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THE ASSESSMENT OF EXPLOITED STOCKS OF CORAL REEF FISHES



By John L. Munro

WorldFish Center PO Box 500 GPO 10670 Penang Malaysia Cover Photograph: Lyretail grouper (*Variola louti*), Blue-banded surgeonfish (*Acanthurus lineatus*), Whitecheek surgeonfish (*Acanthurus nigricans*), and Pale-lipped surgeonfish (*Acanthurus leucocheilus*)

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Contents

1.	Introduction	1
1.1.	Background	1
1.2.	Differences from and similarities to other benthic fisheries	2
1.3.	Stock assessments	6
2.	Data acquisition	7
2.1.	Catch statistics	8
2.2.	Fishery independent methods	8
2.2.1.	Routine test fishing for monitoring trends in stock sizes and mortality rates	8
2.2.2	Observational techniques	9
2.2.3	Depletion experiments	11
2.2.4	Effective area fished	11
2.2.5	Recruitment rates	12
3.	Parameter estimation	12
3.1.	Growth rates	13
3.1.1.	Length-based methods	13
3.1.2.	Hard structures	15
3.1.3.	Mark and recapture methods	18
3.1.4.	The Phi-prime growth performance index	19
3.2.	Mortality rates	20
3.2.1.	Total mortality rates	20
3.2.2.	Natural mortality rates	22
3.2.3.	Fishing mortality rates and catchability	25
3.3.	Population and biomass estimation	26
4.	Stock assessments	26
4.1.	Harvest per unit area	26
4.2.	Surplus production models	27
4.3.	Single-species assessments	28
4.4.	Multispecies assessments	29
5.	Ecosystem models	30
6.	Management of coral reef fisheries	31
7.	Summary and conclusions	33
8.	Acknowledgements	35
9.	References	36
Annov	1 Statement of work	

iv

The assessment of exploited stocks of coral reef fishes

1. Introduction

1.1. Background

There have been several reviews of methods for the assessment of coral reef fisheries in the past dozen years (Russ, 1991; Medley *et al.*, 1993; Appeldoorn, 1996; Munro and Polunin, 1997; Pauly, 1998) and one covering tropical fish stocks in general (Sparre and Venema, 1992). Additionally, Gulland and Rosenberg (1992) reviewed the use of length-based methods for assessing fish stocks. This review will therefore cover all basic topics but will concentrate on several areas where technical advances have changed our perspectives and enhanced our ability to understand the complex processes that occur in exploited coral reef ecosystems. The sampling methods for reef fish that underpin past scientific studies have been reviewed by Cappo and Brown (1996).

There has been much confusion in the literature over what is meant by a "coral reef fishery" or by a "coral reef fish". Clearly, the terms embrace fish that are found in intimate association with living corals. But large areas of coral reef ecosystems are not covered by living corals – rather, the coral is separated by areas of sand or soft sediments, often supporting stands of algae and seagrasses and, rarely, by rocky outcrops with a sparse cover of coral or algae. These intervening areas are the primary feeding grounds of many fish species that are seen on the reef by day and it is clear that, from a management viewpoint, the "super-ecosystem" that produces the fish should be managed as an entity, as suggested by Marshall (1985). This is because many exploited reef fish species are dependent to a high degree upon mangroves, seagrass beds or shallow reefs as nursery habitats and progressively move into deeper water with increasing size (Nagelkerken *et al.*, 2001).

The "super-ecosystem" extends from the beaches and mangroves of the landward fringe, across the seagrass and algae beds in the lagoons of fringing reefs and over the reef flats and down the

slope to the shelf (Munro, 1996). The shelf can be narrow and coral covered or very wide with scattered patch reefs or coral outcrops. The shelf can be bounded by a barrier reef and thus form a lagoon, in itself a complex system. Alternatively, the shelf can be bounded by a sill reef, that might rise from the shelf edge to least depths of 20-40 m. Beyond that is usually an abrupt dropoff to the deep reef, that extends to the edge of the bathyal zone at around 250 m. Oceanic banks or sea-mounts that extend into the euphotic zone can also have extensive coral cover and be inhabited by typical assemblages of reef fish, despite having least depths of 30-40 m. All of this habitat can be described as a "coralline shelf" (Munro, 1978b; Munro, 1984b; Munro, 1996) and is the entity that must be managed cohesively.

1.2. Differences from and similarities to other benthic fisheries

Almost all fishing gears capture many species simultaneously, a fact that was largely ignored in the management of the major commercial fisheries for many decades. In all tropical fisheries, very large numbers of species can be found in the catches, especially in the case of fisheries in and around coral reefs.

However, while tropical multispecies, multigear fisheries for fish and invertebrates have hundreds of species in the catch, it appears to be invariably true that a limited number of species, typically fewer than 20, constitute ~90% of the weight of the catch. For examples, see Munro (1983b), McManus *et al.* (1992), Smith and Dalzell (1993), Jennings *et al.* (1995), Jeffrey (2000) and Sary *et al.* (in press).

This also applies to fisheries that target snappers and groupers inhabiting relatively deep water with a limited array of gears, such as various hook-and-line techniques. Many species are found in these catches but <10 species make up 90% of the weight of the catch (Ralston and Polovina, 1982; Munro, 1983c; Nath and Sesewa, 1990; Mees, 1993; Pilling *et al.*, 2000; Pilling *et al.*, 2003). In all of these fisheries, single species assessments are of limited use and need to be

combined in some way, with each species weighted by value, to provide an optimized harvest strategy (Munro, 1983b; Polovina, 1989; Sparre and Venema, 1992).

Some coral reef fish stocks are harvested only for subsistence, but such fisheries are becoming rare. Most of the fisheries are in developing countries and are exploited at an artisanal level (Munro, 1999a). That is, the fish or invertebrates are harvested by small-scale fishers and sold at the landing place directly to consumers or to dealers who will distribute the catches more widely. The fishing gears often change seasonally and the principal methods used by individuals will depend on their preferences, their economic capital and personal skills. For example, in the Caribbean, some individuals will fish with hand-lines, either because they feel themselves to be particularly skilled in such fishing, or because they do not have the resources to purchase or construct fish traps. Others use combinations of gears on an opportunistic basis. Some gears target particular life stages. For example, small snappers might be caught by gill-nets in sea grass beds, sub-adults can be taken in traps on shallow reefs or large adults can be taken on hand-lines fished on the deep reef slopes. Such "gauntlet" fisheries dictate that fishing mortality rates in the stock are a function of size.

In all of these fisheries, species are targeted according to their desirability and value and may differ in their vulnerability to capture by particular fishing gears. Unfortunately, desirability, value and vulnerability are often a feature of a single species or family. For example, predatory groupers (Family Serranidae) are highly valued as food fish and will readily take hooks, become entangled in nets, enter fish traps (often in order to prey on fish already trapped) and provide a large and obliging target for spear-fishers. They aggregate to spawn and are vulnerable *en masse* at those times. They are also protogynous hermaphrodites, transforming from female to male at relatively large sizes, and males can become a rarity in heavily fished stocks (Sadovy and Colin, 1995). In contrast, herbivorous surgeonfish (Family Acanthuridae) share few of these traits. Thus, in heavily fished systems the classic trophic pyramid can become flattened and distorted as

the complex interspecific relationships and trophic structure of the ecosystem is affected by differential catch rates.

As fishing effort increases over time, catches of the most vulnerable species will peak and decline and a succession of species will become predominant in the fishery which ultimately becomes dominated by the least catchable and least desirable species, usually herbivores or small omnivores. This is illustrated in Figure 1.

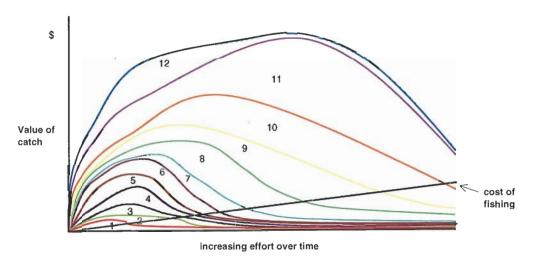


Figure 1. Hypothetical changes in the total value and composition of catches from a coral reef fishery in response to increasing fishing effort over a period of time and with no restriction on the type of gear or mesh size used. Species or groups 1-10 are arranged in declining order of their catchability and/or value. Group 11 might represent miscellaneous "trash fish" and Group 12 the sharks and rays. If the cost of fishing is low, there is no economic constraint that will prevent the most vulnerable species from becoming extinct, at least on a local scale. Adapted from Munro and Smith (1984).

Much interest has been generated in recent years over the degree of connectivity between stocks of marine organisms that inhabit circumscribed habitats, such as coral reef systems, that are separated by large areas of oceanic waters. Clearly, there is some degree of genetic exchange over the range spanned by a species and it is highly likely that many propagules are transferred between reefs that are separated by modest distances. In the latter case, the individual stocks are components of a metapopulation, linked by the spread of their propagules. It is also likely that some stocks on the edge of the range of a species will be "sinks" that are maintained by

upstream "sources". However, in the case of coral reef fish stocks there is no agreement on the degree to which stocks are maintained by self-replenishment (The term "self-recruitment" is avoided here because a "recruit" in conventional fisheries parlance means a fish that has reached the particular age or size at which it becomes vulnerable to capture). That some species are capable of self-replenishment is shown by the existence of species that are endemic to the shallows of isolated oceanic islands. The ability to self-replenish will be much dependent on oceanographic features of the area and on biological features of the adults and of the pelagic larvae (Sponagule *et al.*, 2002). Cowen *et al.* (2000) have argued that the wide dispersal of reef fish larvae originating from a single spawning area, combined with high mortality rates, will greatly reduce the chances of significant numbers of larvae reaching reefs elsewhere and that most will die in the open ocean.

Munro and Watson (1999) have shown that settlement rates of reef fish post-larvae on the heavily-exploited north coast of Jamaica are orders of magnitude less than settlement rates on reefs in the moderately-exploited British Virgin Islands. Furthermore, the only post-larvae that settle on Jamaican reefs in relatively large numbers are those of species that mature before recruitment to the local trap fisheries or larger species that have specialized oceanic pelagic larval stages, such as those of surgeonfishes (Acanthuridae) and goatfishes (Mullidae).

Triggerfishes (Balistidae) also have post-larvae that remain in the pelagic zone for extended periods and jacks (Carangidae) can do so opportunistically by associating with drifting objects.

The conclusion was that the reef fisheries around a relatively isolated island such as Jamaica are very largely dependent on the existence of adequate spawning stock biomasses in local waters.

The corollary is that overexploitation will lead to reduced recruitment to fisheries and, probably, to more variability in recruitment.

Doherty and Williams (1988) concluded that the abundances of most species of reef fishes were limited by the numbers of juveniles that successfully settled into the nursery habitat. Additionally, wide inter-annual variations in settlement rates have frequently been recorded for many species

of fishes in many habitats. This usually does not result in mass mortalities of the abundant yearclasses, suggesting that trophic resources are not normally limiting (Munro and Bell, 1997). Additionally, in exploited stocks in which spawning stock biomasses are significantly reduced, the most likely result will be reduced settlement rates within the area to which the pelagic propagules are dispersed.

1.3. Stock assessments

The purpose of work on fish stock assessment is to provide advice on the combinations of gear and fishing effort that will provide sustainable yields from a stock. These might be the maximum sustainable yield (MSY) or optimum sustainable yield (OSY) or any other level of harvest that is deemed to be desirable by policy-makers. Technically, the status of an exploited stock may lie between being under-fished (a combination of low fishing effort and large age or size at first capture) or over-fished (when effort is high and size or age at first capture is small). Yields in both situations will be less than that which is attainable. Additionally, over-fishing can progressively reduce recruitment to the fishery, leading to a long-term decline in harvests.

The actual catch that is taken from any fishing strategy will be proportional to the numbers of recruits to the fishery within the area under consideration. In the context of coral reef fisheries, this area might be as small as a particular shallow reef if the species is restricted to shallow waters or a much larger area if the species has a large depth range and can move between reef systems. Recruitment rates will be determined by spawning stock biomasses, events in the pelagic phase and post-settlement dynamics. Of these factors, only the maintenance of spawning stock biomasses at prudent levels is realistically within the control of fishery managers.

All of the conventional stock assessment methods described by Ricker (1975), Gulland, 1983, Pauly (1984d), Sparre and Venema (1992), Hilborn and Walters (1992), Gallucci *et al.* (1996) and Gayanilo and Pauly (1997) can be applied to individual species of coral reef fish and

invertebrates. Computer programs, such as FiSAT (Gayanilo *et al.*, 1996), now provide easy access to many of the analytical routines.

All methods require accurate data and parameter estimates. Data acquisition costs are proportional to the degree of sophistication desired. Herein lies the problem for coral reef fisheries managers, mostly located in developing countries, where governments are reluctant to spend large sums of money on the management of small scale fisheries that are not perceived to be of great value. This view is erroneous, however, as demonstrated by Sary *et al.* (in press) who showed that the cumulative cost of non-management of Jamaica's trap fisheries has amounted to US\$1.3 billion over the past 25 years.

2. Data acquisition

As stated above, all conventional methods of stock assessment can be applied to coral reef fisheries. Additionally, given the usual clarity of the water around coral reefs, the use of underwater visual census (UVC) techniques is feasible for estimating stock densities. However, the principal difficulty faced in assessing coral reef fisheries is the acquisition of the required data.

Gulland and Rosenberg (1992) give a good account of the basic approach to data collection, particularly for length-based methods. However, while the need for cost-effective data acquisition systems has long been recognized (Munro, 1983a), little real progress has been made in developing appropriate systems. The greatest problem that is encountered in gathering length-frequency or other biological data is the relatively low numbers of individual species taken in the catch, or delivered to a landing place, in a single day. Thus, obtaining a satisfactory size frequency sample can be expensive and time-consuming, particularly for the larger and more valuable species, such as snappers or groupers or spiny lobsters.

2.1. Catch statistics

Systems for collecting catch and effort statistics are highly advanced in many countries that have industrial-scale fisheries. However, there are very few countries in the coralline zones of the world that gather even the most basic catch data and this is almost invariably aggregated by families or into even broader groups and, consequently, is of very little value for the purpose of stock assessment. For example, data on the total landings of "snappers" may mask the fact that the larger species are being supplanted by small species of lower value. It would be of much greater value if managers of coral reef fisheries identified the top ~20 species in terms of value and concentrated on gathering statistics for those species. As stated previously, this subset of species represents a very large proportion of the total catch. In addition to monitoring the trends in landings of the major species, it would be necessary to include others that are of concern because of their large sizes and high abundances in the past (e.g. large serranids or lutjanids) or their status as threatened species (e.g. sharks and rays or ornamental species, such as angelfish). The remaining fraction can be aggregated as miscellaneous species "not elsewhere included" or "n.e.i." in the jargon of FAO.

This proposed course of action is now much easier because many guides to the identification of reef fish and invertebrates have been published in recent years, pertaining to all ocean areas.

This has simplified taxonomic problems that bedeviled collection of adequate statistics in the past.

2.2. Fishery independent methods

2.2.1. Routine test fishing for monitoring trends in stock sizes and mortality rates

Munro (1983a) advocated the development of cost-effective data acquisition systems that included an element of routine test fishing with standardized fishing gears to monitor trends in stock abundances. This theme was further developed by Munro and Fakahau (1993a). Such a system has been in effect in the Gulf of Thailand trawl fishery for many years (Pauly, 1979). However, no system of this sort is yet in effect in any coral reef fishery.

Although this could be a relatively expensive undertaking it would provide an independent measure of relative abundances, expressed as catch-per-unit-effort, and concurrently provide length-frequency data, spawning information and samples of otoliths. At little extra cost, fish captured by routine fishing done in shallow waters could be tagged and released and would provide an additional source of information on migrations, growth and mortality rates (see Section 3.1.3).

2.2.2. Observational techniques

Underwater visual census (UVC) techniques have reached a high level of sophistication (Samoilys, 1997; Cappo and Brown, 1996). The purpose of UVC is to obtain estimates of population densities and, if these are combined with estimated size frequencies, estimates of the biomass of individual stocks will be obtained. If additional data are available then biomasses can be divided into those of pre-recruits, recruited stock and spawning stock. Recent studies of reef fish using UVC in various parts of the world include those of Zeller and Russ (1998), Nunez-Lara and Arias-Gonzalez (1998); Friedlander and Parrish (1998), Letourneur *et al.* (2000); Kulbicki *et al.* (2000), Gust *et al.* (2001), Pet-Soede *et al.* (2001), Brainard *et al.* (2002) and Spalding and Jarvis (2002).

However, the reliability of fish counts can be variable (Watson *et al.*, 1995) and Samoilys and Carlos (2000) concluded that counts along transects or stationary point counts both yielded data that "were characterized by high variability, low precision and low power". Additionally, there is often a very poor relationship between the species composition that is observed by divers and that which is taken by fishers (Jennings and Polunin, 1995; Cole *et al.*, 2001) or between UVC estimates of abundance and catch rates (Connell *et al.* 1998; Kulbicki, 1995). On the other hand, Kulbicki *et al.* (2000) found a good relationship between UVCs and experimental fishing with handlines (in <20 m) and longlines in deeper water and obtained a good correlation between observed abundances and catch rates.

Differences between the numbers of fish observed and catch rates are often related to diurnal movements of some species to or from deeper water (Cappo and Brown, 1996). In other cases, acquired behavior of fishes can bias census results. Kulbicki (1998) found that fishes exposed to human disturbance avoided observers, that school size influenced detection either positively or negatively according to species, and that detectability decreased with fish size for most species. He concluded that studies using UVC methods "might have drawn erroneous conclusions, especially when comparing reserves with fished areas or when comparing different species or different size classes".

The use of tape recorders in UVCs has been shown to improve accuracy (Greene and Alevizon, 1989) and the use of underwater video improves speed and accuracy of censuses, particularly because evaluations can be done on shore and doubtful counts and identifications reviewed (Parker *et al.*, 1994). However, skilled underwater observers can often recognize behavioral features of species that are not identifiable on videotapes (E. DeMartini, pers. comm.)

Most of the catches of "coral reef fish" are taken in relatively deep waters on open shelves or in lagoons, very often at depths beyond the practical operating limits of SCUBA divers undertaking UVCs. Cappo and Brown (1996) suggest that a depth of 20 m represents the safe lower limit for routine UVCs and considered that UVC techniques are undoubtedly useful and can be precise for shallow-water species such as coral trout, but were of little utility for schooling lutjanids and lethrinids in deeper water between reefs. For species in which all, or a significant component, of the stock is in deep water, remotely operated vehicles (ROVs), submersibles, baited camera stations or other conventional capture methods are necessary for gathering the biological and fisheries data needed for assessing coral reef fisheries (Cappo and Brown, 1996). Willis and Babcock (2000) and Willis et al. (2000) found that baited underwater video stations or experimental handline fishing were much more effective than UVCs in detecting the presence of snapper, *Pagrus auratus*, while the reverse was true for blue cod, *Parapercis colias*.

Estimated fish lengths from UVC have been used to obtain estimates of biomass, although the accuracy of the estimates is highly dependent upon the training and experience of the divers (Bell et al., 1985). Harvey et al. (2002) have shown that the use of stereo-video systems greatly increased the statistical power to detect changes in the mean length of a fish stock and it seems likely that the use of such systems will increase.

There appear to have been no recent reports of the use of submersibles or remotely operated vehicles for populations assessments since Ralston *et al.* (1986) used a submersible to compare hand-line catch rates with observed bottom fish in deep waters at Johnston Atoll.

2.2.3. Depletion experiments

Depletion experiments have been undertaken in a number of fisheries in order to estimate stock abundances, all with a reasonable degree of success. Polovina *et al.* (1985) studied deep-reef fish stocks in the Marinas by intensive fishing of seamounts with hook-and-line and Smith and Dalzell (1993) depleted stocks of shallow-water reef fish in Yap, Federated States of Micronesia by intensive fishing with nets and spears. A different approach was taken by Gaudian *et al.* (1995) who did UVCs before and after a period of intensive hook-and-line fishing. The work produced credible estimates of initial stock densities and catchability.

2.2.4. Effective area fished

Techniques for estimating the effective area fished (EAF) by an item of fishing gear originated with the work of Eggers *et al.* (1982), in which gears were spaced at variable intervals to detect competition between them. Most work has been done in relation to various species of crustaceans caught in traps in temperate waters (Aedo and Arancibia, 2003, and references therein) and appears to have been widely successful. However, the methodology has not been applied to fish traps and, given the non-uniform topography of coral reefs, it might not be a viable technique in shallow waters.

Miller and Hunte (1987), Acosta *et al.* (1990) and Recksiek *et al.* (1991) obtained estimates of EAF by Antillean fish traps by comparing estimates of stock size obtained from UVC with the catch rates in traps. These works showed that it was possible to estimate EAF by this method. However, the estimated EAF appeared to vary with site and season. Consequently, the technique does not appear to hold promise of much utility.

2.2.5. Recruitment rates

The influx of pre-settlement stages of reef fish can be monitored using light traps (Doherty, 1987) and crest nets (Dufour and Galzin, 1993) but variations between sites and seasons can make this an expensive and manpower-intensive exercise. In contrast, UVC techniques can be used in nursery habitats to monitor the abundances of post-larval reef fish (Nagekkerden *et al.* 2001) but variability of settlement and survival between habitats, years and seasons make this an unrewarding exercise. Monitoring of selected sites with small-meshed fish traps might be useful for specific areas, such as fishery reserves (Watson and Munro, submitted). However, little is known about the processes that control survival rates between settlement and recruitment to the fishery.

3. Parameter estimation

The range of methods available for estimation of the parameters required for stock assessment are described by Ricker (1975), Pauly (1984d), Gulland and Rosenberg (1992), Hilborn and Walters (1992), Sparre and Venema (1992), Gallucci *et al.* (1996), Gayanilo and Pauly (1997), Hilborn and Mangel (1997), Pauly (1998) and Quinn and Deriso (1999).

3.1. Growth rates

3.1.1. <u>Length-based methods</u>

Simple graphical methods of estimating age and growth by following modal progressions in length frequency samples date from the early years of fisheries science. The work of Pauly and David (1981) in developing the first computerized method for "the objective extraction of growth

parameters from length-frequencies data" (ELEFAN I) provoked much interest and debate and led in turn to the development of alternative approaches (Shepherd *et al.*, 1987) and refinements (Pauly, 1987). The robustness and reliability of length-based methods in general, and of growth parameter estimation in particular, were reviewed in much detail by Pauly and Morgan (1987) and by Gulland and Rosenberg (1992). An alternative system, MULTIFAN was developed by Fournier *et al.* (1990) and further refined, as MULTIFAN-CL, by Fournier *et al.* (1998).

If fishes have a restricted spawning season and grow quite rapidly with little individual variation and no size-selective mortality, then large, non-selective, length-frequency samples will show clear modes that represent individual year-classes, possibly over several years. Monthly samples will show modal progressions that reflect growth and these can be plotted to describe a growth curve. In the case of coral reef fishes, and other tropical species, the reality is somewhat different. Although spawning seasons are fairly well-defined for most species, for many species some spawning can occur on a daily basis and settlement from the pelagic stage and recruitment to the fisheries can take place over extended periods. Individual growth rates can be quite variable and year-class failures are commonplace. Additionally, it can be exceedingly difficult to obtain large, non-selective, length-frequency samples on a regular basis. The consequence is that modal-progressions in periodic length-frequency samples are often difficult to follow and present a wide variety of alternative interpretations. Hence the need for an objective method that will reveal the growth curve that best describes the data; most commonly expressed in terms of the von Bertalanffy growth equation:

$$L_t = L_{\infty} (1 - e^{-K(t-t_0)}),$$

in which L_t is the length, L_t , at age t, L_{∞} is the asymptotic length, K is the growth coefficient and t_0 is the theoretical age at which $L_{\infty} = 0$ if the equation applied to all ages. A number of alternative growth models have been developed (Quinn and Deriso, 1999) that might better describe growth over the exploited phase, but have not been widely used in stock assessments.

The perceived problem with the ELEFAN I program is that it will produce a best fit to *any* data set, irrespective of the adequacy of the sampling programme. Additionally, no confidence limits are generated. Consequently, in unskilled hands it is liable to produce inaccurate results and, if used in stock assessments, the results can lead to incorrect decisions. However, the same problem is encountered in pencil-and-paper methods and the solutions lies in adequate training of the user.

The ELEFAN I program prompted the development of Shepherd's Length Composition Analysis (SLCA) (Shepherd *et al.*, 1987) which is conceptually similar to ELEFAN I. A modified version of SLCA (Pauly and Arreguin-Sanchez, 1995) is included in the FiSAT package and is stated to give near-identical results to those produced by ELEFAN I (Gayanilo and Pauly, 1997).

The MULTIFAN program had a different genesis, originating with the work of MacDonald and Pitcher (1979), Schnute and Fournier (1980) and Fournier and Breen (1983), who derived growth, age composition and total mortality estimates from single length-frequency samples. The MULTIFAN program (Fournier *et al.*, 1990) derives growth parameters and age compositions from multiple length-frequency samples.

Comparisons have been made between the length-based models by a number of investigators (Rosenberg and Beddington, 1987; Castro and Erzini, 1988; Basson *et al.*, 1988) and the findings were summarized by Terceiro *et al.* (1992). The basic conclusions were that ELEFAN I and SLCA are both sensitive to increasing variation in length at age (which results in multiple age-classes in the larger length groups), that SLCA tended to produce somewhat elevated estimates of the growth coefficient, K, and that ELEFAN I, tended to underestimate both K and L_∞.

Terceiro *et al.* (1992) compared the performance of the original version of SLCA and MULTIFAN, on simulated distributions of exploited stocks with 3 to 13 age classes. They concluded that "as a quick and simple method to examine length-frequency distributions, SLCA provided a good return for the amount of computational resources invested with limited user input". They considered

MULTIFAN a "more complex but more powerful estimation technique with a formalized set of rules for a more objective evaluation of alternative interpretations of the length-frequency data". They suggested that SLCA should be used to obtain initial estimates of the parameter range, followed by application of MULTIFAN. The improved version of SLCA (Pauly and Arreguin-Sanchez, 1995), which gives clearer goodness of fit estimates, should now be used.

No application of MULTIFAN to reef fish species has been reported to date, but it is routinely used for tuna assessments by the SPC (P. Dalzell, pers. comm.) and has also been used for blue shark stock assessment (Kleiber *et al.*, 2001).

MULTIFAN has been extended as MULTIFAN-CL (Fournier *et al.*, 1998), a model that can be used to estimate age composition, growth parameters, mortality and recruitment rates, given inputs of a time series of data on catch and effort in the fishery and length-frequency data. It provides confidence intervals for the estimated parameters. To date, the only published application is to the South Pacific albacore (Fournier *et al.*, 1998) but it is now routinely applied to other tuna species, marlin and swordfish by the SPC (P. Dalzell, pers. comm.; see www.spc.int/oceanfish/html/sctb/sctb15/index.htm). However, there is no reason why it should not be applicable to reef fish stocks, other than the perennial difficulty of obtaining adequate data sets.

3.1.2. Hard structures

The presence of annual rings in otoliths, on scales and in other bony structures has been recognized for many years and otoliths of temperate water fishes have been routinely used to determine age structures of exploited stocks. In coral reef fish, periodic rings have been observed in many species. Munro and Thompson (1983) reported that most species of exploited coral reef fish in Jamaican waters showed some periodic marks and concluded that "given sufficiently large samples taken over the course of some years, it is likely that age and growth estimates could be made for many species".

Pannella (1971, 1974) identified daily rings in fish otoliths. This gave much impetus to age estimations based on daily and annual rings (Gjøsaeter *et al.*, 1984). However, with few exceptions the work has been done in developed countries with access to adequate funding, sophisticated equipment and highly trained staff (Ralston and Williams, 1988; Morales-Nin and Ralston, 1990).

Daily rings have now been reported for a large number of species of coral reef fish (Ntiba and Jaccarini, 1988; Allman and Grimes, 2002; Robertson *et al.*, 1999; McCormick, 1999; Szedlmayer, 1998). The methods have been developed to a high level of sophistication (Iglesias *et al.*, 1997; Morales-Nin *et al.*, 1998) and computerized systems that count daily rings by reading the relative transmission of light through sectioned otoliths are now commercially available and there are age-reading services available in North American and Europe. Counting daily rings in large otoliths is difficult and the system has the greatest utility in determining the ages of juvenile fishes (Ralston *et al.*, 1996). Marks can be detected that indicate the time of settlement from the pelagic phase and thus can reveal the duration of the pre-settlement phase, the date of settlement and the actual age at recruitment to the exploited stocks (Campana and Thorrold, 2001).

Processing techniques for otoliths have also been progressively improved (Cowan *et al.*, 1995) and annual rings have been reported for lutjanids, lethrinids, serranids, scarids and pomacentrids. (Bullock *et al.*, 1992; Davis and West, 1992; Sadovy *et al.*, 1992; McPherson and Squire, 1992); Ferreira and Russ, 1992; Ferreira, Russ, 1993; Morales-Nin, 1994, Fowler 1995; Williams *et al.*, 1995; Choat and Axe, 1996; Hart and Russ, 1996; Newman *et al.*, 1996; Newman *et al.*, 2000a, b; Luckhurst *et al.*, 2000; Newman *et al.*, 2000a,b; Cappo *et al.*, 2000 a,b; Marriott and Cappo, 2000; Pilling *et al.*, 2000; Newman and Dunk, 2002). Generally, this work has been done in areas with significant seasonal temperature variations such as the Great Barrier Reef. However, the work of Pilling *et al.* (2000) on lethrinids and lutjanids was based in the central Indian Ocean and

included species inhabiting deep water where seasonal changes in temperature would be expected to be minimal.

Templeman and Squires (1956) found that there was a relationship between the age of haddock and otolith lengths and weights. However, this topic seems to have not been pursued until Fletcher (1991) observed that there was a relationship between otolith weight and age in the pilchard, *Sardinops neopilchardus*, in Western Australia. Subsequently, a substantial amount of work was done on this topic.

It has been found that otolith weight was a good predictor of age in *Lutjanus* synagris (Luckhurst *et al.*, 2000) and in *Lutjanus russelli* (Newman and Dunk, 2002). Additionally, Pilling *et al.* (2003) have examined the possible use of otolith weights as a predictor of age in *Lethrinus mahsena* and several other commercially important Indian Ocean scarids (2 species), lethrinids (2 species) and a serranid. They found significant variation in the age:otolith weight relationship in *L. mahsena*. Consequently, otolith weight was not a precise indicator age. However, they found that using otolith weights to estimate age frequencies produced distributions that did not differ significantly from distributions derived from counting otolith increments. They therefore concluded that this was a practical and economical method of assessing age structures of this species. The other species examined by Pilling *et al.* (2003) all produced significant age:otolith weight regressions and they concluded that precise relationships could also be derived for these species, given the required investment. Similarly, Strelcheck *et al.* (2003, and references therein) showed a relationship between otolith weight and standard length and age in *Mycteropera microlepis* (Serranidae).

Studies of otoliths of a variety of species have shown that many species of coral reef fishes have high growth coefficients, variable asymptotic lengths and high longevity. The latter feature was regarded with some surprise but has now been widely confirmed. Unexploited stocks of snappers, for example, have been shown to include around thirty year classes. The consequence

has been that the recruitment variability that is a feature of reef fish (and other) stocks only becomes apparent when the stocks are heavily exploited and the failure of a year class results in a significant reduction in catches.

3.1.3. Mark and recapture methods

Methods for deriving growth rates from mark and recapture data are well established and include techniques developed by Gulland and Holt (1959), Fabens (1965), Munro (1982) and Appeldoorn (1987). All are presented in the FiSAT package (Gayanilo *et al.*, 1996). Additionally, Laslett *et al.* (2002) have developed a sophisticated methodology for fitting generalized growth curves to tagrecapture data, with application to southern bluefin tuna. However, given the difficulty of acquiring data for coral reef species, the benefits of using growth curves that cannot be expressed in terms of the von Bertalanffy equation and cannot be used in conventional yield equations, would appear to be limited.

Munro (1999) reported that for the routines included in FiSAT, a preliminary estimate of the asymptotic length, L_{∞} , can be made for each species, based on published estimates of L_{∞} or on the maximum known size, L_{max} , in which case an approximation is $L_{\infty} = 0.95L_{max}$. The Fabens routine can be used to make estimates of L_{∞} and the growth coefficient, K, and to check for the presence of errors or anomalous data points. If the estimates of L_{∞} correspond reasonably well with the preliminary estimates and no anomalous data points are detected, Appeldoorn's method for defining seasonally oscillating growth curves can be used based on default values. Results are generally similar to those given by the Fabens method. Where the resulting estimates of L_{∞} differed markedly from known values of L_{∞} or those derived from L_{max} , the value of L_{∞} can be fixed and the growth coefficient, K, then estimated using Appeldoorn's method. If data are very sparse, or the Fabens method will not converge, Munro's method can be used to obtain an approximation of the growth parameters.

A mark and recapture programme executed within a small marine fishery reserve in Jamaica using Antillean fish traps produced growth estimates for 15 species of reef fish (Munro, 1999b). Marked fish that were captured within the reserve were released and in many cases repeatedly recaptured. Of 6,949 fishes marked, 5,690 recaptures were made, with the high recapture rate being attributable to repeated catches of individual fishes. Consequently, this was a very cost effective exercise. A similar study has recently been undertaken in two Kenyan marine parks (Kaunda-Arara and Rose, submitted). Additionally, a mark-and-recapture study using Antillean fish traps was undertaken in Kavieng, Papua New Guinea and similarly produced high rates of recapture (A. Wright, pers. comm.).

In Hawaii, a low cost mark-and-recapture program, focused on carangids, has had anglers tagging and releasing fish. A return of ~10% was reported, providing information on movements and growth rates (Tagawa and Tam, 2001)

3.1.4. The Phi prime growth performance index

If growth is expressed in terms of the von Bertalanffy equation, a growth performance index can be calculated;

$$\Phi' = \log (K) + 2 \log (L_{\infty})$$

in which K is the coefficient of growth and L_{∞} is the asymptotic length and Φ 'is the growth performance index (Pauly and Munro, 1984).

This has been shown to have a narrow range of variation within genera and families of fishes. If the maximum size of a species is known, and Φ ' is known, then an approximation of K can be calculated. For example, Dalzell *et al.* (1992) obtained values of L_{∞} and K for lethrinids from the literature, derived Φ ' and then estimated K for the species that they were assessing.

3.2 Mortality rates

3.2.1. Total mortality rates

Mortality rates can be derived from four sources of data: age frequency analyses, length frequency analyses, mark-and-recapture data and mean weights of individuals in the catch. All analyses can be confounded by migration from the area sampled but this is perhaps less of a problem in reef fish than in species occupying unbounded habitats, provided that the full depth range of the species is covered.

The increasing use of otoliths for estimation of age and growth rates has permitted the direct estimation of total mortality rates from age frequency data, assuming that samples are non-selectively obtained and representative of the stock as a whole. Most results to date are for a wide variety of exploited Australian snappers (Lutjanidae) (Davis and West, 1992; Newman *et al.*, 2000a,b; Newman and Dunk, 2002; Newman, 2002).

In the absence of large samples of aged otoliths or other bony structures, representative annual average length-frequency samples can be used to estimate total mortality rates. The original equation was

$$Z = K \cdot (L_{\infty} - L_m) / (L_m - L_c)$$
 (Beverton and Holt, 1957)

in which Z is the coefficient of total mortality, K is the coefficient of growth, L_{∞} is the asymptotic length, L_m is the mean length of fully recruited fishes and L_c is the length at full recruitment. This estimator, along with variants, is included in the FiSAT package. However, its usefulness has been supplanted by the development of length-converted catch curves (Pauly, 1984a,b,c), for which routines are also provided in the FiSAT Package (Gayanilo and Pauly, 1997).

Many estimates of mortality rates based on length converted catch curves have been published.

The plots of catch curves are surprisingly robust and excellent fits of points to the linear descending arm of the catch curve are often obtained from relatively small sample sizes. This can be misleading. It is essential that sample sizes are adequate and are representative of the annual

average length composition of the stock. The same limitation applies to age-structured catch curves and it is probably easier to get a very large representative length-frequency sample than to get an age-frequency sample. However, the accuracy of the estimate of Z is highly dependent upon the accuracy of the growth parameter estimates (K, L_{∞}) (Isaac, 1990). High variability in individual growth rates (common in many species of fishes) also limits accuracy, as do seasonal growth oscillations of short-lived species. A routine in FiSAT corrects for the latter factor.

In the absence of reliable estimates of K, the ratio Z/K can be obtained from length-converted catch curves by arbitrarily setting the value of K at 1. The slope of the catch curves then equals Z/K, and this parameter can be used in stock assessments.

The development of accurate ageing of coral reef fishes leads to the possibility of combining reliable estimates of K and L_{∞} with large length frequency samples to obtain good estimates of total mortality rates from length-converted catch curves. An unanswered question concerns the degree to which growth rates are variable between areas and along latitudinal gradients. If variability can be shown to be limited, then growth parameter estimates obtained in one area could be used to obtain mortality estimates from length-frequency data collected in other areas.

Age-based or length-converted catch curves do not necessarily have linear descending arms. If samples are truly representative of the stock, the descending arm should reflect age- or size-specific mortality rates. For example, if fish become too large to pass through the entrance funnel of traps the larger fish should have a lower mortality rates. Also, if fish migrate out of the exploited habitat at a particular size, the catch curves should show an increase in apparent Z, that reflects the outmigration.

Estimating mortality rates from mark-and-release data is difficult because estimates can be compromised by tag loss or tagging-induced mortality, either because of increased vulnerability to capture or due to physical damage caused by tags. Tag loss can be estimated by double-tagging

a proportion of fish. However, this increases the injury to the fish. Mark-and-recapture data based on conventional tags should therefore be used with some degree of caution. Coded microwire tags, that minimize injury to the fish, provide a partial solution to the problem but require special detectors to identify marked fish and this limits their applicability.

The total mortality rate can also be derived from the mean weight of individuals in the catch (Gulland, 1969), provided that the growth parameters and age at first capture are accurately known and the sampled weights are unbiased. Mean weight is a statistic that is fairly easily derived. However, it has seldom been used in stock assessments.

3.2.2. Natural mortality rates

Being small is very dangerous. It has become more evident that M changes with size and age and also when the fish community is exploited and the trophic pyramid is flattened. For example, in Jamaica the stocks of most predatory reef fish have been drastically reduced, except moray eels. Consequently, natural mortality rates must be greatly reduced when compared to stocks in unexploited reefs and, furthermore, must decrease with increasing size as the numbers of predators capable of catching and swallowing a particular fish decrease.

Changes in natural mortality rates have been modeled using the Weibull hazard function (e.g. Appeldoorn, 1988; Caddy, 1991). This equation is

$$M = dt^{c-1}$$

in which M is the coefficient of natural mortality, t is age and c and d are constants.

This function predicts that the logarithm of natural mortality, M, is linearly related to the logarithm of age, with the rate of change declining strongly with increasing age.

Using a different approach, Watson *et al.* (2002) modelled observed post-settlement decreases in the abundance of yellowtail snapper, *Ocyurus chrysurus*, to calculate M day⁻¹ at settlement and the rate of reduction of M with increasing age. The equation is

$$D_t = N_r (1 - e^{-(M + m.t)})$$

in which D_t is the cumulative number of deaths at time t, N_r is the initial number of fish in a single cohort that settles at t=0, and m is the amount by which M decreases each day. $D_t=N_r$ at t_∞ when the last survivor dies. These results also show that M decreases exponentially with age and size.

It is believed that decreasing mortality rates with increasing age or size are a feature of most ecosystems and this is widely applicable in a complex ecosystem such as a coral reef, where the numbers of potential predators decline with increasing size of all potential prey species. Mortality rates would be expected to increase as senility is approached, but few fish seem to attain extreme longevity. Furthermore, as all reef fish species settle from the plankton at relatively small sizes, most species are potential prey of all predatory species at some point in their lives. There are few estimates of age dependent mortality rates for any species. Fournier *et al.* (1998) used increasing rates of age-dependent natural mortality to improve the fit of the MULTIFAN-CL model to data for South Pacific albacore, *Thunnus alalunga*.

Natural mortality rates of stocks of reef fish at unexploited parts of Pedro Bank in the Caribbean in 1969-73 were derived from size frequency analyses (Munro, 1983b). Estimated rates were high and were presumed to reflect the very high biomasses of predatory species that were present at that time. For stock assessment purposes, observed natural mortality rates were presumed to be reduced in proportion to predator biomasses in exploited areas. However, there is no proof for this simplistic assumption. Worldwide, very few pristine coral reef fish stocks remain and the opportunity to replicate the type of observations that were made at Pedro Bank are now greatly diminished. Important exceptions are the unexploited reefs of the North-west Hawaiian Islands and Kingman, Palmyra, Howland, Baker and Jarvis Atolls in which current UVC work, described by Brainard, Laurs and Associates (2002) could provide a basis for estimates of natural mortality rates.

Estimates of mortality rates of two small, unexploited species of snappers were obtained by Newman *et al.* (1996). The rates were M = 0.235 for *Lutjanus adetii* and M = 0.154 for *L. quinquelineatus*. Newman *et al.* (2000b) obtained estimates of M for unexploited stocks of *Lutjanus carponotatus* (M = 0.199) and *L. vitta* (M = 0.342) on the Great Barrier Reef and Newman and Dunk (2002) estimated M = 0.152 in an unexploited stock of *L. russelli* in western Australian waters. Additionally, Hart and Russ (1996) have estimated mortality rates of M = 0.15 in unexploited stocks of *Acanthurus nigrofuscus* on the Great Barrier Reef, and somewhat greater rates in stocks that had been impacted by outbreaks of crown-of-thorns starfish.

Munro (1999b) obtained estimates of M from length-converted catch curves for a variety of species in a small fishery reserve in Jamaica. In this case the reserve was very small (27.5 ha) and mostly shallow nursery habitat and outmigration was a component of the estimates of M. Nevertheless, the study suggested that the collection of length-frequency data by catch-measure-and-release programmes in protected areas would be valuable in obtaining estimates of M.

If a time series of estimates of Z and the corresponding fishing effort, f, are available, then a plot of the regression equation

$$Z = qf + M$$

should yield a straight line in which the slope, q, is the catchability coefficient, equivalent to the mortality caused by one unit of fishing effort. M is the y-axis intercept. However, Arreguin-Sanchez (1996) has shown that q is quite variable in response to stock size and the foregoing equation should therefore be used with caution.

Several empirical methods have been developed to estimate natural mortality rates, based on growth coefficients, maximum size or maximum age (Hoenig, 1983; Pauly, 1980; Ralston, 1987) and have been widely used. The equation of Hoenig produced estimates of M that were very similar to those obtained from age-structured catch curves for *Lutjanus carponotatus*, *L. vitta*, *L. erythropterus*, *L. malabaricus and L. sebae* (Newman *et al.*, 2000a,b; Newman, 2000a) and for *L.*

russelli (Newman et al., 2000a), whereas that of Pauly (1980) yielded estimates that were much greater that those obtained from age-structured catch curves. Newman et al. (1996) reported that the empirical equation of Ralston (1987) gave even more divergent estimates of M than that of Pauly.

In cases where stocks are exploited with very selective gears the pre-recruits to the fishery suffer only natural mortality and the total mortality rate will increase progressively as fishes become fully recruited to the fishing gear. Beyond full recruitment, the slope of a length-converted catch curve will reflect the total mortality rate of the stock. Munro (1984a) proposed a method for estimating natural mortality rates based on the above observations, provided that the selection curve was known. The method was subsequently improved by Moreau (1988). The method would appear to be applicable to reef fish stocks that are exploited by wire-mesh fish traps. However, there have been no applications of the method to coral reef fish to date.

3.2.3. Fishing mortality rates and catchability

Fishing mortality rates, F, have most usually been derived by subtracting independent estimates of M from Z and catchability estimated by dividing Z by f. Thus

$$Z = F + M = qf + M$$
 (Garrod, 1967).

Depletion experiments such as those of Polovina *et al.* (1985), Smith and Dalzell (1993) and Gaudian *et al.* (1995) also provide direct estimates of q. Other estimators are given by Ricker (1975) and there appear to be few recent developments that are applicable to reef fish.

3.3. Population and biomass estimation

As discussed in section 2.2, estimates of population and, more importantly, biomass (B) can be obtained from fishery independent techniques. If catch (C) statistics are also available, then rates of exploitation, E = C/B = F/Z, can be estimated and rapid progress can be made towards a full assessment of the status of a stock, subject always to be usual caveats about the accuracy of

estimates of C, B, and Z. If estimates of biomass have very wide confidence limits (e.g. Kulbicki, 1995) it will be difficult to get useful estimates of E without additional sources of information.

4. Stock assessments

4.1. Harvests per unit area

It is self-evident that harvests from a given area of land are bounded by the ecological conditions of the area, the fertility of the soil, the stock or crop densities and the biology of the animals being farmed or the crop that is grown. Aquatic habitats are no different and the amount that can be extracted from a given area in a given time is circumscribed by the same limiting factors.

Coralline shelves, as described in Section 1.1, are complex and studies of harvest per unit area have been bedeviled by confusions over the depth contours to be included and whether or not the species concerned are "reef fish". Nevertheless, if the stocks that are encompassed, and the depth zones, are clearly described, a planimeter and a nautical chart can give a useful approximation of likely upper bounds of production (Munro, 1978b).

There have been a number of compilations of such estimates (Marten and Polovina, 1982; Munro, 1984b; Marshall, 1985; Medley *et al.*, 1993; Nielson *et al.*, 1999; Dalzell *et al.*, 1996). Harvests in excess of 20 t km⁻²year⁻¹ have been reported for areas of coral, reef flat and seagrass beds from which a very wide range of fish and invertebrates are harvested. Shallow reef flats produce more than 10 t km⁻²year⁻¹, even when overfished, and coralline shelves below the shallow reefs generate harvests of 1-3 t km⁻²year⁻¹ (Munro, 1996). Sary *et al.* (in press) found that the coral reef fishery in the vicinity of Discovery Bay, Jamaica, is producing a harvest consisting mainly of small herbivores and invertebrate-consuming fish totalling over 5 t.km⁻²year⁻¹, despite gross overfishing and degradation of the reef ecosystem. Far lower production rates are achieved if only a limited array of predatory species are targeted, as on the Great Barrier Reef.

4.2. Surplus production models

Surplus production models developed by Schaefer (1954) and Fox (1970) were developed for single species assessments, in which catch rates are regressed against fishing effort to obtain a linear regression from which a parabolic yield curve can be obtained. Variants were developed by Csirke and Caddy (1983), Garcia *et al.* (1987) and Caddy and Garcia (1982).

Such models have been applied to the total biomass harvested in a fishery (Sparre and Venema, 1992). In such cases the catch rates usually decline exponentially, as in the Fox model. With increasing fishing effort, the yield curve takes an asymmetrical form, with the right-hand side of the curve declining progressively and only reaching zero at extremely high levels of fishing effort. This asymmetrical form can be attributed to reduced mortality rates of prey species as predator biomasses are reduced and perhaps to increasing growth rates because of lowered stock densities. However, at extreme levels of fishing effort, recruitment failures of the most vulnerable species would herald a progressive exponential decline in total catch caused by successive local extinctions of species until the last was eliminated. Fortunately, economic constraints would preclude that level of fishing effort but loss of biodiversity can be a consequence of even modest levels of fishing effort in a multispecies fishery.

A variant of the Fox model was developed by Munro and Thompson (1983) for the Jamaica coral reef fishery, in which fishing effort per unit area (fishing intensity) was regressed against the catch rates obtained in ecologically-similar areas in the same year. This concept was extended by Munro (1978a), Ralston and Polovina (1982), Csirke and Caddy (1983), Bayley (1988) and Dalzell and Adams (1994). A composite model was developed by Polovina (1989) that incorporates both space and time and non-equilibrium effects. With regard to this model, Polunin et al. (1996) stated that "with such a powerful tool tropical reef researchers can now estimate sustainable yield wherever enough replicates can be found in time and space". Unfortunately, the needed replicated data remain extremely scarce.

4.3 Single-species assessments

The yield-per-recruit assessment models of Beverton and Holt (1957), the yield-stock prediction model of Thompson and Bell (1934) and Virtual Population Analyses(VPA) (Gulland, 1965) can, of course, be applied to any species of coral reef fish, given the necessary catch statistics and parameter estimates. Length-structured VPA additionally requires good catch-at-length data. However, unless the species in question is of extraordinary value and can be managed separately (spiny lobsters, for example), these formulations are of little use. All of these applications are included in the FiSAT suite of computer programs (Gayanilo *et al.*, 1996; Gayanilo and Pauly, 1997).

4.4. Multispecies assessments

Multispecies formulations of the Beverton and Holt (1957) yield-per-recruit (B&H Y/R) model have been developed by Munro (1983b), Murawski (1984), Shepherd (1988), Silvestre and Soriano (1988), Polovina (1990) and Munro *et al.* (in press). In its simplest form, this consists of summing the yield curves, assuming a single price/kg for all species (Silvestre and Soriano, 1988). Alternatively, the yield curves can be expressed in terms of the value of each species to give weighting to the most valuable species in the catch (Munro, 1983b).

In applying the B&H Y/R model to reef fish stock in Jamaican waters, Munro (1983b) reduced the natural mortality rate, M, from the levels existing in virgin stocks in proportion to the biomass of predators remaining in the system. This is a fairly simplistic approach and no way has been found of testing this assumption. Additionally, it can be expected that growth rates might change in response to decreased stock densities and that mortality rates of larger individuals of prey species might be reduced as a result of reduction of the average size of the predators. These changes cannot be modelled at this stage. However, if realistic and detailed Ecopath models (see Section 5) of exploited reef systems can be developed, a better understanding of the response of prey species to the reduction of predator stocks might be achieved.

An important feature of the B&H Y/R model is that Pauly and Soriano (1986) have shown that the yield curves are highly sensitive to the value taken for L_c, the size at first capture, if the fish are small in relation to the size range covered by the selection curve. This has to be compensated for in the assessments (Silvestre and Soriano, 1988; Silvestre *et al*, 1991). This might be of importance in the application of the B&H Y/R equation to some reef fisheries, such as those using fish traps.

Alternative formulations have been developed that deal with multispecies fisheries in which different gears compete for the same stocks and there are no ecological interactions between the species (Murawski, 1984). This model was developed for a group of predatory species on Georges Bank and would not seem to be applicable to a multi-species, muti-gear coral reef fishery. However, it might be applicable to the more specialized deep-water snapper and grouper handline and trap fisheries, in which the target species are at similar trophic levels. Similarly, Shepherd (1988) combined yield-per-recruit calculations for interacting stocks (cod and haddock) and allowed for predatory interactions between the stocks.

Multi-species Y/R assessments can also be made using the FiSAT software (Gayanilo *et al.*, 1996; Gayanilo and Pauly, 1997). This model is an extension of the Thompson and Bell (1934) model. It does not allow for species interactions. The model requires substantial amounts of data and there have been no attempts to apply the model to coral reef fisheries.

Christensen (1995) developed a multi-species virtual population analysis that was applied to a fishery in Lake Tanganyika. This was developed from the multi-species length cohort analysis of Pope and Yang Jiming (1987). These models require information on diets in addition to size-frequency and catch data and were essentially precursors to ecosystem models.

5. Ecosystem models

Early attempts at ecosystem models such as those of Andersen and Ursin (1977) were extremely complex and required a huge array of inputs. However, the development of the first Ecopath model by Polovina (1984a) and its application to the reef system at French Frigate Shoals in the NW Hawaiian Islands chain (Polovina, 1984b) led to the development of Ecopath II (Christensen, 1991; Christensen and Pauly, 1992) and its widespread application to aquatic ecosystems (Christensen and Pauly, 1993), including coral reefs.

To date, over 140 Ecopath II models have been developed; some reported in the primary literature, others informally. However, only two reef systems have been described in detail: the Bolinao reef in NW Luzon in the Philippines (Pauly *et al.*, 1993; Alino *et al.*, 1993) and the fringing and barrier reefs of the Tiahura sector at Moorea, French Polynesia (Arias-Gonzalez *et al.*, 1998). Additionally, (Opitz, 1993, 1996) developed composite models of Caribbean reef systems, based mainly on biological data from Puerto Rico and the U.S. Virgin Islands, and on trophic data on invertebrate groups extracted from a wide array of literature.

Unfortunately, there have been few recent studies on the trophic ecology of coral reefs and researchers have relied largely on data collected at Eniwetok Atoll (Hiatt and Strasburg, 1960; Hobson and Chess, 1978), in the Hawaiian Islands by Hobson (1974, 1974, 1975) and in the U.S. Virgin Islands (Randall, 1967) and a few more specific studies by Randall and co-workers (Randall, 1965; Randall and Warmke, 1967; Randall and Hartman, 1968; Randall *et al.*, 1978; Randall and Brock, 1980; Randall 1980). Clearly, there is a need for additional studies of trophic relationships in coral reefs before the Ecopath model can be widely applied.

The need for additional studies is emphasized by the development of Ecopath-with-Ecosim (Walters *et al.*, 1997), which enables dynamic simulation models to be run on the mass-balance models produced by Ecopath II. This will enable scientists to predict changes in exploited fish communities in response to management measures, to verify the accuracy of such predictions

and, ultimately, to advise managers of the likely outcomes and consequences of management decisions. Details of the Ecopath program and of work in progress are available at www.ecopath.org.

6. Management of coral reef fisheries

The options available for the management of tropical coastal fishery resources in the tropical Pacific were reviewed by Munro and Fakahau (1993b), with emphasis on coral reef fisheries. The options available in the Indian Ocean and the Caribbean are no different. These include traditional management practices (where they exist), community-based systems, or administrative measures that aim to restrict harvests. These include minimum size limits, catch quotas, seasonal closures, maximum size limits and protection of spawning stock (e.g. berried female lobsters). Additionally, gear restrictions can be implemented, areas can be closed to fishing or limited entry systems enforced. Strategies that aim to influence the fishery by the introduction of taxes or subsidies, by pricing or marketing directives are other options, but have to be approached with great caution lest they yield unexpected consequences. Finally, the development of alternative fisheries has often been advocated, usually to get the fishers "offshore", but with a poor record of success. However, the emplacement of fish aggregating devices (FADs) in deep water has had some success in a number of countries.

The development of fisheries enhancement systems has been considered as a possibility for supplementing natural recruitment and increasing catches. The issue is discussed by Munro and Bell (1997), who point out that this can only be possible in the context of a well-managed fishery. Aquaculture development has also been advocated as a means of reducing pressure on fish stocks and, while successful in some cases (e.g. *Eucheuma* cultivation), it has most often been beneficial in providing income for the community and has not directly reduced impacts on fish stocks.

Clearly, all management strategies need to be tailored to the needs of the fishing communities, the consumers and the interests of other stake-holders (hoteliers, dive operators, sport fishers, etc.). Management measures that do not have widespread support will always be difficult to enforce and the best systems will be those in which the community perceives the benefits of the management measures and persuades recalcitrant fishers to conform with the law, with the involvement of officialdom kept to a minimum. This involves extensive community education and the provision of a stream of information. Failure to do this is the primary reason why almost all coral reef fisheries, worldwide, remain unregulated. The costs of management are consequently quite high. However, as mentioned previously, the costs of non-management are staggering and the cumulative cost of not managing Jamaica's fisheries is estimated to have amounted to US\$1.3 billion, over the 25-year period since management strategies were first recommended (Sary et al., in press).

Marine protected areas or marine fishery reserves have received much attention in recent years and it has been repeatedly shown that there are substantial increases in the size and abundance of fishes within protected areas, provided that they are of adequate size and that protection is enforced (Roberts *et al.*, 2001; Gell and Roberts, 2002; Russ and Zeller, 2003). Successful reserves are expected to increase harvests in adjacent areas as a result of outmigration from the reserve and as a result of increased spawning stock biomasses within the reserve. Outmigration rates are much dependent upon the size and configuration of a reserve and upon the behavior of individual species (Walters, 2000). No stock-recruitment relationship has ever been demonstrated for any species of coral reef fish, but it is self-evident that drastic reductions in spawning stock biomasses as a result of overexploitation will result in reduced recruitment rates in the areas to which propagules are dispersed, whether those areas are local or distant.

Species that aggregate to spawn are extremely vulnerable to overexploitation and, for example, it is clear that the survival of some stocks of groupers (Serranidae) (see Section 1.2) will depend on the creation of fishery reserves, preferably that include spawning aggregation sites and are of

sufficient size to encompass the home range of much of the local stock. An additional factor is that it is becoming increasingly apparent that the degree of connectivity between reef systems and islands might be quite low (Cowen *et al.*, 2000) and that replenishment of stocks is largely dependent upon the existence of an adequate spawning stock biomass. For example, Munro and Watson (1999) found that abundances of the pre-settlement post-larvae of commercial species of reef fish in the moderately-exploited British Virgin Islands were orders of magnitude greater than those recruiting to the north coast of Jamaica, where adults of any moderate-sized reef fish species are very uncommon and large species are locally extinct or extremely rare. Thus it appears that there is little replenishment of reef fish stocks by larvae spawned elsewhere and, if reef fisheries in Jamaica are to recover, it will be dependent on the accumulation of adequate spawning stock biomass in fishery reserves in local waters.

Where reef systems are closely connected by geographical proximity or oceanographic conditions, the stocks of individual species, although isolated, will be components of a metapopulation. The degree of connectivity will vary with the species but it seems likely that if reef systems are under different national administrations, a lack of effective management in one or more parts of the system will have impacts elsewhere. The need for international collaboration in managing and maintaining spawning stock biomasses is therefore evident. However, at a local level, the yield from a reef fishery will be determined by the effectiveness of fishers and managers in managing the stocks that are derived as a result of local settlement and resultant recruitment to the fishery.

7. Summary and Conclusions

It is evident that, while coral reef fisheries are exceedingly complex, they are amenable to assessment by conventional means. Certainly, it is very easy to demonstrate whether or not the principal species are overfished and to initiate preliminary steps towards developing a set of management strategies in close consultation with stakeholders.

The need remains for the development of cost-effective data acquisition systems, which will deliver the information needed for management of the fisheries and concurrently provide estimates of landings that are adequate for statistical reporting.

Although underwater visual census (UVC) methods have been developed to a high level of sophistication, and are widely used for estimating stock densities and biomasses, they have been shown to give variable results for some species. Because of their limitation to relatively shallow waters (usually < 20 m) their applicability will vary geographically and areas with extensive coralline shelves and large, deep, lagoons will need to be studied using other fishery-independent methods.

Methods for estimating parameters required for stock assessment models have advanced in many areas. All exploited species of reef fish appear to have daily rings in their otoliths that are readable in the early life stages and many have annual rings and can be accurately aged. Such age estimates can be used to validate estimates of growth rates based on length-frequency analyses. Sophisticated length-based models have been developed for fishery assessment and should be tested in reef fisheries for which there is adequate data.

If fish traps are used in fishery reserves to undertake mark-recapture-release studies, very high rates of return can be obtained through repeated recaptures of individuals and these can provide excellent growth parameter estimates together with estimates of natural mortality rates.

Mortality rates can be derived from length-converted catch curves, particularly when the required growth parameter inputs are derived from otolith analyses.

There are numerous ways of assessing the status of multispecies fish stocks that have been developed but not yet applied to many coral reef fisheries. These range from simple assessments of harvests per unit area, through total biomass surplus production models to parameter-

demanding yield-per-recruit and allied models. Although multispecies yield-per-recruit models require the application of some simplifying assumptions about species interactions, they will provide a reasonable assessment of the current status of the fishery and a starting point for evaluating changes in response to management measures. There is a wide degree of uncertainty in all fisheries estimation but this should not be an excuse for not exploring assessment methods and improving strategies for obtaining better estimates of the required parameters.

Finally, the development of Ecopath II provides a route towards ecosystem-based coral reef fisheries management and Ecopath-with-Ecosim provides the means for simulating the changes that will result from changes in the fishery. However, additional data on trophic interactions in coral reef systems and better knowledge of life-history parameters and of behavioral interactions of coral reef fish species is needed before these models can be confidently used for fisheries management in the most complex of all marine ecosystems.

Future research needs include continuing efforts to improve techniques for gathering the parameters needed for stock assessment models and for improving their accuracy. Additionally, there is a great need for the development of models that explicitly address the problems of multispecies fisheries. Virtually all of the world's fisheries harvest many species simultaneously but single-species assessments continue to be made that make no serious attempt to address the fact that a management strategy for one species may well have negative effects on others.

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Contract No 02-WPC-021

Statement of Work:

Introduction

The Council finalized its Coral Reef Ecosystem Fisheries Management Plan (CREFMP) in March 2002. It is expected that the final rule or regulations stemming from the CREFMP will be implemented in late 2002 or early 2003. The new FMP will increase the Council's responsibilities under the Magnusson-Stevens Fisheries Conservation and Management Act (MSFCMA), including monitoring coral reef fishery stocks, with respect to MSY and overfishing. Stock assessment of coral reef fish is still very much in its infancy, compared to stock assessments for temperate and cold water fisheries. Several factors together make stock assessment of reef fish stocks difficult. These include the high number of species, gears and landing sites that are typical of these fisheries, allied to little or no biological data on most species in the catch. However, in the past ten years there have been some significant improvements in methods such as ageing of reef fish, estimating fish populations through underwater visual census techniques and the development of more robust computer-based analytical and modeling techniques.

Statement of work

The contractor will review the scientific literature and generate a report on the current status of stock assessments on coral reef fisheries and the methods employed. The review will contain the following elements:

- A brief description of the distinctive features of coral reef fisheries; multi-species, multigear fisheries, poor catch statistics, developing economies with limited human and financial resources.
- Estimating age and growth parameters using marks on otoliths, scales, bones; mark-recapture; length-based methods.
- Estimating mortality rates, from age-based and length-based methods (including estimates based on UVC); mark-and-recapture; M from virgin stocks or MPAs; other estimates of M (e.g. from mesh selection data)
- Recruitment rates based in catch statistics; fishery-independent methods; length and age at recruitment.
- Population and biomass estimates based on catch statistics; estimates based on UVC (advantages and limitations); recruitment and spawning stock biomass; recruitment limitation and connectivity of stocks.
- Estimating potential yields, Maximum sustainable yields (MSY) and Optimum Sustainable Yield (OSY)
- Ecosystem models
- Managing coral reef fisheries; limiting size and age at first capture; limiting harvests; permanent or seasonal closed areas.
- Summary and Conclusions (future research)