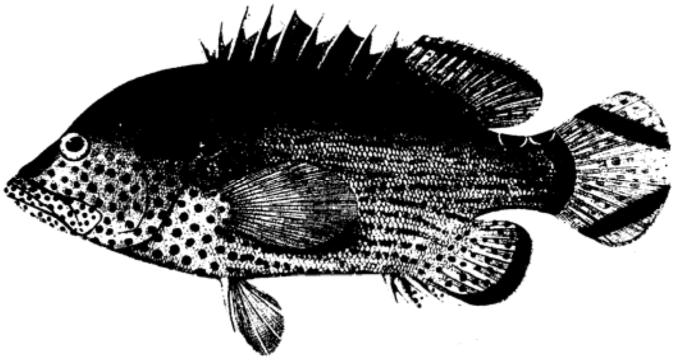
A REVIEW OF CORAL REEF FISHERIES AND THEIR STOCK ASSESSMENT



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Abstract

Although all fisheries are multispecies and spatially heterogeneous, coral reef fisheries are an extreme in both respects. The two main approaches to stock assessment have been either to consider individual species separately or to lump all species together. Both are limited in their predictive power. The lack of ecological knowledge and the large number of parameters required make methods based on single species often impractical or expensive. However where the appropriate information is available, ecological studies do not provide significant improvements on yield-per-recruit or surplus yield models currently used. Alternative community models based on aggregates of species lack predictive power, empirical support and relevant data. Models are further limited since they do not address various economic aspects, fish movement and recruitment, all of which must be spatially resolved. However the ECOPATH model, based on trophic compartments, represents a new approach useful to multispecies assessment, and the only way at present to include predation in stock models. In practice the data available will have the most important effect on the choice of stock assessment model. The major concern for management of many coral reefs is conservation of the habitat and stocks. It seems that this can be achieved with little reference to stock assessment, by using community management and closed areas, which have received increasing support that they are effective. However once the objective of conservation is achieved, stock assessment should have an important role in improving the economic performance of the fisheries. The wider problems of management have no simple solutions, but managers should look to adaptive management, designing their own experiments to choose between management models.

Introduction

Coral reefs are the dominant marine habitat throughout shallow tropical seas where there are no upwellings or inflows of fresh water nearby. Smith (1978) has estimated that coral reefs and associated communities at less than 30m depth cover in total 600,000 km^2. If it is assumed that the average sustainable yield is 15 mt km^{-2} yr^{-1} (Munro, 1984), the potential sustainable global harvest from coral reefs could amount to 9,000,000 mt yr^{-1}. This is about 10% of the world's commercial fish yield (FAO, 1989).

The harvest is perhaps even more important when considering the value of the catch. On first consideration coral reef fisheries may appear to have little economic importance. Many coral reef fish command low prices in markets, and therefore are of low commercial value. However this ignores the relative importance of these resources to some of the poorest people in developing countries. Although the more valuable species might be sold, the remaining catch can be reserved for the fisherman's family, providing an important source of protein in the diet. The importance of the fisheries is further enhanced by the high employment they provide. Since coral reef fisheries are not easily exploited using industrial methods, they tend to be labour intensive. These factors make the social value of coral reef fisheries particularly high.

It is clear that coral reefs are an important resource, but do they require fundamentally different management methods to other fisheries? The catch is often highly diverse and the reef system is extremely patchy, with the yield and species composition strongly dependent on the areas fished. However coral reef fisheries do not present a qualitatively different problem to fisheries science. All fisheries involve more than one species, even though the fishery may be directed at only one. There is always a by-catch or other species interacting with the target species as competitor, predator or prey. The high spatial heterogeneity of reefs again is not qualitatively different to other fisheries. In most fisheries fish and fleets aggregate to distinct areas. However coral reefs are a special case in that they represent an extreme in both species diversity and spatial heterogeneity. No other type of fishery has as diverse stocks or such a complicated spatial structure.

Traditionally fisheries science has assessed and managed each species separately. In general, it was assumed either that interactions between species did not matter much to management of the stock, or if they did matter, little could be done about them. Even where the degree of interaction between species is known, it was thought that management requires monitoring and prediction of the population sizes for all species in the system, a daunting task. The best option may well be to treat changes in stock size due to species interactions as noise in the system. While not ideal, this approach does not seem unreasonable in many temperate fisheries where the diversity of the catch is low. In the case of coral reefs, where catch diversity is particularly high, it may be over-optimistic to make any prediction without some consideration of the effect that species have on each other.

Spatial heterogeneity has received less attention in the sense that it does not appear in any of the standard stock assessment models. However it is a recognised problem, particularly in the analysis of catch per unit effort (e.g. Hilborn and Walters, 1992), and the measurement of interaction between fisheries (e.g. FAO, 1992). Differences in concentrations of fish are fundamental to both monitoring and the economic exploitation of the resource (Clark, 1982). Since coral reefs have an extremely patchy distribution, these factors will be of fundamental importance in understanding their fisheries.

This review concentrates on capture fisheries for finfish, although some of the points made in this paper may be relevant to the management of invertebrates. The extensive literature on fish ecology is reviewed briefly from the point of view of fisheries management and provides background for those not familiar with this area of research. The aim is to see whether studies can suggest any improvements to population models currently used in stock assessment. Using case studies the wider issues of coral reef fisheries management are then briefly discussed. The coral reef environment is beset by a number of environmental and socio-economic problems which may well eclipse those of traditional stock management.

Fishing Gears

Coral reefs are exploited in a wide variety of ways. Fishing for bait or food probably represents the largest single use. The main fishing gears used for catching finfish are set nets, hook and line, traps and spearing. Nets, which tend to be size selective depending on the mesh size used, are set just off the reef and the fish driven in. Hook and line is more effective against predators, such as snappers (Lutjanidae) and groupers (Serranidae). Traps are the least selective of these gears. They take a wide variety of fish or lobster dependent upon their construction and the bait used. Spearing is a selective method for taking larger fish. Another important form of reef exploitation falls under the heading of gathering, when the more sedentary organisms, such as molluscs, crustaceans, coral and algae, are collected from the reef.

Fisheries do not target exclusively for bait or food. Other species for the curio and aquarium trades may be important locally in terms of commercial value. Corals and shells are gathered from the lagoon or reef top, although some more valuable species, such as black coral, are gathered by divers. Aquarium fish are mostly taken by divers with nets, although poison is used widely in the Philippines and some other countries (Randall, 1987).

A number of fishing methods destroy the coral reef habitat. Many poisons, such as bleach or sodium cyanide, not only kill the fish against which they are directed, but all reef organisms they reach before becoming too dilute (Eldredge, 1987). Explosives, used mainly on schooling species, also cause widespread destruction of surrounding coral (Alcala and Gomez, 1987). Another destructive technique, *muro-ami*, is used extensively in the Philippines. Boulders are repeatedly dropped onto the reef surface scaring fish out of refuges in the reef and driving them into nets (Carpenter, 1977; Carpenter and Alcala, 1977). This breaks up the reef surface, killing coral and other benthic invertebrates. Following the destruction of the habitat, the reef is very slow to recover, due to the low growth rate of coral, and poor coral recruitment to these areas because of the rubble produced (Alcala and Gomez, 1987). Until coral cover has increased, the topographic complexity will be severely reduced, probably leading to reduced diversity and production of the fish community (Gomez *et al*., 1987). For these methods of fishing, productivity may decrease more rapidly than a stock assessment would predict.

Observed and Potential Yields

Table 1 gives a selection of published yields per unit area. Despite the wide variation in these numbers, they can give some idea of the potential yield that could be obtained. However, to interpret observed yields in relation to potential yield, it is necessary to understand how this variability might arise.

Turning first to potential yields, an important source of catch variability among reefs may be differences in productivity and community structure. The relatively high biological productivity of coral reefs is generated from two sources. Firstly the primary productivity of benthic algae and symbiotic zooxanthellae is very great (Kinsey, 1983; Larkum, 1983). However there appear to be few mechanisms for transferring this energy through the trophic levels of the community. This suggests that despite high productivity at the base of the food chain, the potential harvests will be relatively small (Polunin and Brothers, 1989). The second source of energy is plankton. Many reef organisms feed on plankton, so a reef system will filter water flowing over it, concentrating energy and nutrients within the system. This productivity provides an important addition to the harvestable resource (Russ, 1984). Caribbean reefs have relatively few planktivorous fish (Bohnsack *et al.*, 1984) compared to the Indo-Pacific region (Russ, 1985; Williams and Hatcher, 1983). This suggests the potential yield from Indo-Pacific reefs should be higher and is in agreement with recent observed yields for the Pacific, which are the highest recorded.

On a large scale, species composition depends upon regional and latitudinal characteristics. For instance, changes in water temperature with latitude affect coral reefs, and ultimately limit their distribution, although the impact of this on productivity and community structure is less clear.

On a smaller scale, Williams and Hatcher (1983) found significant differences in species composition and biomass across the Great Barrier Reef (GBR) from nearshore to offshore reefs. In general, larger and more valuable species were found predominantly on the offshore reefs, smaller species inshore. Although other reefs may be structurally different to the GBR, there are likely to be similar patterns, with low wave energy areas having a different community to high energy unprotected reefs.

Changes in sustainable yields will further depend to some extent on the location of the reef in relation to various local oceanographic features. There may be differences in productivity due to local nutrient supply and the presence of other habitats, such as seagrass beds and mangroves, found nearby. In the case of islands, much variation in productivity can be linked to various factors correlated with their size (Ogden, 1982).

All the influences discussed so far may affect both observed and potential yields. However, in addition there are a number of factors which will primarily affect only observed yields. Observed yields are directly related to the current and historic levels of fishing effort and the fishing gear used. A consequence is that the lowest observed yields may be associated with the both the most lightly and most heavily fished areas. Although the total catch may be similar, these two situations can be distinguished by differences in the catch per unit effort. That said, however, measurement of fishing effort for coral reef fisheries is at least as hard as it is for other fisheries, and generally harder. Another potential difficulty is that observed yields are often interpreted as being estimates of sustainable or equilibrium yields. This may be reasonable if the levels of catch and of fishing effort have remained roughly constant for some time, but if not they can be seriously misleading.

Table 1 Published yields from areas of coral reef (updated from Munro and Williams, 1985).

Place	Fishery Type	Area (km^{-2})	Max. Depth (m)	Species Groups Included	Average (mt km^{-2} yr^{-1})	Reference
Puerto Rico	artisanal	5300	100	neritic fish and crustaceans	0.5	Weiler and Suarez-Caabro, 1980
Ontong Java	subsistence	122	-	all	0.6	Bayliss-Smith (MS) cited in Munro and Williams, 1985
Kapingamar-angi Atoll	subsistence	400	-	not known	0.7	Stevenson and Marshall, 1974
Jamaica 1968	artisanal	3422	200	neritic fish and crustaceans	1.7	Munro, 1977
Jamaica 1980	artisanal	3305	200	neritic fish and crustaceans	1.4	Sahney, 1983
Tanzania	artisanal subsistence	12160	-	all	1.8	Wijkstrom, 1974
Tarawa Kiribati	artisanal subsistence	500	-	reef and lagoon fish	4.4	Marriot, 1984
Kora and Lakeba, Fiji	artisanal subsistence	8.4	-	all	5.0	Bayliss-Smith (MS) cited in Munro and Williams, 1985
Faluk Atoll	subsistence	6	-	-	5.1	Stevenson and Marshall, 1974
Philippines Apo Is.	artisanal	1.56	60	only demersal fish and pelagic fish	5.8 11.3	Alcala and Luchavez, 1981
Philippines Sumilon Is.	artisanal	0.50 0.65	40 60	demersal and pelagic fish	20.2 18.3	Alcala, 1981
American Samoa	subsistence		-	fish and invertebrates	12.0	Hill, 1978
American Samoa	subsistence	3	8	only fish and invertebrates	21.2 26.6	Wass, 1982

Place	Fishery Type	Area (km^{-2})	Max. Depth (m)	Species Groups Included	Average (mt km^{-2} yr^{-1})	Reference
Papua New Guinea Tigak Islands	artisanal subsistence	208	30	only fish	0.42	Wright and Richards, 1985
Papua New Guinea Port Moresby	artisanal	116	7.5	neritic fish	4.5	Lock, 1986b
Philippines Selinog Island	artisanal subsistence	1.26	30	neritic fish	6.0	Alcala and Gomez, 1985
Philippines Hulao-hulao Island	artisanal subsistence	0.5	15	neritic fish	5.2	Alcala and Gomez, 1985
Philippines Cape Bolinao	artisanal	11	18	neritic fish	4.4	Acosta and Recksiek, 1989
Philippines Sumilon Is.	artisanal	0.50	40	all	36.9	Alcala and Russ, 1990
Philippines Sumilon Is.	artisanal	0.5	40	all	19.9	Alcala and Russ, 1990
Philippines Apo Is.	artisanal	0.54	20	mainly fish	48.79	Bellwood, 1988
Philippines Apo Is.	artisanal	1.06	60	mainly fish	24.86	Bellwood, 1988
Philippines Apo Is.	artisanal subsistence	0.7	20	mainly fish	22.1	Savina and White, 1986a
Philippines Apo Is.	artisanal subsistence	1.8	20	mainly fish all	10.7 17.9	Savina and White, 1986a

The size and species selectivity of the gear may also have a profound effect on the yield. Furthermore fishing gears could also alter the yield through their effect on the habitat. Degradation of the habitat often accompanies high fishing effort and is an important problem for management.

Finally, when attempting to estimate the maximum biological yield, some reference to the value and end use of the catch is required. The driving force behind many fishery is the economic incentive, so the landed catch may reflect market accessibility and demand as much as what can be caught. The acceptability of different species to local communities can also be an important factor. For these reasons some account needs to be taken of factors such as species targeting and alternative sources of income for fishermen.

Even where all these factors can be taken into account, consideration will still have to be given to data errors. Data are often missing, particularly in artisanal and subsistence fisheries (e.g. Powers, 1982). Estimates of the total catch where data are absent, will obviously tend to be under-estimates. Other biases may also be present. Comparison between data from different places is made more difficult because there is lack of consistency in the origin of the catch. This is an important source of error in observed yields (Russ, 1991). Data may be in the form of catches aggregated over a number of habitats and different depths. Identifying exactly where fish come from may be necessary for reliably estimating sustainable yields and accounting for the distribution of fishing effort.

Given the large number of factors affecting yields, can any conclusions be drawn from observed yields? Where the quoted yields represent isolated observations from a single year, for example, the answer is almost certainly no. However, where the yields given in Table 1 can be taken to be estimates of sustainable yields, then they do give some indication of a lower bound for the potential yield of each location. The potential yield must be higher or equal to the observed yield because observed yields could increase with different levels of fishing effort or under improved management. However the observed yields are interpreted, their high variability undermines the value of any estimate of the global average maximum sustainable yield for a coral reef. In any case, since there are likely to be large differences in both productivity of reefs and in the way the reef might be used, a global average provides a poor estimate of the potential yield from a particular area.

Effect of Exploitation

A primary concern in fisheries management is how the catch will alter as fishing gears and effort change. Fishing affects abundance of a species in two ways. Firstly there are the direct effects on the species itself independent of the rest of the community. Secondly, there are indirect effects through changes in abundance of other species in the community. Russ (1991) discusses these and wider effects of fishing on the community in some detail, but points out how little is actually known.

The species selectivity of the gear has a major direct influence on catch species composition and how it changes over time. For instance, a species dominating the catch at the start of a fishery may become rare as its population falls due to a high fishing mortality. Other species may therefore increase as a proportion of the catch. Where fishing mortality is high, this effect may be the greatest single influence on the ecological community (Hilborn and Walters, 1992).

Different fishing mortalities will have two further effects. Firstly if a species grows slowly, the average size of individuals in the catch will fall more rapidly than for faster growing fish. Hence even if there is no change in species composition in terms of numbers of fish, a slow growing species may decrease as a proportion of catch weight. Secondly the recruitment of some species may be more heavily affected by fishing than others. Species that take longer to reach maturity (slower growing) will be subject to a higher total fishing mortality before spawning and the spawning biomass will therefore be reduced by a greater amount. The impact this has on recruitment will depend on the stock-recruitment relationship. Slower growing species often have a lower fecundity, which may increase the chance of recruitment overfishing. On reefs, these factors will tend to decrease the numbers of top predators, like sharks, relative to the faster growing herbivores and planktivores. If the growth rates are known for individual species, some estimate of the size of these effects might be obtained.

The main indirect effects are likely to be predation and competition, which can bring about changes in recruitment, natural mortality and growth. For instance, removing a predator could decrease the natural mortality of the prey. Such qualitative hypotheses are easy to advance where the predatory and competitive relationships between species are known. However, quantifying such interactions, which would be necessary in stock assessments, is at best very difficult.

There is some evidence that fishing may have profound effects on the whole coral reef community. Removal of herbivores on a large-scale can result in a rapid increase in algal growth at the expense of corals and may lead to seaweed dominating the benthic community (Parrish *et al.*, 1985). Fishing of sea urchin predators such as pufferfish and triggerfish may account for the high densities of sea urchins found on many heavily exploited reefs (McClanahan and Muthiga, 1988) and subsequent heavy bioerosion. Fishing of Napoleon wrasse on the Great Barrier Reef has even been suggested as a factor in the outbreaks of the crown-of-thorns starfish (Ormond *et al.*, 1990).

Single Species Ecology

There is a large amount of life history information on coral reef fishes, however it tends to concentrate on small, generally territorial, species, rather than larger, commercially important species (Sale, 1991; Thresher, 1984; Munro and Williams, 1985; Richards and Lindeman, 1987; Doherty and Williams, 1988). This section briefly reviews those aspects that are of particular relevance to fisheries management.

The potential sustainable yield from any population depends on three basic processes; recruitment, growth and mortality. These can be studied for each species separately, but the number of species on a coral reef and the range of their behaviours make generalizations difficult. Understanding the differences between species is necessary to interpret changes in the community species composition, but some simplification may be possible. Many species fall into natural groups or guilds (groups of closely related species exploiting similar resources), such as reef-flat dwelling damselfish (Pomacentridae). However, it may still be necessary to taken into account a wide range of factors in fisheries models to obtain accurate predictions.

Recruitment

With a few exceptions (e.g. Fishelson, 1970; Robertson, 1973; de Boer, 1978; Leis and Goldman, 1987) reef fish have an initial pelagic larval stage, which gives a potential for wide dispersal. Subsequently larvae settle out onto a reef (or adjacent habitat) as juveniles, and are eventually recruited to the fishery as adults. Unless otherwise stated, recruitment in this section refers to settlement on the reef. Numbers settling following the planktonic life stage is a function of parental abundance and fecundity, and interactions between oceanographic processes, larvae behaviour, predation, growth and starvation (Richards and Lindeman, 1987).

Egg Production

Fish may have pronounced spawning migrations and produce pelagic eggs, produce pelagic eggs but not migrate, lay demersal eggs or be viviparous (Johannes, 1978). Some species aggregate when spawning, which may increase their catchability[1] at a critical time, an important factor in some fisheries (Johannes, 1978, 1988). Other types of spawning behaviour include nest-building and defending breeding territories.

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[1] Catchability is defined as a species fishing mortality (proportion of the fish population caught) resulting from one unit of effort.

The production and release of gametes and larvae ranges from being a relatively discrete event (Johannes, 1978; Pressley, 1980; Ross, 1983; Doherty, 1983a) to being an almost continuous process throughout the year (Robertson, *et al.* 1981; Victor, 1986a). Fecundity is high in most reef species. For example, egg counts of ripe female groupers have been found to be 160,000 eggs per female (Thompson and Munro, 1978;), and such quantities are typical (Sale, 1980). Larval survival has never been measured directly, but the low observed reef recruitment compared to high fecundity suggests it is poor.

Although no stock-recruitment relationship has been demonstrated for any coral reef species, some theoretical implications have been considered. Many commercially valuable reef species change sex from female to male during their life (Reinboth, 1980). These protogynous species will only be more affected by fishing than a gonochoristic species if the availability of males becomes limiting (Bannerot *et al.*, 1987). The degree to which the sex ratio is affected by fishing will depend upon how the sex-change is triggered. Thompson and Munro (1983) found significant changes in the sex ratios of a number of protogynous species of grouper which were caused by the fishery. For these species the sex change is size or age dependent. Many other species actively change sex to maintain some sex ratio in the population (e.g. the small planktivores *Pseudanthias* spp.) and are likely to be much less vulnerable than those for which the change is dependent on age or size (Munro and Williams, 1985).

Larvae Dispersal and Settlement

With reefs having such a patchy distribution, understanding the mechanisms by which larvae are dispersed is critical to understanding recruitment, and in particular any stock-recruitment relationships that might exist. Mark-recapture experiments with larvae would be an ideal approach to study larvae dispersal, but as these are difficult to carry out, more circumstantial methods have had to be used.

It is not clear why so many species have pelagic larvae. Johannes (1978) has suggested pelagic larvae are a means to reduce mortality from reef associated predators, such as diurnally active plankton feeders. It has also been suggested that this form of dispersal reduces the chance of local extinction, where larval dispersal spreads the risk of failure among local cohorts (Barlow, 1981; Doherty *et al*., 1985). More recent views are, however, that the patterns of geographical and within-site variation, both within and between species, are at present too complex to allow simple interpretation. There is very little known about survivorship and factors affecting it at different stages of the life-cycle and it is possible that it is juvenile, not larval, mortality that adult spawning periodicity is an adaptation to reduce (Robertson 1991).

Once in the water column, the distribution of larvae is primarily controlled by oceanic processes such as currents and tides (Richards and Lindeman, 1987). In this context the retention of larvae within a reef area is difficult to assess, as it may be the accidental result of the interaction between currents, larval behaviour and mortality or a direct result of an active strategy (Leis, 1986). For instance, it has been suggested that species distribution patterns can be explained largely by differential larval mortality alone (Roberts, 1991).

It is still not clear whether larvae are able to control their distribution on a large scale. Leis (1981) tested the hypothesis that lagoons provide a sheltered environment and allow larvae to remain in the same location as the parental population. He sampled larvae around Lizard Island (northern Great Barrier Reef), but found no significant numbers of larvae or juveniles of reef fish in the lagoon and concluded the lagoon was not important in maintaining local recruitment, but that it provided a brief spawning ground. He found that nearshore open waters were important as nursery grounds for several coral reef fish taxa.

A number of alternative hypotheses rely on larvae controlling their distribution by moving in a chosen direction. Larvae may move vertically between currents flowing in different directions at different depths, swim directly against currents or move into the boundary layer close to the bottom where the current flows more slowly (e.g. Hardy, 1953; Leis, 1982a,b). Leis (1986, 1991) assessed the vertical distribution of a number of coral reef fishes and found taxon-specific patterns of vertical distribution, which were similar among related taxa. The vertical distributions were highly structured during the day, yet unstructured at night. A large number of studies have suggested that larvae move away from the reef where they were spawned, then return using eddies created as currents flow over the reefs (Jones, 1968; Sale, 1970; Emery, 1972; Johannes, 1978; Lobel and Robinson, 1983). However empirical support for this hypothesis is limited. Powles (1977) compared the density of larvae of five non-reef species around Barbados, and found that the distribution of one species could be explained by its aggregation within turbulent areas in the lee of the island. Wyatt (1982) found some inconclusive evidence that larvae might be retained in a similar way on the leeward side of Jamaica. A study on the Great Barrier Reef found no significant difference between concentrations within an eddy on the lee of a reef and upstream, although this may be because these eddies are not in existence long enough to achieve a significant effect (Munro and Williams, 1985).

The length of time larvae spend in the pelagic phase has been documented for a large number of reef species. These times were calculated from observations made on spawning and settlement or counting otolith increments (Victor, 1982; Thresher, 1985), and range, for example, from 15 to 121 days in Pacific and Atlantic wrasses (Victor, 1986b). The ability to spend a longer time in the pelagic stage increases the chance of finding a favourable habitat to settle out on. A delay in metamorphosis is common in marine invertebrates (Scheltema, 1986) and is likely to be present in the larvae of many reef fish species. Many reef associated species have prejuvenile stages morphologically adapted for extended planktonic life, which enables them to delay metamorphosis and settlement. Victor (1986b) argued the delay of metamorphosis in the wrasse, *Thalassoma bifasciatum*, was an adaptive response to increase the chance of finding an acceptable site. Kobayashi (1989) suggested that by delaying metamorphosis the larvae of the damselfish, *Dascyllus aruanus*, can exert some control over their own settlement site. In support of this he found a positive relationship between larval distribution and adult habitats. There is also some direct evidence that larvae exercise some choice in their settlement site. *Dascyllus* larvae actively choose their settlement site using various chemical cues (Sweatman, 1988). Similarly Levin (1991) also found larvae are able to select their microhabitat. These studies suggest that larvae control their own distribution to some extent.

Many studies have found correlations between various ecological factors and recruitment to the reef. The settlement of larvae onto the benthos is affected by a vast range of factors including habitat, shelter, presence of con-specifics, predators, territories and currents (Richards and Lindeman, 1987).

In a study on the temperate reef fish genus *Sebastes* (rockfish), Carr (1991) showed that the structural composition of the reef strongly influences the magnitude and species composition of local recruitment. Shulman (1984, 1985a) found that recruitment and early survivorship were strongly limited by the number of refuges on the reef, and therefore were probably related to the predation rate. The presence of adult con-specifics may also affect settlement. In an experiment on territorial damselfish, Shulman *et al*. (1983) found that recruitment decreased significantly when adults were present. Variability in recruitment may also have a species specific component, correlated with social behaviour. Shulman (1985b) found the recruitment of schooling species to be clumped and highly variable compared to non-schooling species.

However some of this variability must be attributed to observation error. Sampling frequency considerably affects estimates of reef recruitment (Booth, 1991), and may obscure any patterns that are present. Therefore there are few conclusions that can be of use in stock assessment. The high variability observed suggests that any stock-recruitment relationship is likely to operate on a large scale, and will therefore probably require an extensive sampling effort to detect it. An exception may be isolated oceanic islands, which may largely depend on local recruitment. Although it is relatively easy to measure both recruitment and the size of the adult population in this case, the sampling effort required to account for outside factors may still be large and prohibit research.

Stock and Recruitment

An important issue to consider is the definition of a stock on a coral reef. Cushing (1968) defines a stock to be a population whose reproduction, growth and mortality are homogeneous. Circumstantial evidence suggests that populations at the scales generally studied by ecologists (patch reefs) are not individual stocks, since they are not exclusively self-recruiting populations (Doherty and Williams, 1988; Sale, 1980). Managers will have to look to larger areas to identify independent stocks on the basis of recruitment.

Whereas it can be imagined that populations are self-sustaining in a complex environment such as the Great Barrier Reef where larvae are likely to find a new potential home on most currents, one might expect isolated oceanic islands to have difficulty sustaining their populations, particularly with a background current. However these islands seem to be self-sustaining (Lobel and Robinson, 1986). On a theoretical level, Black *et al.* (1991) used numerical models on data from the Great Barrier Reef to show that coral reefs in general can be self-seeding, revealing a potential for the maintenance of local populations of various reef organisms.

If two populations are independent and can be treated as separate stocks, it should be possible to detect genetic differences between them. However if genetic differentiation is due to random drift, rather than a stronger force like selection, even small amounts of exchange will maintain the similarity between groups (Falconer, 1980). Electrophoresis has been used to test for genetic differences among populations of reef fish in a number of studies. Soule (cited in Ehrlich, 1975) and Shaklee (1984) found no genetic differentiation between pomacentrid populations separated by as much as 3000 km, with the exception of *Acanthochromis polyacanthus* which has no planktonic phase. Bell *et al.* (1982) did find significant differentiation in the anemone fish *Amphiprion clarkii* over a 1,500 km chain in Japan. Munro and Williams (1985) suggest that this is consistent with the short larval stage of anemone fish compared to other pomacentrids. In addition, since pomacentrids have a shorter larval phase compared to most reef fishes (e.g. Brothers *et al*., 1983; Johannes, 1980; Goldman *et al*., 1983), it is unlikely that other species will show greater differentiation.

Part of the problem might be that discrete stocks do not exist on coral reefs, and fish are distributed in a continuum rather than as isolated populations. If it is not possible to define distinct homogeneous populations, it will become necessary to include heterogeneity explicitly in population models. Unfortunately this would require a more detailed understanding of how larvae disperse.

Temporal and Spatial Variation

The degree of temporal and spatial variation in recruitment depends upon the reef fish species examined and the measurement scales used (Munro and Williams, 1985; Doherty, 1987). The high variability was illustrated by Shulman *et al*. (1987), who reviewed mean annual recruitment rates for a number of species. Rates ranged from 0.1 recruits $m^{-2}year^{-1}$ for *Pomacentrus wardi*, to 250 recruits m^{-2} $year^{-1}$ for *Apogon doederlieni*, a small shoaling species, on One Tree Reef, GBR. General results indicate that juvenile recruitment fluctuates typically within one order of magnitude of the mean (Williams, 1983; Eckert, 1984; Sale *et al.*, 1984; Kami and Ikehara, 1976; Luckhurst and Luckhurst, 1977; Molles, 1978).

Recruitment fluctuations in space and time are probably related. Several studies on the Great Barrier Reef suggest that peaks in recruitment might coincide on the scale of kilometres, but not tens of kilometres (Doherty, 1983b; Eckert, 1984; Sale *et al*., 1984), although generalisations are difficult (Victor, 1984). However recruitment pulses of only a few days duration have been observed to occur simultaneously over large areas of reef. *Thalassoma bifasciatum* larvae settled simultaneously onto reefs within an area of $1000km^2$, although Victor (1984) observed that larvae settling out onto reefs were not the same age, indicating that planktonic dispersal resulted in cohorts of larvae mixing. Some species, such the as the french grunt, *Haemulon flavolineatum*, show distinct and predictable settlement pulses (McFarland *et al*., 1985).

Doherty (1983b), Eckert (1984) and Sale *et al.* (1984) studied recruitment to a number of reefs on the Great Barrier Reef over a number of years. Their conclusions indicate that recruitment is patchy, with little correlation between adjacent reefs. However some reefs may consistently received more recruits than others (Eckert, 1984; Sale *et al.*, 1984; Doherty and Williams, 1988). This may be due to the attractiveness of these sites to the larvae, lower mortalities or their hydrographical position.

Many reef fish have seasonal peaks in breeding activity (Johannes, 1978), although some species seem to breed all year round (Walker, 1975). Seasonal peaks in recruitment or juvenile abundance have been recorded in many reef areas. In the Philippines (Pauly and Navaluna, 1983), Hawaii (Watson and Leis, 1974) and Jamaica (Wyatt, 1982) these peaks appear to be bimodal, whereas on the Great Barrier Reef the seasonal peaks in recruitment are unimodal (Russell *et al.*, 1974, 1977; Williams, 1983; Williams and Sale, 1981; Leis and Goldman, 1983). However, Robertson (1990), studying 8 species of damselfish and one species of blenny in Panama, stated that seasonal cycles of spawning differed from seasonal cycles of larval recruitment in these species.

There have been few published attempts to correlate parental population fecundity with recruitment. Robertson *et al.* (1988) in a 3 year study found no significant correlation between the magnitude of larval production and of subsequent settlement within the study area for a damselfish *Stegastes partitus*. However Doherty (1980, 1983b), in a study of the recruitment of the damselfish *Pomacentrus wardi*, found that it was impossible to know where the larvae came from and consequently the adult population with which settling larvae should be linked. Until an appropriate definition of a stock can be obtained, a stock recruitment relationship cannot be found.

Migration

It has been generally accepted that most coral reef species appear to move little after settlement (Ehrlich, 1975; Sale, 1980), although this may reflect the species studied rather than a general conclusion (Jones, 1991). A great deal of evidence suggests that many species at least have the ability to move into new areas even if under normal circumstances little movement occurs. In a number of experiments, recolonisation of reefs after individuals have been removed has been rapid due to immigration of adults and juveniles to the free area (Brock *et al.*, 1979; Ogden and Ebersole, 1981; Walsh, 1985). This is almost certainly the way in which fishing sites recover in the short term, although it is not clear over how large an area fish will immigrate to a site.

The few tagging studies that have been carried out indicate that many species are capable of moving large distances (Stark, 1971; Bohnsack, 1990), although most movement is typically limited to within a few kilometres. The species itself is one of the most important factors in determining movement. For *Dascyllus aruanus*, a damselfish, it was shown that adult migration is rare (Forrester, 1990). This contrasts with the schooling planktivorous damselfish, *Abudefduf saxatilis*, the distribution of which was largely determined by movement among reefs in an area at least as large as 0.5km^2 (Robertson, 1988a). Similarly, Robertson (1988b) explained the abundances of surgeonfish using relocation, and suggested movement was important in re-organising reef fish communities and should be further examined. In another study Thresher (1983) found that movement of juveniles and subadults as well as predation mortality could explain the distribution of planktivorous fishes.

Movement may also follow predetermined paths as well as be random. The life history of many species include habitat shifts after settlement. For instance, the grunt *Haemulon flavolineatum* in the Caribbean settles in seagrass beds and subsequently moves to the coral reef habitat (McFarland, 1979). Alternatively fish may move to and from feeding grounds. Ogden and Buckman (1973) found adult parrotfish (*Scarus iserti*) migrate diurnally along constant routes to feed. This may be true for other species which have an ordered change of activity during the day.

Recruitment to a fishery may not be limited to juveniles, but include adults. Juveniles will be recruited to a fishery by growing to reach the size at first capture whereas adults will immigrate into the population being fished. When interpreting catch per unit effort data for coral reefs, it will be necessary to take account of fish movement. For sedentary species, continued fishing of a particular area would result in a more rapid decline in catch per unit effort compared to more mobile species, even when their populations within the area were initially the same size. This is because more mobile species are likely to move into the zone from outside, so that the impact of fishing is spread over a wider area. Fish movement has been dealt with for traps in terms of estimating the area effectively fished by a unit of effort (Miller and Hunte, 1987; Appeldoorn and Recksiek, 1990), but needs to be considered for other fishing gear. In such a patchy habitat as the coral reef, it is particularly important to know the degree to which different species move around and whether movement is affected by factors like density.

Growth

The growth of fish is often described using the von Bertalanffy growth model. While other equations may describe growth better in particular cases, the von Bertalanffy model parameters are useful in allowing comparison between species and species groups, as well as enabling growth to be incorporated into various population models (Gulland, 1983).

Parameters for many species have been published in the literature, but confidence intervals are usually missing, making comparisons between species difficult. There are a number of problems with basic data sets, in particular ageing of coral reef fish (Brothers, 1980, 1982; Gjosaeter *et al.*, 1984), which often has not been verified. Different estimation procedures (see Ricker, 1975; Gulland, 1983; Pauly, 1984) may give varying results with the same data. Many estimates rely on length frequency methods rather than direct ageing of the fish (e.g. ELEFAN), and have a number of problems leading to further questions as to the reliability of the estimates (see Rosenberg and Beddington, 1988). Repeats of estimates by different researchers are rare, but would be particularly useful in verifying results.

It might be expected that growth patterns depend to some extent on taxonomic group. For instance the butterflyfish, Chaetodontidae, are invariably small fish with little variation in size compared to emperors, Lethrinidae, which show a wide variation in asymptotic size. However showing that a particular group has a consistent growth pattern has been rare. A tagging experiment in the Virgin Islands (Randall, 1962), where parrotfish (Scaridae) had a significantly higher growth rate than surgeonfish (Acanthuridae) of equivalent size, is a possible exception.

Munro and Williams (1985) found no significant patterns in growth parameters compiled from the literature, except the intrinsic positive correlation between estimates of the asymptotic length and growth rate (Pauly, 1979). However variability of estimates is likely to obscure any patterns which may be present. For instance, growth parameter estimates of the emperor, *Lethrinus nebulosus*, show a wide range of values over three studies at different locations, exceeding the variation between taxonomic groups.

There are a number of other factors which might be expected to affect growth. Location may have a large effect. Stark (1971) found the snapper, *Lutjanus griseus*, tagged on Alligator reef in Florida grew at different rates depending on where they were recaptured. Fish remaining on the reef showed an average growth rate of just 1.7mm per month, whereas those moving to an inshore habitat grew at a rate of 8.4mm per month. At the very least this suggests that parameter values from one area should not be applied to another without careful consideration.

Water temperature is likely to have an important effect over large areas. Warmer water tends to be associated with higher natural mortality rates, and hence lower average size (Beverton and Holt, 1959; Pauly, 1980). Hence estimates of asymptotic size tend to be lower for areas with higher average water temperatures (Munro and Williams, 1985). It is quite likely that temperature affects growth directly, but this factor has not been separated from the effect of natural mortality.

Growth rate may also be related to food availability. This is certainly true in aquaria (e.g. Feddern, 1965). It has also been used to explain variation in growth rate in a number of studies of reef fish (Ralston, 1976; Jones, 1986). For instance, Ralston (1976) found *C.miliaris* grew more slowly in Kaneohe Bay than elsewhere in Hawaii, possibly because the low density of a primary constituent of its diet (calanoid copepods) in other areas.

A further complication will be changes in growth rate due to the sex of the fish. For instance, primary (non sex-changing) males of the parrot fish *Scarus iserti* grow faster than either secondary (sex-changed) males or females (Warner and Downes, 1978). A potentially common phenomenon has been observed for the wrasse *Thalassoma bisfasciatum*, where breeding fish grow more slowly than those not breeding (Warner, 1984).

Within fisheries, density-dependent growth is of particular interest (Jones, 1986). Doherty (1982b, 1983a) has shown that the growth rate of the damselfish *Pomacentrus wardi* is negatively correlated with the increased density of both other juvenile and adult conspecifics. However in this case, lower growth rates were probably the result of having to spend time defending territory rather than an absolute shortage of food. This resulted in a net loss of biomass for all individuals combined and therefore a fall in productivity. Forrester (1990) found a similar inverse relationship between density and growth in the damselfish *Dascyllus aruanus*. It is likely, where the presence of other species reduce time available for feeding, similar results might be observed. For non-territorial species, it will be necessary to show a reduced availability of food results in decreased feeding and growth.

Mortality

There are a number of direct measures of mortality for coral reef fish. Shulman and Ogden (1987) reviewed the mean post-settlement survivorship for a number of coral fish species. They found the proportion that survived to one month ranged from 10-80% and to a year from 0.1-75%. This large variation has a number of causes, including significant observation errors, but some of the variation is caused by genuine differences between species.

Even within families variation in mortality estimates has been large. Eckert (1987) stated that average juvenile mortality among 11 labrid species varied from 25 to 91.8% per year and was highest for abundant schooling species. Several species of plankton-feeding damselfish had a post-settlement mortality of around 50% per year compared to 5-10% per year for the territorial, algal-feeding *Pomacentrus wardi* in the same habitat (Williams, 1979; Doherty, 1980). In addition an ecologically very similar species to *P.wardi*, *P.flavicauda*, living in the same habitat was found to live only half as long (Doherty, 1980). Doherty (1980) also found juvenile *P.wardi* mortality to vary consistently among different habitats within the lagoon, suggesting that mortality may be strongly influenced by the location of the individual.

Predation mortality probably accounts for much of the immediate post-settlement mortality. In a caging experiment which eliminated predation mortality for post-settlement juveniles, Doherty and Sale (1985) found that 25% of fish were lost, presumably to predators, during the first 5 days in the benthic habitat, compared to less than 10% of fish aged between 6-10 days and no losses of fish aged between 11-15 days. The data also showed different rates of mortality for different groupings of fish, where schooling species had a higher rate compared to sedentary solitary species. This may be due to differing vulnerability to predation, caused by different substrate use.

A major concern seems to be whether observed distribution patterns may be more closely related to numbers settling or post-settlement mortality (Jones, 1991). Shulman and Ogden (1987) found that post-settlement mortality had a stronger influence on adult population sizes of *Haemulon flavolineatum* than recruitment variability. Studying *Pomacentrus amboinensis*, Jones (1990) suggested the local effect of good recruitment years on the adult population was limited by density-dependent mortality and migration. These results have not been universal. The distribution of pre-settlement fishes in the plankton influences settlement patterns (Meekan,1988; Roberts, 1991), and may be the most important controlling factor on patterns of relative abundance of juveniles.

Some studies have looked for density-dependent mortality directly. Victor (1986a) observed that juvenile densities of conspecifics of the wrasse, *Thalassoma bifasciatum*, had no apparent effect on juvenile mortality. Similarly Doherty (1983a) found clear density-dependent growth, but no significant changes in mortality in experiments with the damselfish *P.wardi*, when densities were artificially altered. However Hunt von Herbing and Hunte (1991) found evidence which suggests that post-recruitment mortality in *Thalassoma bifasciatum* was density-dependent. These conflicting results, which are common in the literature (Jones, 1991), are perhaps not surprising when considering the potential complexity of relationships between fish. For instance, although Forrester (1990) found survival of *Dascyllus aruanus* recruits was generally inversely related to their density, he also found it was enhanced in the presence of adults. Controlling for all possible effects in these experiments is difficult.

If decreasing density increases growth rates, it might make individuals less susceptible to predation, if predation rate is related to size (e.g. Nikolskii, 1969; Weatherley, 1972). If this were the case and fishing decreased density, the resulting lower natural mortality would compensate for a higher fishing mortality to some extent. However it is likely that a more significant effect will be simply the numbers of predators. In many multispecies fisheries the larger predators are often caught in preference to other species. It may well be that, with heavy fishing, natural mortality for many species will decrease as predators are removed.

Mortality in fisheries models is normally represented by an instantaneous mortality rate (Z) being made up of natural mortality (M) and fishing mortality (F). While there are a number of methods for estimating fishing mortality reasonably accurately, estimating natural mortality is notoriously difficult (see Shepherd, 1988). Perhaps the most useful method to obtain estimates was developed by Pauly (1980) using data on growth and mean water temperature from a range of stocks. Given growth and mean water temperature for a particular stock, the natural mortality can be estimated. Estimates using this method cannot be particularly accurate, but very often this is the only way to obtain some idea of natural mortality. Other methods are available (see Shepherd, 1988), and where comparisons have been made, tend to give different estimates. Furthermore parameters derived from this source are not likely to provide much insight into patterns of mortality. Any patterns based on Pauly's (1980) method will not differ significantly from the growth rate patterns, since they are derived from the species growth parameters.

No clear patterns in mortality have been identified, except perhaps that the highest mortalities occur immediately after settlement. Since this takes place before recruitment to the fishery, it is unnecessary to include it directly in fisheries models. Yield-per-recruit and dynamic pool models normally assume a constant natural mortality, ignoring age specific, density dependent (e.g. starvation and disease) and predation effects. While it is clear this has theoretical shortcomings, practically it is the only reasonable option when more detailed information is unavailable.

Community Models

The reductionist approach is to treat a community as the sum of its species, with no extra properties of its own. If this is accepted as the null hypothesis, any theory will have to explain significantly more community behaviour than can be explained by models where each species is treated as a separate variable. With highly diverse communities such as coral reefs, this leads to an extremely complex system with potentially hundreds of parameters. This, together with the logistical problem of recording catches down to species level, has encouraged the search for models which deal with groups, rather than single species.

This section looks at two general approaches to modelling communities that have been used in the past and discusses the possible applications of these models to coral reef management. In general models have been proposed for two closely related purposes. Many models aim to explain how the community evolved. In the case of coral reefs, they have to show why this community is particularly diverse. Secondly models have addressed ecological mechanisms that explain how the diversity is maintained. This last problem is of greater interest to management, since disruption through fishing could result in fundamental changes in the community ecology.

Trophic Level Models

Lindeman (1942) considered the community to be chain of different trophic levels through which matter and energy flow. Due to inefficiency in transfer (e.g. respiration within a level) energy is lost as it moves through the chain reducing the amount available to higher levels, hence the biomass decreases with the trophic level. Increasing the amount of detail to represent the community structure more accurately led to the development of compartment models (e.g. Dobben and Lowe-McConnell, 1975; Wiegert, 1976). Primary productivity and energy flow through food webs has been used to estimate potential yield from fisheries (Steel, 1975; Cushing, 1975; Polovina, 1984).

The main problems result from the allocation of compartments, which must represent the major structural components of the community. A trophic chain imposes an artificial structure, which may be difficult to reconcile with the real community structure. For many communities aggregation of species to different compartments may be inappropriate (Cousins, 1986), arbitrary (Ulanowicz and Radach, 1981) or impossible (e.g. heterotrophs; Rigler, 1975). Even if the model structure does give a reasonable description of the community, it will be static, and therefore will ignore community dynamics and be unable to predict how the structure might change under perturbation (Hubbell, 1971; Wiegert, 1976).

An interesting extension to this basic approach uses the size spectrum of the community (Platt, 1985). Using the positive correlation between the density of organisms and their size (see Sheldon *et al.*, 1973), Platt and Denman (1978) built a model employing only organism size, growth, turnover and respiration. However in practice biological attributes of species important to the community structure, but not represented by size, provide a limit to this method (Sainsbury, 1988).

An important consideration for all these models is whether the species groups capture significant changes in the value of the underlying components. For trophic models, this will be the case to a certain extent, since piscivores tend to fetch a higher price than the herbivores and planktivores upon which they feed, and therefore may form a natural group, with species having similar prices. Even so, the optimum management strategy suggested by these models may result in catches of lower value than ultimately could be the achieved.

The ECOPATH model (Polovina, 1984, Christensen and Pauly, 1991), which is available as a computer package, appears to be at present the only practical way to look at and use trophic relationships within the community. The model calculates biomass and production of various user-defined trophic compartments based on diets and the efficiency with which energy is passed along the food chain. The method provides a useful way to estimate production largely independent of fisheries data, and a way to explore different ways of fishing the community. The published test (Atkinson and Grigg, 1984; Grigg *et al.*, 1984) suggests the model provides a good description of a coral reef (French Frigate Shoals, Hawaii).

The model's disadvantages stem from its static nature and the data required to estimate necessary parameters. Data required demands estimates of observed diet for different species groups, as well as data more usually available such as non-predation mortality and growth rates. Although additional sampling is needed, the model only needs to use catch data peripherally and provides an independent assessment of the ecosystem. It should be emphasised that it is impossible to get around these extra data requirements. If trophic relationships are to be included in any analysis, data on the diet is a minimum requirement. It is likely in any case that many fisheries will have either too little or unreliable fisheries data for accurate stock assessments (e.g. Powers, 1982), so some special sampling will have to undertaken in any case. A second problem is that the model may not have much predictive power. For instance, increased fishing of a group might well result in a change in diet of that group's predators (e.g. Shpigel and Fishelson, 1989), invalidating the model if the diet change moves from one compartment to another. However, ECOPATH represents the simplest approach incorporating trophic relationships and it is a useful addition to tools available for analysis of potential fishery yield.

Multi-species Models

The ecological niche stands as the present paradigm of community structure. Hutchinson (1965) described the niche in terms of the multi-dimensional 'space' occupied by a species, each dimension representing an ecological resource. The concept partitions resources among species, such that each species has resource space in which it can persist. Quantitative niche theory was developed using sets of the Lotka-Volterra equations with parameters describing the impact of the size of each species population on every other species in the community through use of shared resources (see Levins, 1968; May, 1984).

It is a simple matter to extend the model to allow mutualism and predation, and hence describe a food web (Pimm, 1982). These food web models provide a reasonable approximation to a wide range of possible deterministic models when close to equilibrium, but away from equilibrium they may provide a poor description.

Pope (1979) looked at a model based on the Lotka-Volterra equations with the addition of harvesting (i.e. the Schaefer model), assuming it fully described the dynamic behaviour of a multi-species fishery. He demonstrated a number of features of model, also found in the individual equations. Total equilibrium yield is a parabolic function of fishing effort. Given constant catchabilities, maximum yield is obtained when the catch per unit effort is half its initial value, and maximum possible yield occurs where fishing effort and catchabilities are adjusted to reduce each individual species CPUE to half that species initial level. Similarly Powers and Crow (1982) studied a more specific theoretical model describing the harvesting of two competing species which included migration and dispersal. The model illustrates the possible behaviour of the populations to fishing. An important result was that the species with the higher catchability was more vulnerable than the other with which it competes.

The Lotka-Volterra model discussed above is linear and deterministic, assumes homogeneous populations and has no external driving variables, such as seasonal environmental changes. Relaxing these assumptions can result in a wide variety of behaviours, giving the general theory little predictive power. Non-linear or stochastic models may give what appear to be regions of attraction rather than equilibrium points, resulting in potentially highly complex behaviour. Many non-linear models can exhibit a range of behaviours, including limit cycles of variable frequency and deterministic chaos, as well as the more familiar equilibrium points.

Although food web fisheries models cannot be applied directly, there are some very general conclusions which can be drawn (Kirkwood, 1982):

■the multispecies MSY is less than the sum of the single species MSY.

■the sensitivity of the system to environmental fluctuations increases as the level of exploitation increases.

■the models that do exhibit 'unexpected' and irregular behaviour normally are those that include strong non-linear inter-species interactions.

The practical implications are that managers should perhaps be a little more conservative with multispecies stocks. These models also suggest that yield can be increased by adjusting the relative catchabilities of different species as well as controlling effort. This is most likely to be achieved by controlling fishing gears and the times and areas fished.

Including Spatial Heterogeneity

The fact that populations in fisheries are never homogeneous is perhaps of greater immediate interest, and can have a profound effect on population dynamics (Nisbett and Gurney, 1982). Many fisheries models are age structured, but fewer are structured spatially. In theoretical ecology, spatial heterogeneity has been put forward as a major stabilising factor, and is considered to be important in population dynamics. For instance, Ives and May (1985) showed that contagion in distributions could allow greater coexistence between competing species through greater overlap in resource use. Spatial effects on fisheries have also been widely discussed (e.g. Clark and Mangel, 1978; Allen and McGlade, 1986), particularly in the interpretation of catch per unit effort data. However, in contrast with many ecological studies, fisheries studies have concentrated on how spatial heterogeneity might decrease rather than increase stability.

Spatial heterogeneity is increasingly recognised as an important factor in coral reef ecology. Many phenomena operate in different ways at different spatial scales, although observations are usually made on one scale only (Reichelt, 1988). For instance, whereas fish species abundances and distributions might appear random on the scale of tens of metres, more consistent patterns emerge on the scale of tens of kilometres (Lowe-McConnell, 1987; Roberts, 1991). However at this stage it is unlikely that spatial heterogeneity will be included in stock assessment until special methods are developed to cope with this complex issue.

Models of Coral Reef Communities

A number of authors have suggested that coral reef fish populations are relatively stable and maintained by competition and predation between species in much the same way as has been proposed for temperate communities (Smith and Tyler, 1972; 1973a; 1973b; 1975; Ehrlich, 1975; Gladfelter and Gladfelter, 1979; Gladfelter *et al.*, 1980; Anderson *et al.*, 1981; Ogden and Ebersole, 1981; Shulman *et al.*, 1983). For example, Robertson and Gaines (1986) found competition for food in surgeonfish (Acanthuridae) and habitat partitioning among species. Targett (1978) found similar results for two species of pufferfish. However such results are not universal, and in many cases clear evidence of competition has not been found. Ogden and Ebersole (1981) suggest that this is partly because experiments on a small spatial scale will fail to detect interactions which are present.

Grigg *et al.* (1984) concluded from their trophic model that predation was a major determining factor of coral reef community structure. Experimental work also suggests predation is important, at least in immediate post-settlement fish (Doherty and Sale, 1986; Shulman *et al*., 1983). Although there is no experimental data for predation during other parts of the life-history, it seems likely this form of mortality is high and plays an important role in the life history of many species (Glynn, 1988; Shulman and Ogden, 1987). Paine (1966) showed that predation can have a significant impact on the community, potentially preventing exclusion by competition.

Fishing may be a source of community instability and could change community structure (e.g. Goeden, 1982). However the coral reef food web is complex, with predation rates very different to observed abundances of prey (Parrish *et al.*, 1985). This complexity has prevented the development of food web models, most work being based on the analysis of single species, or species groups.

As well as more general ecological theories, coral reefs have attracted a number of special theories to explain their high diversity. Connell (1978) proposed an intermediate disturbance hypothesis, adapted from widely accepted theories of forest dynamics. He suggested that there is some level of random disturbance which prevents domination of a community by a small number of species while not substantially increasing the extinction rate, hence maximising diversity. While the theory mainly attempts to explain coral diversity, it might explain fish diversity if fish diversity depends on the benthic community and structural complexity of the reef.

Connell's (1978) intermediate disturbance hypothesis only has application in the sense that large perturbations, which may be induced through fishing, will decrease the diversity of the reef, an empirical fact which has a wide support (Dahl and Salvat, 1988). On a large scale this may have profound implications for species conservation, particularly where fishing is accompanied by destruction of the reef habitat. On a small scale disturbance is likely to lead to increasing dominance of small, fast growing fecund fish which will be of lower value than larger, more slow growing species.

Sale (1978) proposed a hypothesis based on work with territorial damselfish. In its simplest form the theory requires that there are a limited number of sites available to fish on a reef, and once a fish settles in a site, all other settlement there is prevented until it is released again. If all species have an equal chance of recruitment and the population is large enough, coexistence will be achieved. Hence the distribution of species will reflect past recruitment rather than competitive interaction. The theory requires, among other things, a rapid increase in mortality as the density passes some threshold, a result which has not been found for damselfish (Doherty, 1982a), the group to which the hypothesis is most likely to apply.

Sale's (1978) theory suggests a population model based on space limitation or strong density dependent mortality. With no shortage of larvae, the stock would be rapidly replenished up to the limits of the resources available. Given a carrying capacity (unexploited stock size) of a reef, growth rate and mortality, this could be modelled reasonably accurately. However, since it has been questioned whether this model is a reasonable description of territorial fish populations for which it is most appropriate, it would not seem fitting to apply it to more mobile fish which make up much of the catch.

Observations on settlement to patch reefs and the inability to consistently find significant competition in reef fish populations has lead to the proposal that adult stocks are limited by recruitment, so that densities on the reef are largely a result of previous settlement patterns rather than interaction between and within adult fish populations. This hypothesis has received some empirical support through studies which have largely been directed at demonstrating that expected competitive interactions are not present or that observed densities can be directly related to known recruitment patterns (Williams, 1980; Doherty, 1982a; Victor, 1983; Munro *et al.*, 1973). The theory does not address the possibility of a stock-recruitment relationship or interactions between pre-settlement populations.

Populations may never reach sizes necessary for significant competition if they are held below their carrying capacity. The carrying capacity represents the largest population size that a particular area can sustain, which in the Schaefer model is the unexploited biomass. As the carrying capacity is approached the level of competition between individuals within the same species increases mortality or decreases growth and recruitment until a balance is reached. According to niche theory the level of competition between any two individuals from the same species must exceed competition between two individuals from different species because of the greater niche overlap. Therefore if there is little competition within each species, there will be even less competition between species. Species might be held below their carrying capacity by a variety of factors, including predation, disease and non-density-dependent fluctuations in mortality due to changes in the environment, as well as recruitment.

If competition and predation are not important, a dynamic pool model with constant natural mortality and an appropriate stock-recruitment relationship may provide a reasonable description of the stock for many species. However predation may well be significant, so natural mortality may have to be re-estimated when fishing effort or selectivity changes significantly. In addition, any stock-recruitment relationship would need to be spatially resolved, which would require research on hydrography and larvae behaviour, a daunting task since the population dynamics of pelagic larvae are even harder to observe. Most reefs are set in a spatially complex environment, so that how larvae are distributed and the effect on recruitment of fishing a particular area are unknown. However isolated atolls maintain resident populations, which suggests they are supported by local recruitment. It is for these isolated populations that a stock-recruitment relationship might be most clearly demonstrated. In the meantime yield-per-recruit assessment methods may be the best approach.

Implication for Fisheries Management

Much of the research in coral reef ecology may be valuable in the long term as understanding improves, but it is of little help now in formulating appropriate models or management advice. Hence results can only be included in a very general way. Considering the large and detailed research effort that has been put into studies of coral reef ecology compared to other marine systems, this suggests that pure ecological studies cannot be relied upon to answer questions in tropical fisheries in all but the long term.

There are a number of problems with using the results from coral reef ecological studies in fisheries models. Perhaps the most obvious is that theories are based on a very narrow range of species. In general it is easier to undertake experimental work with the smaller less mobile fish species. This has led to significant amounts of work being carried out on, for instance, damselfish, but very little on species that are important in catches (e.g. groupers, snappers and emperors). Most research has therefore been directed at explaining the ecology of the highly diverse territorial damselfish guilds and it is unclear how relevant these results are to other species in the community.

The conflicting results of ecological studies provide little clear evidence favouring one community model over another (Jones, 1991). In particular, there is no evidence that models other than those already used in stock assessments, such as yield-per-recruit, will provide significantly better advice.

Choosing the model is an important management decision, since different models can give radically different results. For instance, single species models will obviously not lead to a recommendation to fish down the predators to reduce mortality on species lower down the food chain. Since there is no way to test models with the available information, the models used will probably continue to reflect the data available rather than theoretical considerations.

It would be reasonable to assume single species stock assessments to be the default analysis unless interactions between species are significant. For coral reef fisheries, there are several important arguments against using single species models. Firstly predation rates are high on coral reefs, indicating significant trophic relationships. However, the impact of predation may not be so great if sources of mortality are not additive. For instance, predators may selectively take diseased individuals that are likely to die anyway or density-dependent effects may reduce the impact of predation. The effect of competition between species is even less clear. Competition is almost certainly greatest within guilds of species. For damselfish Doherty (1982b) showed that growth was density-dependent, since at higher densities fish had to spend more time defending their territory and less feeding. If such competitive interactions are present within and between species, the impact of fishing will be significantly reduced and a higher fishing mortality might be attained before the total yield begins to decrease.

Even if it could be guaranteed that single species models would give an accurate description of the system, if none of the parameters are known *a priori*, the problem of estimation is enormous. Neglecting interaction parameters, the cost of obtaining accurate information for sets of single species models will be prohibitive. If it is assumed that 20 species make up the catch, and 5 parameters are needed to describe each species' population changes (2 mortality, 2 growth and 1 for recruitment), the model would require 100 parameters. Allowing for interactions between species may require population models for species not present in the catch and this would be simply impractical. This makes other simpler approaches, such as aggregating species in the catch much more attractive.

Simpler models may even be more accurate, since increasing complexity does not automatically increase accuracy. Very often simple models will result in better management advice than complex models, even if complex models are a more accurate description of the system (Ludwig and Walters, 1985). Considering the complexity of the coral reef community and the potential inaccuracies in describing the system, it is likely that the best models will be very simple.

Multi-species Stock Assessments

Single species models are probably the most commonly used models in stock assessment. Sparre *et al.* (1989) describe methods available for this approach. Many papers describe the biology of individual species and give parameter estimates useful for analysis on a species by species basis (e.g. Wright *et al*., 1986; Lablache and Carrara, 1988; Manooch and Drennon, 1987; Morize and Caillart, 1988; Sadovy and Figuerola, 1989), but they concentrate on a small number of commercially valuable species.

Huntsman *et al.* (1983) fitted a series of yield-per-recruit models for the nine most important species in the South Atlantic Bight snapper-grouper fishery. Results for all species were very similar and indicated one management strategy might maintain yields for all species. Munro (1977) used the Beverton and Holt yield-per-recruit model for a set of single species, assuming no interaction. Results defined the general gear selectivity and fishing mortality required to improve yields. Similarly Polovina and Ralston (1986) used a dynamic pool model with separate catchabilities for each species to estimate potential yield from a previously unexploited deep slope fishery. Results also gave some indication of the expected changes in species composition of the catch as the fishery progressed.

Polovina (1989) developed a method to deal specifically with multispecies or multiarea problems. This method estimates simultaneously parameters for the Schaefer model for several areas and species, allowing a more powerful multivariate approach to estimation. However, species interactions have largely not been included in stock models. An exception is competition for hooks which has been studied in a deep slope fishery (Polovina, 1986). This is a specific problem where catchability for one species depends on the abundance of another. This form of interference may be important where saturation of hooks or handling time is an important feature of the gear.

At the other extreme all species might be combined into a single catch. The surplus yield approach, where the biomass is undifferentiated, has been widely adopted (e.g. Munro, 1977; Lock, 1986a). Although the method has shortcomings, it is robust and valuable in providing a simple indication as to the state of the fishery. It captures the fact that there is a maximum yield obtained between no fishing effort and some level of effort so high that it drives the populations and therefore production down to a very low level. However there are two main problems with the model. Usually data on catches at the higher effort levels are lacking, since there is an economic disincentive to fish at these levels. This effect together with increasing variability in catches at higher effort levels makes the MSY estimate less reliable. Secondly the model only allows one control variable, effort, when a number of others are possible; for instance species and size selectivity of gear, which may change the optimum fishing effort considerably.

A slightly more refined approach is to group only similar species together. The argument that this approach is valid makes use of the fact that closely related species tend to have similar parameter estimates for population models (e.g. growth and mortality estimates) and species guilds behave in a similar manner to single species populations in that larger slow growing individuals are replaced with smaller fish, whether of the same species or not (Appeldoorn and Lindeman, 1985). Such species grouping is common in tropical multispecies fisheries and by default, assessments are often forced to use these sort of data.

Appeldoorn and Lindeman (1985) present an example of this approach, aggregating species for an assessment of the Puerto Rico haemulid fishery where fourteen species have been accumulated into a single catch estimate. The method still identifies general overfishing already uncovered by other methods. A more objective method is to use cluster analysis to identify species groups occupying the same habitat. Ralston and Polovina (1982) applied the Schaefer stock-production model to species clusters after first demonstrating that the model was inadequate when used on a species-by-species basis. The clusters performed only slightly better than aggregating all species together.

The main attraction of grouping species together lies in the low cost involved in data collection. The method also seems to give reasonably sensible results when using a robust surplus yield model. More detailed economic analysis would still require the species composition, however, unless the prices for all species were the same. A more subtle problem lies in the response of a heterogeneous population to fishing.

Estimating catchability for a group of species combined may lead to under-estimates of the remaining population size as fishing progresses. Different species are likely to have different catchabilities, and the species with higher catchabilities would decline at a faster rate. This would lead to a decreasing catchability for a group of species as fishing pressure increased, and current catchability would be overestimated. Since catchability relates the catch per unit effort to population size, if the catchability is too large, the population size will be higher than estimated.

Other inaccuracies may be more important to the issue of conservation. Even if a group of species reacts in a similar manner to a single species population when fishing effort is low and increasing, this may not be true at high fishing intensities or when fishing intensity is decreasing. The recovery time may be much greater. Species pushed close to local extinction may take many generations to recover, whereas a single species recovering from growth overfishing will take only one generation. Furthermore local extinctions in multispecies fisheries are a real possibility. Economic constraints that would usually prevent a rare species being fished to extinction will not operate when the catch rate remains high, supported by alternative species. Completely ignoring catch composition may not be a wise choice.

Management Case Studies

It is important to understand the circumstances under which coral reef fisheries operate to make meaningful suggestions for research. Ideally scientists need large amounts of data on age, growth, abundance, mortality and trophic relationships under a wide range of regimes, but in reality such data are always imperfect and incomplete. The lack of data for artisanal and subsistence fisheries is a particularly acute problem, and yet these types of fishery dominate coral reefs. Perhaps more fundamentally, managers do not always see stock assessment as the priority concern. To give some idea of the types of fishery and range of problems, case studies of fisheries in Papua New Guinea, Philippines and the Caribbean are discussed.

The two studies in Papua New Guinea presented here illustrate an important point common to coral reef fisheries. Few artisanal or subsistence fisheries collect data on a permanent basis, because of the difficulty in implementing a fishing log-book system to measure catch and effort. This means data has to be obtained through specific surveys. If any stock assessment is undertaken, it may often be based on length-frequency samples, which are relatively easy to obtain. The information in the Papua New Guinea studies was the result of specific surveys lasting about one year.

Papua New Guinea

Wright and Richards (1985) describe a subsistence and artisanal coral reef fishery in the Tigak Islands, Papua New Guinea. Four gear types were used; nets, hand lines, spears and trolling. 253 species from 43 families were recorded in the catch. Only one, the mullet *Valamugil seheli*, made up as much as 20% of the catch; all other species made up 5% or less. Even at the family level the catch is highly diverse. The most commonly caught families were mullets, jacks, snappers, emperors, groupers and parrotfish, which vary from 20 to 8% of the catch respectively. Fish production for the market was found to be inversely related to the price for copra, which is the main source of cash for islanders. A lack of infrastructure, together with seasonal bad weather, also limit fish supply and distribution to markets. There was no evidence of overfishing and observed finfish yields (0.42 mt km^{-2} yr^{-1}) were well below those given elsewhere (see Table 1).

The artisanal fishery at Port Moresby, described by Lock (1986a,b,c,d), is the most highly developed in Papua New Guinea. The fishery consisted of five villages and several reefs of varying distance from the port. The catch was again highly diverse, but differed in composition to that in the Tigak Islands. 23 families were represented, with only 7 making up more than 5% of the catch, and the largest, the lethrinids, comprised 30% (this group comprised 10% in Tigak). In contrast to the Tigak Islands fishery, fishing continued throughout the year despite changes in the weather, although fishermen changed their gear and target species. The fishery had developed despite the lack of ice and cleaning facilities. This was in contrast with elsewhere in PNG where such infrastructure had been provided, but failed to stimulate an increase in production. This was probably due to the high demand for fish in Port Moresby, coupled with the strong tradition of fishing in the area. Fishing intensity dramatically decreased with distance from the market and increasing reef exposure. There was a corresponding increase in catch per unit effort. Lock identified reef habitat types using, among other things, satellite information, and concluded the reefs were ecologically similar. He then fitted the Schaefer model to the total catch and effort for each reef (depth < 7.5m), and estimated the MSY to be 8 mt km^{-2} yr^{-1}.

Species composition was observed to change as fishing intensity increased most clearly in the net fishery. As fishing effort increased the catch changed from being dominated by large herbivorous acanthurids to smaller predatory lethrinids, and then to small herbivorous siganids. In all cases there was a consistent decline in the value of the catch, from slow growing valuable fish to smaller fish with higher fecundity and lower market value. Lock suggested that the actual abundance of small fish, such as siganids, had increased despite the increased fishing mortality as a result of reduced predation and competition.

A common feature of most coral reef fisheries, including those above, is that fishing effort concentrates around towns or villages. This is presumably because it is more costly and difficult to fish further away from home. There are a number of other factors that influenced the behaviour of the fishermen. Lock (1986d) indicated that prices change with time of day, season, market, species, size and the fortnight pay cycle, so that these factors may well be important driving forces in supply. However, Wright and Richards (1985) found that maximising the catch rate may not be the main objective for subsistence fishermen. Since there is no observable price for fish caught in the subsistence fishery, it will be even more difficult to understand its dynamics.

Philippines

Coral reef fisheries in the Philippines are much more developed than those in Papua New Guinea, and face a different set of problems. They are particularly intensive and provide income for a large number of people (Murdy and Ferraris, 1980). As well as the usual hand lines, nets, spear and trolling, the Philippines have a particularly large fishery gathering invertebrates in the lagoon and on the reef flat.

Habitat destruction associated with deforestation, damaging fishing methods and other forms of exploitation is of as much concern in the Philippines as direct overfishing. Fishing using explosives, poisons and breaking up the reef to scare fish into nets reduce live coral cover which has, independent of fishing mortality, a large impact on the fish community (Bell and Galzin, 1984).

Although controls on dynamite fishing exist, they are not well enforced and incentives to ignore them are high (Galvez, 1989). The set net techniques of *muro-ami* and *kayakas* also cause damage (see Gomez *et al.*, 1987 for a description). To increase the catch rate the reef in front of the net is hit with boulders, forcing the fish from cover. Another problem in the Philippines is the use of poisons to collect aquarium fish and even some food fish, which kill surrounding benthic invertebrates (Albaladejo and Corpuz, 1981; Rubec, 1986). It is estimated that 150 mt of assorted poisons like bleach and sodium cyanide are used each year on Philippine reefs (McAllister, 1988).

In studies of two island fisheries with contrasting reef quality, Savina and White (1986b) and White and Savina (1987) suggested that potential yield is decreased by low coral cover and indicate that prevention of destructive fishing practices may be the key to improved management. Controls on gears is an important management requirement in many Philippine fisheries (White, 1984). McAllister (1988) conjectured that yields in the Philippines have declined by 160,000 mt (US$ 80 million) as a result of reef destruction and that this represents a fall of 127,000 in employment. This problem has exacerbated the poverty of coastal communities, where up to 59% of children suffer from malnutrition. McAllister attributes these problems mainly to habitat destruction rather than fishing beyond the optimum yield.

Because of deterioration of reefs in the Philippines, much effort has gone into the creation of effective marine reserves. Where these have been successfully implemented, they appear to increase stock size and catches. White (1988) reports how community managed reserves resulted in an increase in species richness and abundance within the reserve. The basic principle, now used in a number of community reserves that have recently been established in the Philippines, is to designate a small area in which fishing is prohibited, surrounded by a larger area in which fishing is allowed, but only with ecologically sound gears. Russ and Alcala (1989) found an increase in fish yields outside a reserve in Sumilon Island, suggesting reserves may be useful in increasing yields as well as protecting the reef. A key factor in the success of a reserve appears to be involvement of local people (Savina and White, 1986b). Co-operation of local people is necessary for enforcement, but depends upon benefits which they perceive they get from the reserve.

As well as stock reduction through habitat loss, reef fish are being harvested well beyond the optimum. Del Norte *et al.*, (1989) indicate that overfishing is a problem on many reefs and that there are no adequate stock assessment tools to deal with a fishery in this state. In particular they found when fishing mortality is high, there are too few length frequency classes to obtain reasonable estimates of growth and mortality parameters. The problems of coral reef fish stock assessment are well documented in the

Philippines. Species composition and magnitude of yields have been found to vary considerably among reefs and with season (e.g. Bellwood, 1988; Alcala and Luchavez, 1981; Acosta and Recksiek, 1989; Alcala and Russ, 1990).

Caribbean

In the Caribbean reef deterioration and overfishing are equally of great concern. However, compared to other areas, there is a much longer history of interest in reef fisheries and consequently a greater literature on stock assessments and biology of commercially important species (Sadovy, 1989; DuBois, 1985; Appeldoorn and Lindeman, 1985; Huntsman *et al.*, 1982; Munro, 1977). In this region, fishery regulations have been largely orientated towards improving the economic efficiency of the fishery. Protection and management of the reef habitat is seen as the responsibility of agencies concerned with establishing national parks and reserves. The Caribbean also provides examples of the problems caused by open access to fisheries.

Barbados and Jamaica illustrate the major problems of controlling access to avoid overcapitalization and overfishing (Berkes, 1987; Berkes and Shaw, 1986). While in Barbados catches have been increasing, this is mainly due to the exploitation of pelagic resources. The reefs have been degraded and overfished to the extent that the fishery is switching to offshore resources. The Jamaican fishery is more stable and still reef orientated, although increases in catching power of vessels has led to decreases in catches, and many areas have been heavily overfished (Koslow *et al.*, 1988). These fisheries face a problem commonly found elsewhere, which is how to redirect excess fishing effort to alternative resources as catching power increases, before rather than after the reefs are degraded.

In the Caribbean, as in the Philippines, protected areas can play an important role in managing fisheries. Perhaps the best documented is the Virgin Islands Biosphere Reserve. Boulon and Clavijo (1986) report that subsistence fishermen use mainly traps, bottom longlines and hand lines within the reserve, although the total effort is very low since commercial fishermen mainly fish elsewhere. The reserve regulations prohibit commercial fishing, but allow subsistence or recreational fishing. The main value of the sanctuary is thought to be as a nursery and breeding reserve to maintain recruitment over a wider area (Boulon, 1986) rather than directly improving catches nearby. For this to be the case, a minimum requirement would be that the parent stock would have to be higher in the reserve than in exploited areas. Clark *et al.* (1989) found in a Florida fishery, as in the Philippines, that the reserve directly increased abundance of a number of exploited species. However reserves tend to be primarily a conservation measure, and enhancement of the economic value of fisheries is only a secondary objective.

Management Controls

It is clear from these case studies that management of coral reef fisheries is beset by a number of social, economic and biological problems. Methods are required to cope with the limited resources available in developing countries. Realistically management regimes will have to be simple, require little data and be easy to enforce. This probably rules out many of the management controls developed for industrial and commercial fishing (see Beddington and Rettig, 1984).

Any successful management system would have to solve two important problems. First, it would have to provide for habitat protection, recovery should reef damage occur and conserve vulnerable exploited species. Secondly the regime will have to protect the livelihoods of the fishermen, and if possible, increase their income from the resource. More generally, coral reef management must also deal with conflicts among users of the resource, most notably between fisheries and tourism. These objectives will require a combination of management approaches, the selection of which will depend on the characteristics of the fishery, including the socio-economics of the community involved. However, the role played by stock assessments in setting appropriate management regimes is not clear. The following is a brief overview of some of the approaches in use at present.

Limited Entry and Quotas

Limited entry and quotas are difficult to enforce in reef fisheries, where large numbers of species are being taken with a variety of gears and landed at numerous points. In addition, lack of biological information for many species means that it would not be possible to set quotas for these species with any accuracy. Finally quotas may be inappropriate where gears are unselective, since fishing may have to cease once the first quota is reached, even when other species remain virtually unexploited. Effort control through limited entry is likely to lead to overcapitalisation where fishing power is able to increase. In the context of reefs, these methods are used mainly in recreational fisheries or fisheries targeting high value invertebrates, such as lobster or conch.

Limited entry is a common control for restricting the number of boats or fishermen in a fishery. Lock (1986a) recommends this control for the Port Moresby artisanal fishery, and for such fisheries it may be a good first control because it is relatively easy to implement and enforce, although effective enforcement can still be costly. In subsistence fisheries it is simply inappropriate without providing alternative sources of food for those excluded from the fishery. This is the case in many fishing villages in the Philippines.

Catch quotas in their traditional form would represent the most costly management control. Total Allowable Catch (TAC) quotas are probably the most common form of management, although they include no economic controls and tend to lead to economic inefficiency. An alternative is an Individual Transferable Quota (ITQ) system, whereby fishermen buy quotas of the TAC which they then catch in the most economically efficient method possible (Clark, 1980). The quotas can be freely bought and sold, so that the least efficient fishermen tend to be replaced and the total value of the fishery increases. Management by TAC is not appropriate and could not be applied in most coral reef fisheries (Mahon, 1989). ITQ is very sophisticated and requires exact enforcement, and would therefore again be inappropriate for coral reefs and other highly diverse fisheries.

Gear Controls

Elimination of damaging fishing methods, as the case studies have shown, is of very high priority. If alternative methods of equal efficiency are not available, enforcement may be extremely difficult. This is particularly true in the case of dynamite fishing, which has high catch rates even on heavily exploited reefs. Greatest success has been achieved where thorough public awareness programmes have been implemented (e.g. some parts of the Philippines and Indonesia) and where communities themselves manage the fishery. Similarly poisons are slowly being eliminated from the aquarium fishery in the Philippines using education programmes for the collectors, which teach alternative more sustainable methods for catching fish.

Gear controls, for instance trap mesh size limits (Mahon, 1989), can be used to control both size and species selection, and would be essential for implementing recommendations from most stock assessments. Gear controls for commercial fisheries can be enforced at sea or at landing sites, if there are relatively few. However most other fisheries will not be able to support this sort of enforcement and must rely on a commitment from the community. On the north coast of Jamaica fishermen are being asked to trade each of their small mesh traps for two large mesh traps. After a period of initial reluctance, most members of the community are now taking part (Woodley, 1992).

Controlling species selectivity is likely to be a key component of a multispecies fishery. Food web multispecies models suggest that the sustainable yield can be increased by adjusting fishing mortalities for each species. This can be achieved through changing their catchabilities, which might be controlled by restrictions on gears as well as on the time or place of fishing. Without strong theoretical support, adjusting catchabilities among species to improve yields will be a major challenge. However the immediate management concern appears to be conservation, so the more subtle problems of species selectivity will probably only be resolved in the long term.

Closed Areas

Closed areas are a important control in coral reef management and are being used to conserve both areas of reef habitat as well as stocks. As shown in the case studies for the Philippines, catches in the vicinity of a closed area can improve. An important advantage lies in the comparative ease with which they might be enforced, particularly in the context of community management. Roberts and Polunin (1991) give a detailed review of reserves in coral reef stock conservation and their affect on yields. There are a variety of closed areas, ranging from sanctuary areas in which fishing is totally banned, to zoned areas in which fishing is permitted, but only under certain conditions or using certain gears. However it is unclear how results from stock assessment could be used to improve zonation unless methods are developed to take explicit account of the spatial distribution of stocks. This will be necessary to determine the relative benefits of different zones, as well as where they should be located and how large they should be.

Closed areas could be beneficially established in many reef fisheries immediately. This is happening in many places in the Philippines and has been recommended for Florida (Bohnsack, 1990), spurred on by the urgent need for habitat protection for reefs in most parts of the world.

Seasonally closed areas may be useful in protecting spawning aggregations. However good information would be required on the location and duration of aggregations if such methods are to be effective (Mahon, 1989). Alternatively such sites could be included in permanently closed areas.

Community Management

In many societies, most notably in Oceania, reef fisheries have been managed under customary marine tenure (CMT) systems, with family and clan groups controlling the rights to fisheries on reefs adjacent to their land. These systems are only now being fully documented and show much variety in detail, but have the common characteristic that the community which uses the resources controls its exploitation (Ruddle and Johannes, 1990). Fishing rights usually apply to areas, with rights to species and gears sometimes superimposed. Management measures include restricting harvests from particular areas or of particular species, the live storage or freeing of surplus fish caught in spawning migrations, and taboos on certain areas and closed seasons.

The extent to which different societies recognised the problems of free and uncontrolled access to reef fish and expressly implemented measures to limit this appears to vary. In some cases management regimes may have been an indirect effect of other social and political activities (Polunin, 1984). However, whether direct or indirect, many community managed systems have provided a good basis for dealing with contemporary problems in coral reef management (Ruddle and Johannes, 1990; Johannes *et al.*, 1991).

Christy (1982) used the term territorial use rights fisheries (TURFs) to describe management systems which allocate areas' fishing rights to particular communities. These have some similarities to ITQs, except an area of reef is allocated instead of a catch quota. Although in some cases such arrangements are formalised through legislation, no authority is involved. TURFs encourage good management of the stocks by fishermen as sole owners, but they have several problems. TURFs may slow development of resources where they are not allocated to those who might make best use of them (Lock, 1986a). They may also hinder the implementation of national fisheries policies where this is important to the management of fish stocks as a whole. For instance, the protection of spawning areas may be of wide interest, but the sites may lie in TURF areas whose owners may be unwilling to accept such controls (Munro and Fakalau, 1988).

The role of stock assessment within community managed systems is not clear. TURFs assume that the owners know best how to harvest the resource. In contrast, the stock assessment for ITQs is still carried out by a central authority which sets the size of the quota. Given the complications already discussed it is unlikely that fishermen will be able to find the economic optimum, so a central fisheries body may have some role in providing advice and education. Perhaps the greatest value of CMTs or TURFs is the devolution of the decision-making to a level where people are familiar with the fish, fisheries and socio-economic realities. Given our present understanding of coral reef ecology, community management may well be as close to the optimum as could be achieved at present.

Stock Enhancement and Diversification

Although it is beyond the scope of this review, it should be noted that coral reef fisheries have the potential to be enhanced. Artificial reefs increase the area of suitable habitat for fish and invertebrates and may thus increase the size of the stock (see reviews: Polovina, 1991; White *et al.*, 1990). However, further research is required to determine to what extent they increase the size of the stock as opposed to acting as aggregation devices.

Mariculture techniques are being developed mainly for reef invertebrates such as giant clams and *Trochus*, but some experimental work is under way on cage culture of groupers and other finfish. Supplementary stocking of reefs with juveniles of commercially valuable species has yet to be proved worthwhile. The returns could be low if losses go up as a result of higher densities increasing migration and mortality or decreasing growth.

Conclusion and Future Research

Research on coral reef community ecology suggests that interactions between species, in particular predation, are significant. However community dynamics are not well understood, and so current results cannot be used to improve on models already used in stock assessment. To make stock assessments more effective, two areas of research need to be addressed.

The dynamics governing the behaviour of fishermen has been rarely studied, but is necessary to understand how a fishery operates. For instance, a particular problem in coral reef fisheries management is to improve the spatial distribution of fishing effort. A consistent observation has been that the heaviest fishing takes place close to areas of human habitation. Predicting how the distribution of fishing effort will change as a fishery's infrastructure or gear changes will be valuable in the economic analyses and interpretation of catch data. There may be some value in using models for this purpose in the management of artisanal fisheries, but it is unlikely this approach will be effective in subsistence fisheries without a better understanding of their economic structure.

A second fruitful area of research would require recording changes in species composition within a fishery, which may provide additional useful information for monitoring the fishery as a whole. It is widely accepted that under increasing fishing pressure the catch will become dominated by small, faster growing species. For instance, Munro and Smith (1984) demonstrated this using a simulation based on simple population models to show how the catch composition might evolve as effort increases. However there are no quantitative estimates of these changes, so these observations at present are of little use in interpreting catch data.

The catch species composition will depend on the initial ecological community, the direct and indirect effects of fishing and targeting by the fishermen. The direct effects of fishing and targeting may well be tractable to research, and allow an extension of the analysis of catch data to include species composition alongside other methods, including length frequency and catch per unit effort analysis. However the accuracy of species composition analyses will depend on the strength of the indirect effects of fishing on the catch composition. The indirect effects are largely unpredictable at present, and certainly beyond current stock assessment methods. A database of current observed species compositions for individual coral reef fisheries would be valuable in identifying patterns and could be useful in the development of stock assessments for multi-species fisheries.

Fishing mortality may be the largest single factor governing species abundance, if it is high. The direct effect of fishing where catchability varies among species has been largely unstudied (Hilborn and Walters, 1992). The theoretical effect is simple; species which are vulnerable to the fishermen will initially make up a high proportion of the catch, but as their populations decline other species will come to dominate. The main reason for studying this effect is that it is tractable, and the appropriate parameters (the species catchabilities) can be estimated directly. This approach will not be able to explain all observations, but accounting for changes in species composition caused by differences in fishing mortality is a necessary prerequisite for further work.

As well as specific research, coral reef management requires a general approach to deal with the wide variety of issues it faces. It would seem that pure ecological research cannot be relied upon to solve the problems of stock assessment and management. Existing ecological research is not advanced or specific enough to answer questions posed by fisheries management. Detailed scientific work on reef ecology will probably be useful in identifying models, but only in the long term, as the structure of the coral reef community becomes better understood. Although most innovations are likely to come from this source, ecological research cannot be expected to provide answers for more immediate management questions, or be specific enough to apply to individual fisheries.

The obvious alternative is to use past catch and effort data, and look for relations between different time series variables. Models using catch and effort information can be improved to some extent, but ultimately they are limited by two fundamental problems. Firstly, good parameter estimates require wide variation in the independent variables, which is rarely available. Secondly, other factors of which there are no records might be changing and affecting the catch independent of fishing effort, so that these analyses may provide a poor estimate of the degree to which variables, like effort, control catches.

A third alternative, adaptive management, represents a powerful approach for dealing with fisheries and ecological management (see Walters, 1986; Sainsbury, 1988; Hilborn and Walters, 1992) and has been suggested as particularly appropriate for coral reefs by several authors (Powers and Crow, 1982; Russ, 1991). It involves designing experiments to discriminate between a range of models and therefore, by extension, management actions. The essence of this approach is that instead of relying on research from outside, management takes upon itself to identify and answer problems directly.

Adaptive management is not a simple recipe for success, but is a highly flexible approach that tailors regulation to current needs and encourages constant improvement in management. Walters (1986) gives four basic issues involved in the designing of adaptive management strategies. First, problems, objectives and the limits on what management can achieve need to be defined. This should avoid wasted research effort on areas that management is unable to control or problems which are considered relatively unimportant. Second, quantitative models representing the current understanding of the fishery dynamics need to be proposed. This should produce explicit assumptions and predictions about the fishery so that current thinking can be tested. Third, uncertainty should be introduced, both in the form of observation and process errors for the current model, and alternative models against which the current model can be tested. The data obtained from monitoring the fishery can be used to constantly update models and therefore alter policies through learning. Finally policies should be designed not just for sustainable production, but also to test models and find ways in which production can be improved.

The particular advantage of adaptive management for coral reef fisheries lies in the low cost of obtaining accurate information, if different reef areas can be treated as nearly identical and independent (e.g. Lock, 1986b). While larger areas of coral reef are made up of replicate units, this assumption is not entirely true. Differences between reefs are probably not critical since these can be taken into account in the design of the experiment. The inter-dependence between plots is a more difficult problem. This will depend upon larval recruitment and migration, which in turn should affect appropriate time and spatial scales for experiments. Careful experimental design will be able to account for some interaction between different areas, but such interactions will reduce the amount of information obtained, and suggest the method will not be easy to implement. Although it still needs to be demonstrated that an experimental approach is appropriate to coral reef management in developing countries, it is likely that any drawbacks will be outweighed by the advantages. Adaptive management will allow managers to address their own research needs directly, providing guidance on problems which have so far defeated other methods.

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