L., and Evans, C. W. 1994. Reefs in Kaneohe Bay, Hawaii: two centuries of western influence and two decades of data. *In* Proceedings of the Colloquium on Aspects of Coral Reefs: Health, Hazards, and History, pp. 339–345. Compiled by R. N. Ginsburg. University of Miami. 420 pp.

Jameson, S. C., McManus, J. W., and Spalding, M. D. 1995. State of the Reefs: Regional and Global Perspectives. NOAA, Silver Springs, MD.

Jennings, S., and Polunin, N. V. C. 1997. Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. Coral Reefs, 16: 71–82.

Johannes, R. E., and Riepen, M. 1995. Environmental, economic and social implications of the live reef fish trade in Asia and the western Pacific. Bonnet Hill, Tasmania, Australia: R. E. Johannes Pty. Ltd. and Wellington, New Zealand: Fisheries Development Associates.

Kinsey, D. W. 1988. Coral reef system response to some natural and anthropogenic stresses. Galaxea, 7: 113–128.

Kleypas, J. A., Buddemeier, R. W., Archer, D., Gattuso, J. P., Langdon, C., and Opdyke, B. N. 1999. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. Science, 284: 118–120.

Kleypas, J. A., McManus, J. W., and Meñez, L. A. B. 1999. Environmental limits to coral reef development: where do we draw the line? American Zoologist, 39: 146–159.

Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. American Zoologist, 32: 674–679.

Lapointe, B. E. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnology and Oceanography, 42: 1119–1131.

Lewis, S. M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. Ecological Monograph, 56: 183–200.

Liddell, W. D., and Ohlhorst, S. L. 1986. Changes in benthic community composition following the mass mortality of *Diadema* at Jamaica. Journal of Experimental Marine Biology and Ecology, 95: 271–278.

Littler, M. M., and Littler, D. S. 1984. Models of tropical reef biogenesis: the contribution of algae. Progress Phycological Research, 3: 323–364.

McClanahan, T. 1997. Primary succession of coral-reef algae: differing patterns on fished versus unfished reefs. Journal of Experimental Marine Biology and Ecology, 218: 77–102.

McClanahan, T. R., and Muthiga, N. A. 1998. An ecological shift in a remote coral atoll of Belize over 25 years. Environmental Conservation, 25: 122–130.

McClanahan, T. R., Kamukuru, A. T., Muthiga, N. A., Gilagabher Yebio, M., and Obura, D. 1996. Effect of sea urchin reductions on algae, coral, and fish populations. Conservation Biology, 10: 136–154.

McClanahan, T. R., and Muthiga, N. A. 1988. Changes in Kenyan coral reef community structure and function due to exploitation. Hydrobiologia, 166: 269–276.

McManus, J. W. 1980. Philippine coral exports: the coral drain. ICLARM Newsletter, 3(1): 18–21.

McManus, J. W. 1989. Earth observing system and coral reef fisheries. Proceedings of the 6th Symposium on Coastal Ocean Management, 5: 4936–4949.

McManus, J. W. 1996. Social and economic aspects of reef fisheries and their management. *In* Coral Reef Fisheries, pp. 249–281. Ed. by N. Polunin, and C. Roberts. Chapman and Hall, New York.

McManus, J. W. 1997. Tropical marine fisheries and the future of coral reefs: a brief review with emphasis on Southeast Asia. Coral Reefs, 16: S121–S127.

McManus, J. W., and Noordeloos, M. 1998. Toward a global inventory of coral reefs (GICOR): Remote sensing, international cooperation and ReefBase. Proceedings of the 5th International Conference on Remote Sensing of the Marine Environment, pp. I-83–I-89. San Diego, CA.

McManus, J. W., and Vergara, S. G. (eds) 1998. ReefBase: a global database on coral reefs and their resources. Ver. 3.0. ICLARM, Manila, Philippines.

McManus, J. W., Nañola, C. L., Reyes, R. B., and Kesner, K. N. 1992. Resource Ecology of the Bolinao Coral Reef System. ICLARM Studies and Reviews, 22.

McManus, J. W., Nanola, C. L., and Reyes, R. B. 1995. Effects of some destructive fishing methods on coral cover and potential rates of recovery. Environmental Management, 21: 69–78.

Miller, M. W. 1998. Coral/seaweed competition and the control of reef community structure within and between latitudes. Oceanography and Marine Biology: an Annual Review, 36: 65–96.

Miller, M. W., and Hay, M. E. 1998. Effects of fish predation and seaweed competition on the survival and growth of corals. Oecologia, 113: 231–238.

Morse, D. E., and Morse, A. N. C. 1993. Sulphated polysaccharide induces settlement and metamorphosis of *Agaricia humilis* larvae on specific crustose algae. Proceedings of the 7th International Coral Reef Symposium, Guam, 1: 502.

Morse, D. E., Hooker, N., Morse, A. N. C., and Jensen, R. A. 1988. Control of larval metamorphosis and recruitment in sympatric agariciid corals. Journal of Experimental Marine Biology and Ecology, 116: 193–217.

Neudecker, S. 1979. Effects of grazing and browsing fishes on the zonation of corals in Guam. Ecology, 60: 666–672.

Pauly, D., Silvestre, G., and Smith, I. R. 1989. On development, fisheries and dynamite: a brief review of tropical fisheries management. Natural Resources Modeling, 3: 307–329.

Pauly, D. 1979. Theory and management of tropical multi-species stocks: a review with emphasis on the Southeast Asian demersal fisheries. ICLARM Studies Review, 1: 35 pp.

Pauly, D. 1990. On Malthusian overfishing. Naga, ICLARM Quarterly, 13(1): 3–4.

Pennings, S. C. 1998. Indirect interactions on coral reefs. *In* Life and Death of Coral Reefs, pp. 249–297. Ed. by C. Birkeland. Chapman and Hall, NY. 536 pp.

Polunin, N. V. C., and Roberts, C. M. 1996. Reef Fisheries. Chapman and Hall, London, UK. 477 pp.

Randall, J. E. 1965. Grazing effects on seagrasses by herbivorous reef fishes in the West Indies. Ecology, 46: 255–260.

Randall, J. E. 1974. The effects of fishes on coral reefs. Proceedings of the 2ND International Coral Reef Symposium, 1: 159–166.

Reese, E. S. 1994. Reef fishes as indicators of conditions on coral reefs. *In* Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History, pp. 59–65. Compiled by R. N. Ginsburg. University of Miami, Florida. 420 pp.

Richmond, R. H. 1997. Reproduction and recruitment in corals. *In* Life and Death of Coral Reefs, pp. 175–197. Ed. by C. Birkeland. Chapman and Hall, New York.

Saila, S. B., Kocic, V. L., and McManus, J. W. 1993. Modeling the effects of destructive fishing practices on tropical coral reefs. Marine Ecology Progress Series, 94: 51–60.

Sale, P. F. 1991. The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, CA. 754 pp.

Sammarco, P. W., and Carleton, J. H. 1981. Damselfish territoriality and coral community structure: reduced grazing, coral recruitment, and effects on coral spa. Proceedings of the 4th International Coral Reef Symposium, Manila, 2: 525–535.

Sammarco, P. W. 1982. Echinoid grazing as a structuring force in coral communities: whole reef manipulations. Journal of Experimental Marine Biology and Ecology, 61: 31–55.

Stevens, J. D., Bonfil, R., Dulvy, N. K., and Walker, P. A. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyes), and the implications for marine ecosystems. ICES Journal of Marine Science, 57: 476–494.

Stimson, J., Larned, S., and McDermit, K. 1996. Seasonal growth of the coral reef macroalga *Dictyosphaeria cavernosa* (Forskal) Borgesen and the effects of nutrient availability, temperature, and herbivory on growth rate. Journal of Experimental Marine Biology and Ecology, 196: 53–77.

Wells, S. M., and Alcala, A. C. 1987. Collecting of corals and shells. *In* Human Impacts on Coral Reefs: Facts and Recommendations, pp. 13–28. Ed. by B. Salvat. Antenne Museum E.P.H.E., French Polynesia.

Wilkinson, C. (ed.) 1998. Status of Coral Reefs of the World. Australian Institute of Marine Science, Cape Ferguson, Australia.

Yamaguchi, M. 1986. *Acanthaster planci* infestations of reefs and coral assemblages in Japan: a retrospective analysis of control efforts. Coral Reefs, 5: 23–30.

Yap, H. T., and Gomez, E. D. 1988. Aspects of benthic recruitment on a northern Philippine reef. Proceedings of the 6th International Coral Reef Symposium, Townsville, 2: 279–283.