The Assessment and Management of Caribbean Coral Reef Fisheries

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ABSTRACT

Caribbean coral reef fisheries are distinctive because of the extensive use of traps, which catch most species of fish and invertebrates. Small mesh sizes mean that most species with deep bodies are subjected to severe overfishing. Current evidence strongly suggests that reef fish are structured as meta-populations. However, connectivity between reef systems is low and recruitment overfishing impacts mostly on local stocks.

Although the assessment of multi-species stocks is not a simple task there is a huge amount of information available about the biology and fisheries characteristics of the important species. This is certainly sufficient for making reasoned management decisions. However, most fisheries in the region are not managed. The enormous cumulative costs of non-management should be widely publicised.

KEY WORDS: Stock assessment, populations, connectivity, MPA, fish traps

INTRODUCTION

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. 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). Also, 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. 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 drop-off 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 1978, 1996) and is the entity that must be managed cohesively.

About 180 species of coral reef fishes can be found in Caribbean fish markets, but in most areas about 20 species often make up 90% of the catch by weight. The remaining species are either rare, difficult to catch or of insignificant size.

Although a wide variety of gears are used to catch reef fishes, such as hook and line, spears and nets of various types, the dominance of wire mesh fish traps in most fisheries is unique to the Caribbean. Fish traps are used in many parts of the Indian Ocean, in S.E. Asia, in West...
Africa, and in a few places in the South Pacific but, with some notable exceptions, are small structures constructed from woven cane. The common chevron- or arrowhead-shaped and the double arrowhead or Z-trap derive their shapes from traditional woven designs, probably originating in south Asia (Hornell 1924).

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 or muddy shelves that do not support coral growth. 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 meta-population, 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. Cowen et al. (2000, 2003) have argued that when reef fish larvae originating from a single spawning area are dispersed offshore, the high mortality rates (about 20%/day) will greatly reduce the chances of significant numbers of larvae reaching reefs elsewhere and that almost all will die in the open ocean.

Watson and Munro (2004) 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 (Acanthuridae) and goatfishes (Mullidae). Triggerfishes pelagic larval stages, such as those of surgeonfishes trap fisheries or larger species that have specialized oceanic exploited species will often be negligible. Furthermore, the fisheries or larger species that have specialized oceanic exploited species will often be negligible. Furthermore, the fisheries who manage their stocks will be the main beneficiaries of any gains in production.

Figure 1. Hypothetical structure of a meta-population consisting of a core stock with strong self-replenishment, peripheral stocks with variable self-replenishment and terminal stocks that are unable to replenish themselves.

All reef fish species differ in their vulnerability to fishing, depending on body shape, feeding habits, behaviour, size at maturity relative to size at first capture, catchability and spawning behaviour. The most vulnerable species undoubtedly include the hinds and groupers. They are relatively deep-bodied and therefore are caught in traps well before maturity, they are aggressive predators and will enter traps to prey on the catch and willingly take baited hooks, they are easily taken by spearfishers and they form highly vulnerable spawning aggregations (Sadovy 1994). Thus, they have a high catchability (q) in many different gears and the larger species are caught at sizes (l) well before the size at first maturity (l0).

As a result of the differences in vulnerability to fishing, changes will occur in the composition of exploited coral reef fish and invertebrate communities as stocks of the most vulnerable species are reduced and as prey species respond to the removal of predators.

FISH STOCK ASSESSMENT

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) (Figure 2). Yield per recruit in both situations will be less...
The actual catch of any species that is taken from any fishing strategy will be proportional to the numbers of recruits to the local stocks. 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 and protection of nursery areas is realistically within the control of fishery managers.

All of the conventional stock assessment methods described by Ricker (1975), Gulland (1983), Sparre and Venema (1992), Gayanilo and Pauly (1997) and Gayanilo et al. (2002) can be applied to individual species of coral reef fish and invertebrates. Software such as FiSAT II (Ver. 1.2.0 available at www.fao.org/fi/statist/fisoft/fisat/downloads.htm) now provides easy access to many of the analytical routines. Recent reviews of assessment methods aimed specifically at coral reef fisheries include those of Medley et al. (1993) and Appeldoorn (1996) and the reader is referred to these works for technical details. Here I will concentrate on those aspects that will expedite the stock assessment process and encourage those concerned to take steps to assess the stocks for which they are responsible.

**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 absolutely no value for the purpose of stock assessment. It would be of much greater usefulness 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.

**Harvests Per Unit Area**

If the stocks that are encompassed in an area of shelf and the depth limits are clearly described, a planimeter and a nautical chart can give a useful approximation of likely upper bounds of production. There have been a number of compilations of such estimates (Marten and Polovina 1982, Munro 1978, Marshall 1985, Medley et al. 1993, Nielson et al. 1999, Dalzell et al. 1996). In the Indo-Pacific, harvests in excess of 20 t/km/year have been reported for shallow areas of coral, reef flat and seagrass beds from which a very wide range of fish and invertebrates are taken. Shallow reef flats produce more than 10 t/km/year, even when overfished, and coralline shelves (0 - 50 m) generate harvests of 1 - 3 t/km/year (Munro 1996). Sary et al. (2003) found that the fishery on the narrow coral-covered shelf 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/year, despite gross overfishing and degradation of the reef ecosystem. Far lower productions rates are achieved if only a limited array of predatory species are targeted, as on the Great Barrier Reef.

**Fishery Independent Methods**

Underwater Visual Census (UVC) techniques have reached a high level of sophistication (Samoilys 1997, Cappo and Brown 1996, Ault et al. 2000), sometimes using tape recorders or video to improve speed and accuracy. 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. However, the reliability of fish counts can be variable, 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). The most important limitation of UVC is that most of the catches of “coral reef fish” are taken in relatively deep waters (> 20 m) on open shelves or in lagoons, in depths beyond the practical operating limits of SCUBA divers. The overriding feature of UVCs is that
yield per recruit-effort curves. These will show if the individual stocks are over- or underexploited. In many cases, the required input parameters (K, L∞ and t0) can be obtained from published data, subject to later refinement. M can be approximated using Pauly’s (1980) equation. All of this can be done using the FiSAT II software. The length at first capture (Lc) and the corresponding age (t0) must be obtained from the actual fishery. Total mortality rates (Z) can be obtained from length-converted catch curves, mean lengths, or mean weights of individuals in the catch. Yield curves can be expressed in terms of the value of each species and summed to assess the overall situation in the fishery (Munro 1983).

Beyond this point, data must be collected from the fishery on a continuous basis to evaluate changes resulting from management actions and to monitor changes in the fishery. Depending on the data collected, other conventional analytical models can be applied to any species. However, unless the species in question is particularly valuable and can be managed separately (spiny lobsters, for example), these formulations are of little use in a multispecies fishery.

As discussed above, 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. However, this is subject to the usual caveats about the accuracy of estimates of C, B, and Z, and if estimates of biomass have very wide confidence limits, it will be difficult to get useful estimates of E without additional sources of information.

Surplus production models were developed for single species assessments (Schaefer 1954, Fox 1970) 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 of all species harvested in a fishery (Sparre and Venema 1992).

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 Ralston and Polovina (1982), Csirke and Caddy (1983), Bayley (1988) and Dalzell and Adams (1994). A powerful composite model was developed by Polovina (1989) that incorporates both space and time and non-equilibrium effects. Unfortunately, the needed replicated data remain extremely scarce and the model unused.

**Ecosystem Models**

The development of the first Ecopath model and its application to the French Frigate Shoals in the NW Hawaiian Islands chain (Polovina 1984) led to the development of Ecopath II (Christensen and Pauly 1992). 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 on data extracted from a wide array of literature.

Unfortunately, there have been few recent studies on the trophic ecology of coral reefs, and 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 and 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.

**MANAGEMENT OF CORAL REEF FISHERIES**

The options available for the management of coral reef fisheries 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.

A glance at the catches in almost any Caribbean fish market or landing place shows that most species are being captured before maturity and before they have attained an optimum size relative to their growth and natural mortality rates. This is usually a consequence of too many fishers entering the fishery and progressive reductions in the mesh sizes of traps or nets or of hook sizes.

The sizes at which fish are first captured by a fishery (Lc) should be matched to the prevailing fishing effort to maximise catches and also to permit fishes to attain maturity. The most drastic solution to the problem of undersized fish in catches is to ban the use of the offending fishing gears. For example, the ban on the use of fish traps in Bermuda saved their grouper stocks from destruction (Burnett-Herkes and Barnes 1996, Luckhurst 1999).

The use of escape gaps as a means of increasing Lc in multispecies coral reef fisheries has been suggested by Munro et al. (2003) and is being used in the black sea bass fishery in Florida (Shepherd et al. 2002). Rectangular or diamond-shaped fish traps offer the manager two dimensions as a tool for regulating Lc; the height or diagonal of the gap and the width.
Rectangular escape gaps can be expected to have significant effects on the catches of deep-bodied reef fish. For example, the mesh size most commonly used in Jamaica has a maximum aperture of 4.2 cm. All of the deep-bodied species such as surgeonfish, angelfish, triggerfish, porgies, many grunts, and jacks are retained at extremely small sizes and most are simply discarded. Calculations show that the progressive introduction of increasingly large escape gaps could increase catches on the north coast of Jamaica by 42%, with even greater increases in the value of the catch. Changes in catch composition would also result in the recovery of stocks of many deep-bodied species that have been virtually destroyed locally.

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). While outmigration from a reserve might have some impact on harvests in adjacent areas, the increased spawning stock biomasses within the reserve are of overwhelming importance. 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. Fisheries stock enhancement systems for supplementing natural recruitment and increasing catches may be feasible in the future but can only be possible in the context of a well-managed fishery (Munro and Bell 1997). All marine protected areas should encompass the full depth range inhabited by the important species, from the shallows to the base of the deep reef. The prohibition of fishing in shallow back-reef areas would also enhance recruitment and catches.

Species that aggregate to spawn are extremely vulnerable to overfishing and, for example, it is clear that the survival of some stocks of hinds and many groupers will depend on the creation of fishery reserves, preferably that include spawning aggregation sites and are of sufficient size to encompass the home range and depth range of much of the local stock.

Fish licensing systems exist in many Caribbean countries but there is no evidence that they are used to limit fishing effort or that the lack of a license is a serious deterrent to people who are desperate to earn some income. Individual transferable licenses (Munro and Smith 1984) (ITLs) have been adopted in a few fisheries but not with great success because the schemes have been poorly conceived. However, if ITLs were restricted to individuals and particular areas or fisheries and could not be purchased by entrepreneurs, and if all fishers on a boat had to have a license, the licenses would acquire a market value. Governments could buy back licenses to establish those values. This would achieve a measure of prosperity for the existing fishers but at the expense of impoverished people for whom fishing would no longer be the occupation of last resort.

If economic development can get ahead of population growth, fishing intensity will be reduced, as young people are attracted to better-paying and less arduous shore jobs. However, overpopulation is already a serious population in many countries, and there are few signs of an economic solution to overfishing.

Clearly, all management strategies need to be tailored to the needs of the fishing communities, the consumers, and the interests of other stakeholders (hoteliers, dive operators, sport fishers, etc.). Management measures that do not have widespread support will always be very 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 officials 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 effective management are quite high. However, the costs of non-management are staggering. Sary et al. (2003) estimated that the cumulative cost of not managing Jamaica’s fisheries amounted to US$1.3 billion, over the 25-year period since management strategies were first recommended. What would that figure amount to if applied Caribbean-wide?

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 unreliable results for many species. They are expensive and are limited to relatively shallow waters (usually < 20 m) and areas with extensive coraline shelves and large, deep, lagoons will still need to be studied using other fishery-independent methods.
they are expensive, particularly in terms of manpower. Nevertheless, where substantial funding is available, very detailed UVCs using SCUBA Nitox have been used to assess multiple coral reef fish stocks (Ault et al. 2002, 2005).

Other fishery-independent methods include depletion experiments aimed at estimating stock abundances and catchabilities (Polovina et al. 1985, Smith and Dalzell 1993). Gaudian et al. (1995) did UVCs before and after a period of intensive hook-and-line fishing. The work produced credible estimates of initial stock densities and catchability.

Miller and Hunte (1987), Acosta et al. (1990) and Recksiek et al. (1991) obtained estimates of effective area fished (EAF) by Antillean fish traps by comparing estimates of stock size obtained from UVC with the catch rates in traps. These works showed that the estimated EAF appeared to vary with site and season and the technique does not appear to be of much utility.

Routine test fishing with standardized fishing gears can be used to monitor trends in stock abundances. Although this might 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 could provide an additional source of information on migrations, growth and mortality rates.

**Parameter Estimation**

Simple mathematical evaluations of yield per recruit are essential for assessing the status of stocks. The basic parameters required for stock assessment are the growth parameters, most commonly expressed in terms of the von Bertalanffy growth equation \((K, t_0, L_\infty)\), and the natural mortality \((M)\) and fishing mortality \((F)\) rates. The other parameter determining harvest size is \(R\), the annual number of recruits to the fishery. However, \(R\) is largely uncontrollable, other than by maximising spawning stock biomass and conserving nursery habitats.

**Growth rates —** Because coral reefs are the domain of artisanal fishers, harvesting multiple species with diverse gears, 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. Obtaining a satisfactory sample of size frequencies or otoliths can be expensive and time-consuming, particularly for the larger and more valuable species, such as snappers or groupers or spiny lobsters. On the positive side, a very large number of estimates of growth parameters have been published, covering most of the important species. FishBase (www.fishbase.org; Froese and Pauly 2000) has extensive compilations of published growth parameters and, for example, these have been used to good effect by Ault et al. (1998, 2002, 2005).

Methods for estimating growth parameters from length-frequency data include ELEFAN I (Pauly and David 1981), SLCA (Shepherd et al. 1987) and MULTIFAN (Fournier et al. 1990). Terceiro et al. (1992) 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. ELEFAN and SLCA are included in the FiSAT II software.

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. 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.

Daily rings in otoliths have now been reported for many species of coral reef fish (Iglesias et al. 1997, Morales-Nin et al 1998). Automated systems are now commercially available. The rings are most useful for estimating the ages of juvenile fishes (Ralston et al. 1996) and indicate the time of settlement from the pelagic phase and thus 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).

Annual rings in otoliths have been reported for many species of lutjanids, letherinids, serranids, scarids and pomacentrids. Most of 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 letherinids 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.

The relationship between fish age and otolith weights was discovered by Templeman and Squires (1956). For reef fish, it has been found that otolith weight is a good predictor of age in *Lutjanus synagris* (Luckhurst et al. 2000), in *Lutjanus russelli* (Newman and Dunk 2002), and in *Mycteroperca microlepis* (Strelcheck et al. 2003). Additionally, Pilling et al. (2003) have examined the possible use of otolith weights as predictors of age in several commercially important Indian Ocean species. They found significant variation in the age:otolith weight relationship in *Lethrinus mahsena* and, otolith weight was not a precise indicator of 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 economi-
Studies of otoliths of a variety of species have shown that many species of coral reef fishes have high growth coefficients, variable individual 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.

Methods for deriving growth rates from mark and recapture data are well established. All are presented in the FiSAT package. 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 1999). 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. Consequently, this was a very cost effective exercise.

**Mortality Rates** — Mortality rates can be derived from four sources of data:

i) Age frequency analyses,
ii) Length frequency analyses,
iii) Mark-and-recapture data, and
iv) Mean weights of individuals in the catch.

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 various Australian snappers (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 using length-converted catch curves. The alternative is to use the method of Ehrhardt and Ault (1992), based on the mean length of fishes in the catch. Routines for both methods are provided in the FiSAT II software. It is essential that sample sizes are adequate and are representative of the annual average length composition of the stock.

The accuracy of any estimate of the total mortality rate ($Z$) is highly dependent upon the accuracy of the growth parameter estimates ($K, L_{\text{inf}}$) (Isaac 1990), but the development of accurate ageing of coral reef fishes leads to the possibility of combining reliable estimates of $K$ and $L_{\text{inf}}$ with large length frequency samples to obtain good estimates of total mortality rates from length-converted catch curves.

The mean weight of individuals in the catch (Gulland 1969) will also yield estimates of $Z$, again dependent on the precision of estimates of growth parameters and also on the size of first capture. Mean weight can be estimated accurately from large annual accumulations of measurements.

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.

Mortality rates can also be obtained from mark-and-release data, but results are often compromised by tag loss or tag-induced mortality.

Pauly (1980) described the correlation between natural mortality rates ($M$), growth parameters, and mean environmental temperature, which has been widely used to obtain a first approximation of $M$.

Natural mortality rates can only be directly estimated from the age or size frequency distributions of unexploited stocks, but such stocks are becoming increasingly rare. The conventional assumption is that $M$ is constant, but it is evident that $M$ changes with size and age and also when a fish community is exploited and the trophic pyramid is flattened. However, we have very few estimates of these changes and this remains an area of uncertainty.

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 $M$. Alternatively, UVC techniques could be used in such areas.

Estimates of fishing mortality rates ($F$) and catchability ($Q$) have most usually been derived by subtracting independent estimates of $M$ from $Z$ to get $F$ and catchability estimated by dividing $Z$ by fishing effort ($f$). Thus $Z = F + M = Qf + M$. Depletion experiments such as those of Polovina et al. (1985), Smith and Dalzell (1993) and Gaudian et al. (1995) also provide direct estimates of $Q$.

**Analytical Models**

The most useful first step that can be taken in assessing the status of the principal stocks in a multispecies fishery is to use the Beverton and Holt (1957) yield per recruit formulation to construct yield isopleth diagrams or
Methods for estimating parameters required for stock assessment models have advanced in many areas and estimates of growth parameters have been published for many species. 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. Sophisticated length-based models have been developed for fishery assessment and should be tested in reef fisheries for which there are 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, or calculated from mean lengths or mean weights, 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 and Ecopath-with-Ecosim provides a route towards ecosystem-based coral reef fisheries management, including a means for simulating the ecosystem 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 coral reef ecosystems.

Inaction at a political level seems to underlie the non-management of most Caribbean coral reef fisheries, perhaps resulting from a lack of appreciation of the value of the fisheries and of the cumulative costs of non-management. If more attention was given to publicising these issues and bringing them to public attention, the situation in which fishers find themselves might be improved.

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