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REVIEW OF THE IMPACTS OF FISHING ON CORAL REEF FISH POPULATIONS

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Cover Photograph: Samoan fishermen demonstrate how to throw an upega (cast net)

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Executive Summary

The impacts of fishing on coral reefs are receiving increasing attention as the pressure on these resources has grown. Large-scale surveys of coral reef fisheries throughout the tropical world have generally detected a decrease in target species abundance, biomass and mean size in response to fishing pressure and often reverse trends for site-attached species within marine protected areas (MPAs). Fishing can have indirect effects through predator-prey interactions and competition, and habitat-destructive techniques are being widely used. There is need of greater management, however the resources and time are not available to carry out the data collection achieved for many temperate regions. As the life history (LH) traits of species are useful indicators of their vulnerability to exploitation and propensity to recover when protected, simple surrogates of these traits could be a fruitful avenue to explore for data-unintensive coral reef fisheries management.

Species with 'fast' life histories are generally expected to be less vulnerable to exploitation and have higher rebound potential than species with 'slow' life histories. Marine organisms display a huge variety of LH strategies and some traditional ecological principles, such as of *r*-selected and *k*-selected species, can not be applied in the marine realm. The most important LH parameter in terms of vulnerability to decline and potential to recover from intense fishing is the intrinsic rate of population increase (*r*). LH invariants enable constancy between traits to be described. Research in temperate and tropical waters suggests that maximum theoretical or observed size is a good surrogate to many other LH traits and is a good predictor of a species' vulnerability to exploitation and rebound potential, although phylogenetic comparative approaches should be employed to account for the heritability of traits in related species. Maximum size is an easily obtainable parameter for coral reef fisheries management in data-poor situations.

The great diversity of coral reefs and their accessibility has resulted in specific fisheries issues becoming prominent. These include the live reef fish trade for food and aquaria, where regulation and monitoring are needed. Malthusian overfishing needs to be addressed at the local level and community-based MPAs may serve as useful tools in reducing the impact. The indirect effects of fishing are prominent on coral reefs, which through bycatch and fish removal can ultimately result in potential trophic cascades and phase shifts. Although prey release in fish does not appear to be happening at the aggregated level, species level effects are detectable and need further study. Spawning aggregations can be fished out rapidly and protection of these should be a management priority. Specialist species will be most at risk from widespread habitat degradation and so should be carefully monitored and protected.

MPAs are especially important where target species are valued for other purposes such as diving tourism. However, poor knowledge of the extent of species' mobility in particular hampers informed planning of MPA design for fisheries management. For mobile species only very large areas are considered likely to be effective in increasing abundance and thus generating spillover and larval-recruitment effects. Understanding of the dynamics of whole ecosystems is very shallow, in spite of the wide use of terms such as keystone predation and trophic cascade. Predators do widely control abundances of prey, but so do other processes such as recruitment which are very variable spatially and temporally. This means that the scientific underpinnings of broad ecosystem-based fisheries management (EBFM) are weak. However ecosystem-level metrics including size spectra have been used in temperate situations and might be applied to reef fisheries. Development of such techniques to provide reference points and control rules for EBFM is needed.

Avenues for research development in this field are explored, with suggestions for each topic covered in the review. Two specific research ideas that would be feasible and highly advantageous in the short term are discussed in some detail. The first would ultimately develop a predictive method of assessing abundances of large target species through a standardised measure of fishing intensity. The second would further understanding of ecosystem dissembly through predator-prey interactions and elucidate characteristics that render certain species more likely to 'outbreak' or 'dropout' in response to changes in predation pressure. Availability of long-term data sets in the South Pacific region needs to be assessed, but comparisons at large spatial scales across fishing-pressure gradients offer the greatest scope at present for appropriate work.

Introduction

The world's fisheries provide important food sources for many countries (Watson & Pauly 2001) and coral reef associated fisheries are extremely important to many less industrialised nations (Russ 1991; McManus *et al.* 2000). Globally, fish are often being taken from progressively lower trophic levels to maintain catches, a process termed fishing down the marine food web (Pauly *et al.* 1998). With the majority of the coral reefs of the world occurring in countries where the population is likely to double within the next 30-50years, the situation is likely to get worse (McManus 1997). Despite this, knowledge of the direct and indirect effects of reef fishing is limited (Munro & Williams 1985; Jennings *et al.* 1995; McClanahan & Kaunda-Arara 1996). Direct effects include removal of fishes, and indirect effects are mediated by predator-prey or competitive interactions and/or habitat modification. Both direct and indirect effects can act at the population, community or ecosystem levels (Russ 1991). Due to the decline in reef fisheries productivity, the establishment of marine protected areas (MPAs) has become a popular management option (McClanahan & Mangi 2000; Jennings 2001; Russ 2002). In terms of fisheries management it is hoped that protection will increase the abundance and species richness of fishes, provide breeding grounds and export fish biomass by both adult emigration and larval dispersal (Bohnsack 1993, 1998; Russ & Alcala 1996a; Roberts 1997).

Direct effects

Successful fishing will lead to a reduction in the abundance, biomass and mean size of species targeted by a fishery (Jennings & Polunin 1996b), while increases are sometimes apparent in marine reserves of sufficient size (Watson & Ormond 1994). Such responses to fishing and marine reserve protection have been documented for coral reef systems in East Africa (McClanahan & Shafir 1990; McClanahan 1994; Watson & Ormond 1994; McClanahan & Kaunda-Arara 1996; McClanahan *et al.* 1996), Florida (Clark *et al.* 1989), the Caribbean (Koslow *et al.* 1988; Polunin & Roberts 1993; Hughes 1994), the Seychelles (Jennings *et al.* 1995, 1996), Fiji (Jennings & Polunin 1996a; Jennings *et al.* 1999a), the Philippines (Russ & Alcala 1989, 1996a, 1998, 1999), and the Great Barrier Reef (Craik 1981;

Williamson 1999, Evans, Williamson & Russ, unpublished data) and local extirpations have also been indicated (McClanahan 1994a; Dulvy & Polunin unpublished data). Evidence of increases in abundance and catch rates outside MPAs is also building, although this is typically close to the reserve boundary (Alcala & Russ 1990; Russ & Alcala 1996b; McClanahan & Mangi 2000; Roberts *et al.* 2001). These studies provide strong evidence of a decrease in target species abundance and biomass due to increasing fishing pressure and increases in target species due to protection (Halpern 2003)(Fig 1).

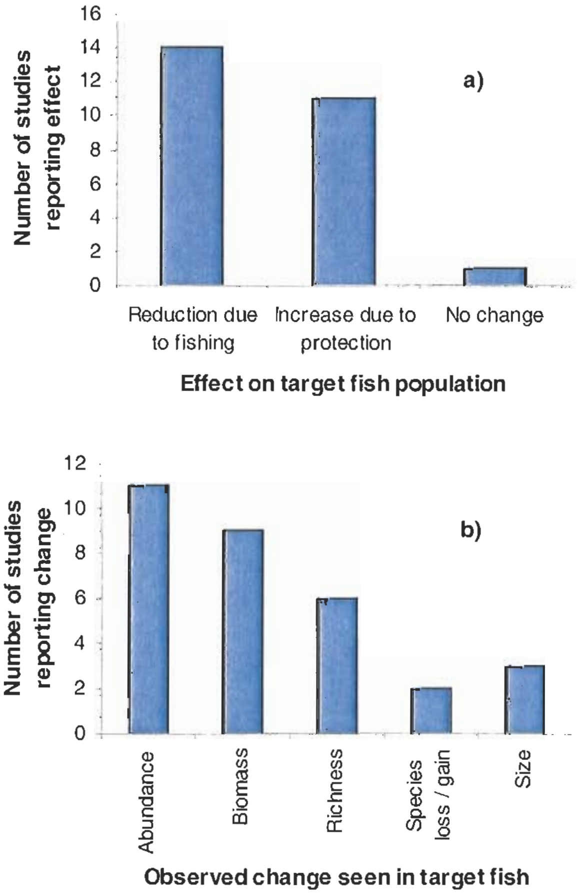


Figure 1. Current literature available on the effects of fishing and marine reserve protection on target fish species on coral reefs. **a)** Number of studies reporting a reduction in target species due to fishing, an increase due to protection or no change. **b)** Number of studies reporting changes in abundance, biomass, species richness, species loss or gain, or size in target fish groups.

Indirect effects

Fishing may have indirect effects on non-target species. For example, a decline in predatory fish due to fishing may result in 'prey release' characterised by an increase in the species normally preyed upon (Jennings & Lock 1996; Jennings *et al.* 2001a). Such responses have been indicated in fish-urchin communities in the

Caribbean (Hay 1984; Hughes 1994) and Kenya (McClanahan & Shafir 1990; McClanahan & Obura 1995). Some evidence of a similar response when fish are the prey species has also been documented (Koslow *et al.* 1988; Caley 1993; Hixon & Beets 1993; Watson & Ormond 1994; Carr & Hixon 1995; Graham *et al.* 2003). Similarly, limited evidence exists of increases in predators in MPAs causing a decrease in prey abundance (Watson & Ormond 1994; Graham *et al.* 2003). Such interactions coupled with other driving forces such as competition and disease can evidently lead to 'phase shifts' from coral dominated to algal dominated communities (Hughes 1994). However, much uncertainty still surrounds the topic, particularly in more complex systems such as the Indo-West Pacific (Russ & Alcala 1989; Jennings & Polunin 1997; Jennings & Kaiser 1998).

Spatial and temporal scales

It is necessary to highlight the importance of the spatial and temporal scale of studies on direct and indirect effects of fishing on coral reefs. Fisheries studies need to be temporally and spatially large scale, particularly with the high variation in recruitment indicative of coral reef fish populations (Doherty 1991). Many of the existing studies are small-scale manipulative experiments (eg Caley 1993; Hixon & Beets 1993; Carr & Hixon 1995), and the majority are 'snap-shot' one-off surveys (eg McClanahan & Shafir 1990; Jennings & Polunin 1997; Graham *et al.* 2003). As a result of natural variability between sites, the most convincing studies of fishing effects on fish communities will be those that span the implementation of a marine reserve or the commencement of fishing. Due to the extent of exploitation of today's coral reefs, the likelihood of finding a previously unexploited reef is slim. However, scope for monitoring sites before and after implementation of a marine reserve is much more tangible. In all the literature reviewed above, only Clark *et al.* (1989) spanned the opening of a marine reserve. To a certain extent Russ & Alcala's (see 1999) work on the opening and closing of Sumilon Island reserve in the Philippines also meets these aims. Furthermore, the only examples of suitable temporal scaled work in the present literature are those of Russ & Alcala (see 1999) at Apo and Sumilon islands in the Philippines, and the currently unpublished work being conducted by the Australian Institute of Marine Science long term monitoring team. Further development of such data sets will be necessary to fully elucidate the implications of reef fisheries on both target and non-target species.

Life history proxies

To effectively conduct resource studies, at suitable temporal and spatial scales, for all reefs is an impossible goal and would not yield results for the foreseeable future (Johannes 1998). Clearly methods for assessing and conserving coral reef fisheries that are much more realistic and achievable in the short term are needed. Labour unintensive techniques and rules of thumb are potentially available for management (Reynolds *et al.* 2001). Life history (LH) traits of animals are often associated with their vulnerability to exploitation (Jennings *et al.* 1999a; Purvis 2001; Reynolds *et al.* 2001), their rarity (Jones *et al.* 2002) and their risk of extinction (McKinney 1997; Roberts & Hawkins 1999; Dulvy & Reynolds 2002; Dulvy *et al.* 2003). There is growing evidence that this also holds for marine taxa. Simple identifiable surrogates of LH traits would therefore be immensely useful to the management of fisheries on coral reefs worldwide.

Use of terms

Before going any further it is necessary to define some terms and address certain pertinent issues surrounding coral reef ecology at present. It is important to note that the boundaries of a reef fish "population" have yet to be defined for any species (Box 1). For the purpose of this review we use the word "population" to refer to the sum of post-settlement individuals of a species occurring on a reef. Fishing pressure is also a fairly vague term in that it encompasses a range of different techniques. Coral reef fisheries are among the most diverse of fisheries (Johannes 1998) and techniques can range from selective methods, such as hook and line and spearfishing, to non-selective and destructive methods, such as

Box 1. Coral reef fish dispersal: open or closed ?

Dispersal of coral reef fish, both through adult movement and migration and through the pelagic larval phase, is a hotly debated topic in coral reef ecology. Pelagic species that frequent reefs have the ability to migrate and move between reefs freely, however, recent research on more reef attached demersal families (such as Serranidae and Lethrinidae) has shown much less movement. Work on the movement of predators, such as coral trout, has demonstrated large intra-reefal movements, but little movement between reefs across channels (Davies 1995). Furthermore, a study of *Plectopomus leopardus* demonstrated that although home range size may be large, there is often a preference for a number of smaller locations within that range (Zeller 1997). Dispersal by larval export is a strong argument for marine reserve protection, and under increasing scrutiny with increasing evidence of moderate to high levels of self recruitment to natal reefs (Jones *et al.* 1999; Swearer *et al.* 1999; Mora & Sale 2002). This is an area in need of further research and has implications for both sustainability and management of reef fisheries.

explosives and drive nets (Russ 1991). With the continuing depletion of resources and the increasing fishery-dependent populations in coastal regions, Malthusian overfishing, practiced by fishermen attempting to maintain their catches and incomes, is resulting in destructive techniques increasing in occurrence particularly in South East Asia (Pauly *et al.* 1989; McManus 1997). For the purpose of this review we assume that the fisheries tend to select larger fish species. Dispersal abilities of coral reef fish are also an important issue which has implications for local vulnerability to exploitation and for various management techniques, in particular marine protected areas (Box 1).

Aims

This review assesses the current understanding of LH traits in marine fishes, evaluating the reasons for looking at them examining useful surrogates to describe various important traits and how this relates to vulnerability to exploitation, with particular emphases on coral reef fish populations. Evidence from temperate water systems, deep water fisheries and the growing evidence in tropical waters is reviewed and this is related to the management of coral reef fisheries. Particular attention is paid to the evidence of size as a predictor of fishing vulnerability in both temperate and tropical coral reef fisheries. Specific issues related to coral reef fish exploitation, including the live fish trade, Malthusian overfishing, indirect effects, spawning aggregations and specialisation, are examined in section II with attempts to derive some lessons for management plans. Section III explores the implications for sustainability, focussing on threats to larger species, the use of MPAs, the ecosystem effects of exploitation and ecosystem-based fisheries management. In section IV we examine the type of data required to further understanding in the field and suggest some suitable avenues for research development.

I. LH Traits in Reef Fish and Implications for Sustainability

All organisms invest energy surplus to maintenance and repair in growth and reproduction. A whole suite of LH characteristics are thought, through natural selection, to favour individuals which produce the highest per capita rate of increase or fitness (Hutchings 2002). LH characteristics of organisms include body size, longevity, survival, fecundity, gestation period, growth rates, age at maturity, distribution, dispersal ability, reproduction in aggregates, specialised habitat preferences and abundance (McKinney 1997; Begg *et al.* 1999; Purvis *et al.* 2000; Hutchings 2002). It is generally accepted that animals with faster life histories, ie those with early maturity, small body size, fast growth and high reproductive potential, are less vulnerable to exploitation and have greater rebound potential than those with slow life histories, ie those with large body size, slow growth, late maturity and low fecundity (McKinney 1997; Jennings *et al.* 1998, 1999b; Russ & Alcala 1998; Dulvy *et al.* 2000; Purvis et al. 2000; Kokko *et al.* 2001; Purvis 2001; Sadovy 2001; Denny *et al.* 2002; Reynolds *et al.* 2002).

Not only do LH traits affect vulnerability to exploitation, but exploitation can ultimately affect the LH traits. Chronic intense fishing causes evolution of phenotypic traits of fish and additive genetic variation (Law 2000, 2001). Intensive exploitation results in earlier age of maturation in fish (Rochet 1998; Rochet *et al.* 2000; Trexler & Travis 2000; Heino & Godø 2002) and invertebrates (Murphy & Rodhouse 1999), slower growth (Buxton 1993; Heino & Godø 2002)(although see Jennings 1999b), reduced mean size of adult fish (Rochet 1998), skewing of sex ratios (Buxton 1993), reduced egg size (Rochet *et al.* 2000), and changes in behavioural and even morphological traits (Heino & Godø 2002). Slower growth is expected on the grounds that fish enter vulnerable size classes later, however this results in lower overall fecundity and smaller size at age later in life (Heino & Godø 2002). Change in LH traits in response to exploitation obviously has implications for the management of fisheries, however this subject deserves the attention of a full review and so we will only touch on some of these issues in this review, concentrating rather on the effect of life histories on species vulnerability to exploitation, and not vice versa.

I. I. Why look at life histories?

In general terms larger bodied animals are targeted through exploitation as they are more valuable and obvious to hunt. Also, animals active during daylight hours and those with larger home ranges are more likely to be encountered by hunters (Purvis 2001). Some species are targeted for specific purposes, such as seahorses for Chinese medicinal markets (Vincent 1996), the humphead wrasse for the live reef fish trade (Sadovy & Vincent 2002) and the emperor angelfish for the aquarium trade (Chan & Sadovy 1998). Although such species are clearly vulnerable to exploitation due to their value, how they respond to that exploitation will be influenced by their biology. For example seahorses are vulnerable to decline as they are site attached, monogamous and the males give birth to fully formed young (Lourie et al. 1999). Aside from these specialised markets, fisheries on coral reefs are often localised, artisanal and targeted at a multispecies assemblage (Choat & Robertson 2002). LH traits play an important role in determining which species succumb to the pressures of exploitation and which are more resistant to increased mortality. With the difficulties in collecting data on coral reef fisheries (Johannes 1998), LH traits are an avenue to predicting the response of these rich communities to exploitation.

The diversity of organisms on Earth displays an enormous array of LH 'strategies' (Roff 1992). LH strategies refer to the coordinated evolution of all the LH traits together, and although originally it was expected that the outcomes would be relatively few, it is now apparent that this is far from the case (Stearns 1992). Fish communities exhibit a huge variation in numbers and sizes of eggs (Hutchings 2002). Egg sizes range from 0.3mm to 6-7cm among species and the number of offspring can range from two to several millions per female (Hutchings 2002). Huge variability between species is also exhibited in size at maturity, ranging from 8-10mm to several metres, and in age at maturity, with some species maturing in weeks while others can take many years (Hutchings 2002). Aside from this huge variability between species, variation within populations of the same species can also be considerable (Hutchings 2002).

The original perception that marine fishes are extremely resistant to population reductions has been largely falsified for many species that have shown little recovery from prolonged declines (Hutchings 2000a). Furthermore, the perception that highly fecund species will be more resistant to declines and recover at accelerated rates is also being questioned (Sadovy 2001; Dulvy *et al.* 2003). Indeed maximum reproductive rates appear consistent across fish species displaying a variety of fecundities and are also similar to other vertebrates, producing a median of 1-7 spawners per spawner each year (Myers *et al.* 1999; Denny *et al.* 2002; Dulvy *et al.* 2003). Evolutionarily, whether a species is highly fecund or not results on average in the same outcome – replacement at equilibrium (Hutchings 2000b) and so fecundity *per se* has little influence on cohort strength in highly fecund teleost broadcast spawners (Dulvy *et al.* 2003). In fact, highly fecund species may have lower intrinsic rates of increase than less fecund species due to the correlation between large body size and the intrinsic rate of increase and of absolute fecundity (Denny *et al.* 2002). Early age at maturity seems to be a stronger correlate of resilience to exploitation and rebound potential than simply fecundity (Smith *et al.* 1998; Hutchings 2000a) and this correlates directly with small maximum body size (Denny *et al.* 2002).

The intrinsic rate of increase (r) (often highest in early maturing smaller species) is the main determinant of population increase and recovery, but is largely dependent on the initial population size and the degree of compensation or depensation (Jennings 2001; Reynolds *et al.* 2001)(Box 2). However, r and K are difficult parameters to measure, particularly with the wild variations in recruitment seen in fish populations (Reynolds *et al.* 2001; Denny *et al.* 2002). Furthermore, the traditional method of assigning some species as r-selected and others K-selected has received increasing criticism and is subject to difficulties (Stearns 1992), particularly in the marine environment (Reynolds *et al.* 2001; Choat & Robertson 2002). A female Atlantic cod *Gadus morhua*, for example, may produce millions of tiny eggs, but not until she matures as late as seven years old (Reynolds *et al.* 2001). Having said this, r, providing the potential for depensation is accounted for, is an extremely important LH trait for assessing the recovery and sustainability of exploited populations (Smith *et al.* 1998).

Box 2. Intrinsic rate of increase and spawner-recruit relationships

The intrinsic rate of natural increase (***r***) is a measure of the potential growth rate of a population. It may be estimated from the slope of the spawner-recruit relationship when spawner abundance is low (Jennings 2001). This is usually the fastest period of population growth (although see depensation).

K is the 'carrying capacity' of a population, reached when the death rate equals the birth rate and the resources that limit population growth maintain the population at this stable equilibrium (Begon *et al.* 1996).

Depensation (or the Allee effect) may affect populations at low population density, resulting in lower than expected recruitment from a given spawner biomass. This may occur for example when females fail to find mates (Jennings 2001; Petersen & Levitan 2001; Denny et al. 2002; De Roos & Persson 2002).

Compensation results in an increased per capita growth rate in depleted populations (Jennings 2001).

Modern fisheries in temperate waters are managed using huge data sets and sophisticated models with insatiable appetites for information (Jennings *et al.* 1999a; Pope *et al.* 2000; Reynolds *et al.* 2001). However, the detailed and enormous quantity of data required for this kind of management are impossible in many situations, particularly in tropical environments (Johannes 1998; Jennings *et al.* 1999a; Reynolds *et al.* 2001). Tropical inshore fisheries involve the most species, greatest complexity and diversity of habitat, most fishers and the greatest variety of gear types (Johannes 1998). The value of these fisheries at a global scale is low (Jennings *et al.* 1999a), huge areas of tropical reef have not been studied (Jennings & Polunin 1996b) and relative to the complexity of the resource few agencies have the resources or expertise to conduct the necessary research; in most cases research would be cost-ineffective anyway (Johannes 1998; Jennings *et al.* 1999a). Even in the data-rich temperate fisheries there is a strong bias towards economically important species at the expense of by-catch species that may also be declining rapidly with the fishery (Reynolds *et al.* 2001; Denny *et al.* 2002). Indeed, of the estimated 7000 species of fishes exploited in fisheries, aquaculture, sport fishing and the ornamental trade, basic LH data on growth and maturity are only available for around 1200 (Froese & Binohlan 2000). Techniques to assess fisheries with minimal data requirements that can be applied in a variety of situations are needed (Pope *et al.* 2000; Reynolds *et al.* 2001). LH traits have been highlighted as useful indicators of vulnerability to exploitation and work is progressing on simple surrogates of LH traits that may be used as rules of thumb to predict species vulnerability (Jennings *et al.* 1999a; Pope *et al.* 2000; Reynolds *et al.* 2001; Denny *et al.* 2002).

LH invariants

Surrogates of LH parameters may also be termed LH invariants whereby constancy among LH traits is sought from which generalisations can be drawn (Hutchings 2002). The first LH invariants demonstrated in fishes were based on the positive relationship between body growth (k) and the rate of natural mortality (M), the negative correlation between body growth and asymptotic size (L_∞) and occurrence of length at maturity (L_{mat}) at a similar proportion of asymptotic length (Beverton & Holt 1959; Beverton 1963). As previously discussed, the intrinsic rate of increase (r) largely determines a population's resilience to exploitation and its rebound potential from decline. This important LH characteristic is correlated with other LH traits such as age and size at maturity, growth rates and asymptotic body size (Smith *et al.* 1998; Frisk *et al.* 2001; Jennings 2001; Reynolds *et al.* 2001; Denny *et al.* 2002). It has also been suggested that species with large range-sizes will be larger-bodied, be found in greater local abundance and be less specialized (Pyron 1999), although the situation may not be as clear for coral reef fishes (Jones *et al.* 2002). There are strong relationships to predict L_{mat} from L_∞, optimum length (L_{opt})

from L_{∞}, L_{opt} from L_{mat}, life span (t_{max}) from age at first maturity (t_{mat}) and L_{∞} from maximum recorded length (L_{max})(Froese & Binohlan 2000). Correlation between L_{∞} and L_{max} (Fig 2) is now regarded as common knowledge (Stamps *et al.* 1998; Jennings *et al.* 1999a; Jennings 2001).

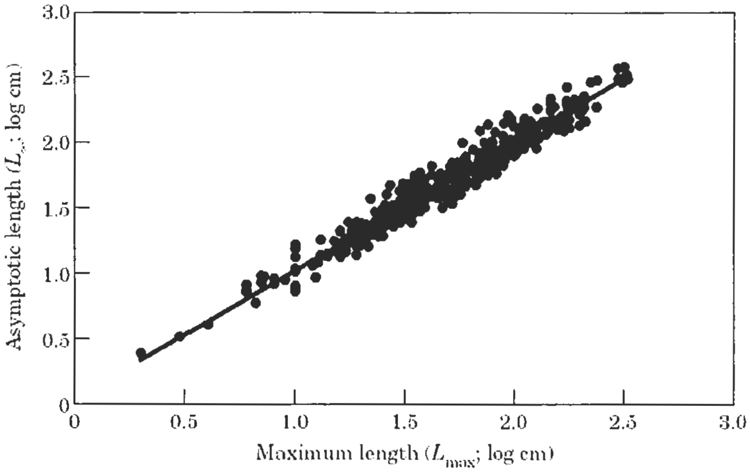


Figure 2. Relationship between L_{∞} and L_{max} in marine fishes (from Froese & Binohlan 2000)

The simple parameter of maximum body size is related to extinction risk in many taxa (McKinney 1997; Purvis *et al.* 2000; Purvis 2001; Dulvy *et al.* 2003) and can be correlated with survival, growth rate, age at maturity, fecundity, fertilization success, ability to provide parental care, probability of attracting mates and ability to acquire and defend nest sites (Roff 1992; Hutchings 2002). In fish, maximum observed size is most commonly negatively correlated with growth, age at maturity, reproductive output and natural mortality (Jennings *et al.*1999a; Jennings 2001; Denny *et al.* 2002). A recent study has also shown that body size alone, regardless of the species involved, is a good predictor of trophic level in fish communities (Jennings *et al.* 2001b). In relation to vulnerability to exploitation is the relationship between maximum size and *r* (Frisk *et al.* 2001; Denny *et al.* 2002; Dulvy & Reynolds 2002; Dulvy *et al.* 2003). These correlations between body size and LH parameters, and the fact that larger species are in general more heavily targeted, has prompted many workers, both in temperate and tropical regions, to promote maximum body size as a good indicator of species' vulnerability to exploitation and/or extinction risk (Jennings *et al.* 1998, 1999a; Dulvy *et al.* 2000, 2003; Frisk *et al.* 2001, 2002; Jennings 2001; Reynolds *et al.* 2001; Denny *et al.* 2002; Dulvy & Reynolds 2002; Jones *et al.* 2002).

The comparative method

The problem with looking at size in general is that it is influenced by phylogenetic / evolutionary ancestry (Harvey & Pagel 1991; Jennings *et al.* 2001b; Reynolds *et al.* 2001). The comparative method pioneered by Harvey & Pagel (1991) tackles this problem by correcting for phylogenetic relationships between species. Paired independent contrasts of the difference in a particular measurable trait between two related species are made (Reynolds *et al.* 2001). This technique has now been used to corroborate the relationship between LH characteristics, including size, and vulnerability to exploitation in both temperate (Denny *et al.* 2002; Jennings *et al.* 1998) and tropical coral reef fisheries (Jennings *et al.* 1999a). Again, the use of observed maximum size to predict species vulnerability to exploitation is advocated (Jennings *et al.* 1998, 1999a; Denny *et al.* 2002).

With strong evidence pointing towards maximum body size as a simple 'rule of thumb' of vulnerability to exploitation, it seems that data intensive fisheries assessment techniques, often used in temperate fisheries, do not necessarily need to be employed in the tropics where it would be impractical to do so (Johannes 1998). Let us now look at the evidence of size as a predictor of fishing vulnerability in both temperate and tropical coral reef fisheries a little more closely.

I. II. Evidence for LH correlates with vulnerability to exploitation

a. Temperate-water fisheries

A great deal of the work carried out in temperate waters comes from the North Sea and northeast Atlantic. The phylogenetic comparative approach has shown that among 18 intensively-exploited fish stocks from the north-east Atlantic, larger, later maturing species with lower potential rates of population increase are less resistant to given levels of exploitation than smaller earlier maturing relatives (Jennings *et al.* 1998). Growth rate and fecundity were not important traits dictating response to exploitation (Jennings *et al.* 1998). The use of theoretical or observed maximum size as a predictor of susceptibility of stocks to exploitation has been promoted as a labour-unintensive and effective management technique (Jennings *et al.* 1998).

The comparative method demonstrated an increase in mean growth rate and a decrease in mean maximum size, age at maturity and size at maturity, all linked to trends in abundance in the demersal fish community of the North Sea between 1925 and 1996 (Jennings *et al.* 1999b). Not only have LH characteristics apparently changed in response to exploitation, but also they have affected species' responses to exploitation compared to their nearest relative. The greatest declines seen in those species that matured later at a greater size, grew more slowly to a greater size and had lower values of r (Jennings *et al.* 1999b).

The phylogenetic comparative approach has also demonstrated that among 63 exploited fish stocks in the northeast Atlantic, a greater rate of recruitment per adult is significantly associated with small body size, increased growth rate and earlier maturity (Denny *et al.* 2002). High recruitment is correlated with low fecundity as the relationship between body size and fecundity is strongly positive (Denny *et al.* 2002). Indices of body length and growth rate are the strongest predictors of r resulting in the use of body size being advocated as an indicator of r in data-poor situations (Denny *et al.* 2002).

b. Sharks and rays

Many elasmobranch fishes are heavily exploited worldwide both directly and as bycatch (Frisk *et al.* 2001, 2002; Reynolds *et al.* 2001). They have very 'slow' life histories with late age at maturity, large size, low fecundity and long gestation period aswell as being live-bearers (Reynolds *et al.* 2001). They are also not morphologically designed to avoid modern fishing pressures (Reynolds *et al.* 2001; Schindler *et al.* 2002). Empirical relationships have been determined in elasmobranch fishes between body size and both length and age at maturity and larger species also have lower growth rates and r values (Frisk *et al.* 2001). The vulnerability of elasmobranchs can be categorised by maximum length, with larger species being more vulnerable to decline or local extinctions (Dulvy *et al.* 2000; Frisk *et al.* 2001; Dulvy & Reynolds 2002). Indeed, locally extinct species of skate have large body sizes compared with other skates, perhaps a response to higher mortality rates and correlations with other LH parameters (Dulvy & Reynolds 2002). The smallest of these locally extinct species can therefore be used as a benchmark to identify other species potentially at risk (Dulvy & Reynolds 2002). Of the remaining five species in the north-east Atlantic skate fishery, the three larger species have declined in abundance while the two smaller species have increased, perhaps as a result of 'competitive release' (Dulvy *et al.* 2000). It has been suggested that a size limit of 100cm be applied to the elasmobranchs in general, over which species are characterised by life-history traits which render them more vulnerable to declines in response to exploitation (Frisk *et al.* 2001). In contrast, a study looking at the rebound potential of 26 species of Pacific sharks found that age at maturity had the greatest influence on recovery from exploitation (Smith *et al.* 1998). Fishing related mortality of sharks has grown considerably over the last decade due to the rapid increase in finning operations (Schindler *et al.* 2002). Species with the lowest rebound values were late-maturing medium to large-sized coastal sharks, those with the highest rebound values were small coastal, early maturing species, whereas the species with mid-range values were large pelagic species that are relatively fast growing and early maturing (Smith *et al.* 1998). Although size is obviously important, age at maturity seems to be the overriding driver of rebound potential, although if the same species were subject to phylogenetically controlled analysis a clearer picture of the influence of size might emerge.

c. Deep sea fisheries

The orange roughy (*Hoplostethus atlanticus*) is exploited at depths greater than 600m mainly off the coasts of New Zealand, Australia and Namibia (Branch 2001; Clark 2001). Orange roughy are slow-growing, extremely long lived (reaching ages greater than 100 years), late maturing (between 22-40 years), have exceptionally low natural mortality, large eggs, and low fecundity and they reproduce in large spawning aggregations, all of which make them vulnerable to exploitation and slow to recover from depletion (Tracey & Horn 1999; Clark *et al.* 2000; Branch 2001; Clark 2001). The orange roughy fishery initially developed on flat bottom habitats; however as populations contracted it soon moved to the spawning aggregations found on seamounts and by 1995-1996, 70% of the New Zealand catch came from such sea mounts (Clark 1999; Clark *et al.* 2000). Catch rates and stock biomass have plummeted for most orange roughy fisheries, with the populations on sea mounts on the Chatham Rise of New Zealand being estimated to be 20% of their original biomass (Francis & Smith 1995; Clark et al. 2000). Clearly the LH of this species leaves it exceptionally vulnerable to exploitation, particularly its longevity and age at maturity (Clark 2001), raising concerns about development of further deep sea fisheries.

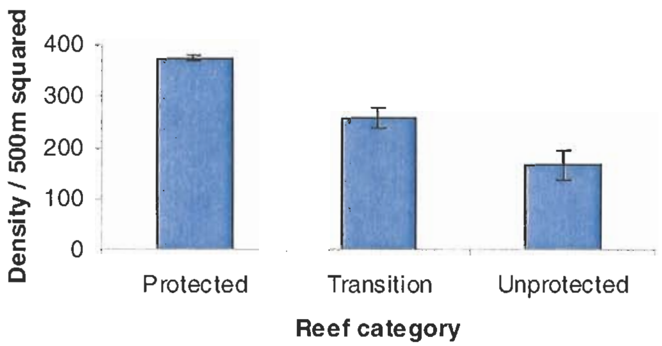
d. Coral reef fisheries

Apo and Sumilon Islands in the central Philippines provide the longest term data sets examining effects of fishing and marine protected areas (MPAs) on coral reefs. When protective management of Sumilon MPA broke down in 1984 the fishing resulted in significant decreases in the species richness of large piscivores (serranids, lutjanids, lethrinids and carangids), labrids and chaetodontids, the last probably due to reduction of live coral cover by destructive methods (Russ & Alcala 1989). The MPA was protected again for almost 5 years from 1987-1992 and then opened to municipal fishers for 2 years (Russ & Alcala 1996a). The density of large predatory reef fish increased 3 times in response to protection, and decreased 3 times when areas previously protected were opened to fishing (Russ & Alcala 1996a). Declines in response to fishing were rapid, whilst recoveries during protection were slow (Russ & Alcala 1998). Fish have continued to build up since protection commenced at Apo Island MPA, and local fish yields have increased (Russ & Alcala 1999).

The rates of decline and recovery in the heavily targeted large predators (epinepheline serranids, lutjanids, lethrinids and carangids) in response to exploitation are linked to vulnerable LH traits (low rates of natural mortality, growth and recruitment)(Russ & Alcala 1998). Caesionidae also declined rapidly with fishing pressure despite having a 'fast' LH, however they are extremely heavily targeted, making up 70% of the yield from Sumilon Island and 14% from Apo Island, and recovered rapidly. Thus LH traits alone are insufficient to predict responses to exploitation, with other influences, in particular recruitment effects, playing a key role (Russ & Alcala 1998). The study shows in general, however, that LH traits are important for predicting coral reef fish population responses to exploitation, if other factors are accounted for, particularly for larger predatory species (Russ & Alcala 1998).

Although not yet directly linked to LH traits, a substantial quantity of work on the effects of fishing coral reef fish populations has been carried out in East Africa. Eight families of reef-associated fish were surveyed on Kenyan reef systems between three MPAs, four sites with unrestricted fishing and one transition reef which had received protection 1-2 years prior to the survey (McClanahan 1994a). Five showed a significant decrease in fish abundance in unprotected verses protected reefs and combined data of all censused species indicated approximately a 50% reduction in abundance on fished reefs (fig. 3)(McClanahan 1994a). A total of 118 species were identified in the eight families of which 100 were found on MPA reefs, 86 on the transition reef and 66 on the fished reefs, resulting in 44 species being unique to the MPAs (McClanahan 1994a).

Figure 3. Total abundance of fish for eight families combined in protected, transition and unprotected reefs in Kenya (Redrawn with data from McClanahan 1994a).



Another study demonstrated that individual fish wet weights were lower on unprotected reefs than reefs protected in MPAs for all studied families except Diodontidae (McClanahan & Kaunda-Arara 1995). A study by McClanahan & Shafir (1990) showed that finfish populations were ca. four fold denser on MPA compared to unprotected reefs. This was attributed to the inclusion of human predators in unprotected reefs adding an additional consumer and trophic level to the reef (McClanahan & Shafir 1990). When three similar reefs with differing intensities and histories of fishing were surveyed, removal of sea urchins was incorporated into the design (McClanahan *et al.* 1996). Wet weights, population densities and species richness of fish were highest in low fishing areas, attributable primarily to fishing, and secondarily and indirectly to high sea urchin abundance (McClanahan *et al.* 1996).

Abundances of commercial fish species (Lethrinidae, Lutjanidae and Serranidae) were found to be up to 10 times greater in a MPA as opposed to a fished reef in Kenya (Watson & Ormond 1994). Evidence of larger individuals occurring within the MPA was also reported. Some reverse trends, with higher abundances of certain species outside the MPA are apparent and are thought to be predator-prey effects (Watson & Ormond 1994). No potential effects of poaching are explored, thus the influence of any poaching on the results is unclear.

A higher biomass of the families Lethrinidae, Lutjanidae and Serranidae occurs in more lightly fished grounds in Fiji (Jennings & Polunin 1996a, 1997). The phylogenetic comparative approach has shown the roles of LH traits in dictating response of species of grouper (Epinephelinae), snapper (Lutjanidae) and parrotfish (Scaridae) to exploitation (Jennings *et al.* 1999a). Species that declined more than their nearest evolutionary relatives had significantly greater maximum size (Fig. 4). The relationship was much stronger for the groupers and snappers than the parrotfish, which is expected to reflect the greater exploitative pressure exerted on these families (Jennings *et al.* 1999a). Size may thus be a predictive measure of heavily targeted species' response to exploitation if a standardised measure of fishing pressure can be achieved (Jennings *et al.* 1999a). The further development of such techniques would be of huge value to coral reef fisheries, particularly in new, developing or lightly exploited fisheries (Jennings *et al.* 1999a).

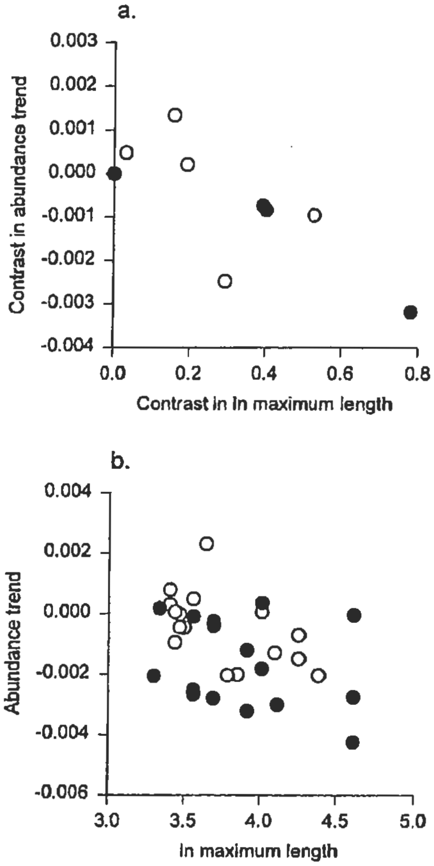


Figure 4. a) Relationships between contrasts in trends in abundance (measured as biomass) and contrasts in maximum size and **b)** traditional cross-species relationships between trends in abundance (as biomass) and maximum length for Fijian reef fishes. Open circles represent parrotfishes; shaded circles represent groupers and snappers (from Jennings *et al.* 1999a).

I. III. Coral reef fisheries management lessons: translation of scientific knowledge to policy

There is a need to develop very simple, yet reliable, techniques that can be used as rules of thumb to help sustainably manage fisheries on coral reefs (Johannes

1998). From the current understanding in marine fishes, maximum size appears to be the most suitable proxy of LH traits. Theoretical maximum size data are available for the majority of reef fish and are easily accessible through resources such as FishBase (Froese & Pauly 2003). Observed maximum size is well correlated with asymptotic maximum size (Fig. 2) and so simple assessments may also be possible site by site. Much of the work above highlights the importance of taking into account species phylogenetic relatedness (Denny *et al.* 2002; Jennings *et al.* 1998, 1999a, 1999b). Future studies related to management should take this into account. Maximum observed size may thus be used specifically to monitor those species that are likely to be most at risk, reducing the labour intensity of monitoring. The potential for closing the fishery to certain large species that are declining rapidly is also a possibility.

The establishment of MPAs has increasingly been considered a management option (Clark *et al.* 1989, Jennings 2001). The general idea of MPAs is to stop all fishing, however some may protect only certain species or protect against specific kinds of fishing (Bohnsack 1996). The motivations for establishing MPAs vary from country to country, but high on the list are economic benefits to tourism, maintenance of fisheries, conservation of coral reef ecosystems, and protection of traditional use rights (Clark *et al.* 1989). In terms of fisheries management it is hoped that protection will increase the abundance and species richness of fishes, provide breeding grounds and export fish biomass by both adult emigration and larval dispersal (Russ & Alcala 1996a).

As a management technique, MPAs are the least labour intensive and simply provide a spatial refuge for sedentary reefal species from harvest (Bohnsack 1998). In many regions of the world, where fishers have been driven to Malthusian overfishing and destructive techniques are causing habitat degradation, conventional fisheries management measures such as size limits and quotas are not an option. It is hoped that MPAs will promote recovery of the sensitive habitat and increase fish stocks, although clearly the effects may not be so great for mobile species. Much debate has been fuelled by the potential speed at which fish stocks will recover and thus how quickly fishers may expect results. Some recent reviews have suggested that MPAs will provide very rapid and lasting increases in target species biomass and fisheries enhancement (Roberts *et al.* 2001; Halpern & Warner 2002). However this is in contrast to other findings, particularly for larger longer-lived predatory species (Russ & Alcala 1998). Both Clark *et al.* (1989) and Russ & Alcala (1998) highlight the extended periods needed to allow target fish species to return to natural levels in MPAs, with the increase in some species still not slowing after 21 years of protection at Apo Island in the Philippines (Russ pers comm.). It seems LH characteristics can play a key role in assessment of which species may respond more rapidly to protection and which will need longer (Roberts 2000). The overriding factor contributing to the speed of recovery in MPAs is the intrinsic rate of increase (*r*) of individual species. As this is directly correlated with maximum size in marine fish (Denny *et al.* 2002), this simple proxy of LH traits can again be used as a rule of thumb to predict which species will rebound more rapidly and which slowly in response to protection.

II. Coral reef specific issues

a. Live reef fish trade

The live reef fish trade, transporting species alive to markets for use as table food and in aquaria is relatively new, affecting reef fisheries mainly in the Indo-Pacific (Sadovy & Vincent 2002). Live food fish are taken from Southeast Asian and Australian reefs and the trade has developed greatly in the Pacific with sporadic activity from the Federated States of Micronesia, Fiji, Kiribati, Marshall Islands, Palau, and Papua New Guinea (Anon 2002; Sadovy & Vincent 2002). The cost of transporting the fish is high, however the trade is worth millions of dollars annually and could potentially boost the incomes of subsistence fishers, with values being up to ten times that for dead fish (Anon 2002; Sadovy & Vincent 2002). The fishery is highly specific with regard to species and size, often with rarer species and those with life histories rendering them vulnerable to heavy exploitation being favoured (Sadovy & Vincent 2002). Live food fishes are common in Asian restaurants, particularly in Hong Kong, Taiwan, Singapore and Japan, where a diner can select their meal directly from the aquarium tank within the restaurant. The trade is mainly made up of species of Serranidae, Labridae and Lutjanidae, with certain species such as the humphead wrasse being particularly prized (Halim 2001; Sadovy & Vincent 2002). The fishery uses various techniques, from non-destructive methods such as hook and line, to destructive fishing such as cyanide and mortality rates on route can be considerable (Halim 2001; Thorburn 2001; Sadovy & Vincent 2002).

The fishery can target juveniles and mid-size fish, with a size preference range of 0.6-1.5 kg (Sadovy & Vincent 2002). Juveniles are increasingly also taken for mariculture grow-out in Southeast Asia. The targeting of spawning aggregations is of particular concern, fishing some populations out very rapidly and altering sex ratios in others (Sadovy & Vincent 2002). The humphead wrasse has been particularly hard hit, fished down to very low levels in many regions (Donaldson & Sadovy 2001). Reductions in fish size have been reported from many regions of Southeast Asia, particularly in groupers and some wrasses (Donaldson & Sadovy 2001; Sadovy & Vincent 2002). Although the scope for intensive coastal aquaculture of live reef fish such as groupers has been highlighted (Bell & Gervis 1999), development of such initiatives are not common. Regulation of the live reef fish trade is needed to sustain the trade. As with overexploitation in normal fisheries, those species with vulnerable LH characteristics are going to be most severely impacted. The evidence for size as a useful proxy of vulnerability suggests that species larger than their phylogenetically nearest relative will decline at faster rates. Taking fish at smaller sizes is of particular concern for the larger species if this is below size of maturation. Also, those species that are particularly prized should receive specific research and management attention to avoid catastrophic declines. The continued build up of databases and monitoring by CITES is also essential and this is also a role that national NGO's could play.

b. Aquarium trade

Live reef fish are also used for the aquarium trade, which has its strongest markets in the USA, western Europe and Japan, mostly for use by hobbyists (Chan & Sadovy 1998). As with the live food fish trade, the aquarium trade is an increasingly important fishery, worth millions of US dollars a year and originates primarily from Southeast Asia and certain other countries such as Sri Lanka (Chan & Sadovy 1998; Wijesekara & Yakupitiyage 2001; Bolker *et al.* 2002; Sadovy & Vincent 2002). The aquarium trade differs from the food trade in that it targets smaller species / individuals, exploits a broader range of species (over 1000) and is better monitored (Sadovy & Vincent 2002). The fishery can be extremely selective, with rare or unusual species often the targets (Sadovy & Vincent 2002). As with the live reef fish food trade, capture methods vary from non-destructive to destructive and mortality rates are high, although in the aquarium trade the market for non-destructive methods is growing (Sadovy & Vincent 2002; Kolm & Berglund 2003). Small size indicates

LH characteristics resilient to exploitation, but there are certain species that are particularly vulnerable to the fishing pressure and others that are so heavily targeted that numbers are rapidly reduced. Species such as the endemic Banggai cardinalfish, *Pterapogon kauderni*, those with extremely specific habitat preferences such as seadragons, naturally rare species and some high value species such as the pygmy angelfish, *Centropyge resplendens*, are of particular concern (Sadovy & Vincent 2002; Vagelli & Erdmann 2002). The Banggai cardinalfish for example, is not only highly endemic, it has limited habitat preferences, is a paternal mouthbrooder living in groups and lacking a pelagic larval phase, thus having limited dispersal ability (Kolm & Berglund 2003) and yet is subject to trade of at least 50,000 specimens a month (Vagelli & Erdmann 2002). There are various examples of declines in abundance of aquarium trade species from Hawaii, Indonesia, the Philippines and the Maldives, although other studies have detected no differences in Fiji and the Cook Islands (Sadovy & Vincent 2002). Clearly the decline will be influenced by multiple factors including LH traits. Strategically-located MPAs with local stakeholder input may be the only suitable and feasible management option to protect many of these species and they obviously have multiple impacts, benefiting other fisheries also. Much interest is growing in the potential for aquaculture production of aquarium fish, however, although 90% of freshwater aquarium fish are now reared in captivity, the production of marine species is still minimal (Bell & Gervis 1999; Tlusty 2002). As with the live reef fish food trade, monitoring of the trade and inclusion of species by CITES and NGO's will be important to help quantify movement of different species. More accurate data is necessary and this could be obtained through the introduction of log book systems or countries reporting regularly to information systems such as the Global Marine Aquarium Database (GMAD). Finally, species with low population densities should be protected from exploitation on a country by country basis.

c. Malthusian overfishing

Malthusian overfishing occurs when fishermen lacking any alternative are faced with declining catches and initiate resource destruction in their effort to maintain their incomes (Pauly *et al.* 1989). This may include use of illegal gears and mesh sizes, gears that destroy the resource base and methods such as dynamite or sodium cyanide that damage habitat and endanger the fisherfolk themselves (Pauly *et al.* 1989). Destructive fishing techniques including blast-fishing and cyanide are now widespread, reported from over 40 countries (McManus 1997). Such methods have large community-level impacts and those species which are dependent on physically fragile habitats are most seriously affected. Size as a proxy of LH traits should be a useful proxy for distinguishing those species expected to decline most rapidly. This problem is however a localised one that needs to be addressed with coastal zone management schemes that integrate village-level management with government policies (McManus 1997). Small-scale MPAs are likely to be a useful management tool here (Russ & Alcala 1989, 1999).

d. Indirect effects

The indirect effects of fishing can result from bycatch, habitat modification or altering predator-prey or competitive interactions (Russ 1991). Bycatch is the result of accidental catch or damage of organisms when fishing for target species (Dayton *et al.* 2002). It is of particular concern in trawl fisheries and has been blamed for the decline of sea turtles (Dayton *et al.* 2002) and some species of skate (Frisk *et al.* 2002), but the impacts on the majority of non-target species are poorly known (Pope *et al.* 2000). Destructive, non-selective fishery methods on coral reefs such as blasting also kill not-targeted species, which thus are also bycatch and effectively discarded. Destructive techniques themselves, such as blasting and trawling, not only remove target and non-target species but also destroy large areas of habitat. Habitat destruction has been the primary driving force behind extinctions and biodiversity decline over the past century (Dayton *et al.* 2002). The decline in abundance and diversity of species as a result of bycatch and habitat loss is of grave concern to marine environmental managers. Techniques that require minimal data to assess the indirect effects of fishing on non-target species are necessary as the resources available to study these species are often even more limited than those available to assess the target species (Pope *et al.* 2000). Maximum size is a method for assessing the vulnerability of elasmobranch fishes to exploitation, whether as targets or as bycatch (Dulvy *et al.* 2000; Frisk *et al.* 2001; Dulvy & Reynolds 2002). The use of maximum size as a strong surrogate to many other LH traits in marine fishes highlights that this may also be the best avenue to explore the effects on non-target species that need to be assessed with the minimum of expenditure.

Another possible indirect effect of fishing is through predation, where it governs the abundance of post-settlement fish (Hixon 1991). The thin body of literature available on reefs is surprising considering the importance of understanding such a system both from a conservation point of view and for maximising yields (Jennings & Lock 1996). For example, if a fishery is directed at species other than top predators, yield may be enhanced by removing their predators (Marten 1979; Jones 1982). Conversely, if a rare prey species is in need of protection, a marine reserve may not be the solution, as the associated increase in predators could further add to the plight of the species.

Evidence for the trophic effects of fishing is available for tropical lakes (Marten 1979) and temperate seas (Estes *et al.* 1998), but is not conclusive for reef fish assemblages (Jennings & Kaiser 1998). This is surprising as piscivorous fishes are probably the most significant consumers of fish biomass in reef ecosystems (Jennings & Lock 1996). It has been suggested that the absence of a detectable trophic trend may be a result of predators and prey not being as tightly coupled (Jennings & Kaiser 1998; Jennings *et al.* 2001a). In complex systems with a greater diversity of species, carnivores are often generalists and highly opportunistic in their feeding habits (Russ 1991). As a result, the effect of a change in abundance of a small number of species might not be great. It is therefore possible that fewer trophic effects of fishing will be seen in the more complex reefal systems of the Indo-West Pacific than on simpler reefal systems elsewhere (Jennings & Kaiser 1998).

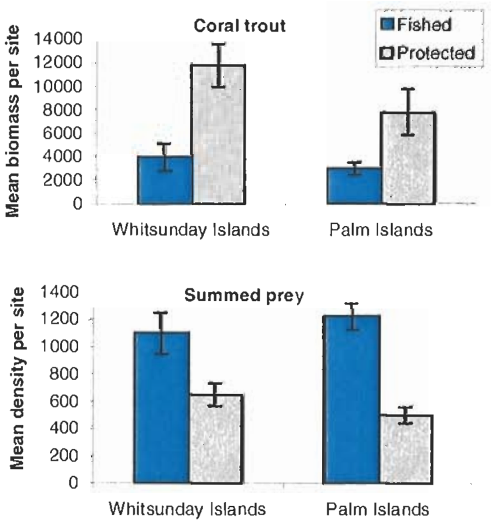


Figure 5. Mean coral trout (*P. leopardus* and *P. maculatus*) biomass (grams per 1500m^2 ± SE) between zones at each island group (top graph) and mean density (per 1500m^2 ± SE) of the prey species summed together (excluding *N. azysron*) at the same sites at each island group (bottom graph)(From Graham *et al.* 2003).

Release of sea urchin populations from predation pressure has been demonstrated in the Caribbean (Hay 1984; Hughes 1994) and East Africa (McClanahan & Shafir 1990; McClanahan & Obura 1995), the latter highlighting the possible role of 'keystone predators' controlling sea urchin populations (Box. 3).

Outbreaks of invertebrate species such as sea urchins (McClanahan & Obura 1995) and crown-of-thorns starfish (Ormond *et al.* 1991) have been linked to predator decline, ultimately resulting in trophic cascades and phase shifts in the ecosystem (Hughes 1994), with likely consequences for sustainability (Box. 3).

Studies looking at prey release in coral reef fish have produced varied results. Small scale manipulative experiments have sometimes demonstrated prey release (Caley 1993; Hixon & Beets 1993; Carr & Hixon 1995), as have larger-scale studies addressing the issue from the species level (Koslow *et al.* 1988; Watson & Ormond 1994; Graham *et al.* 2003). However, when species have been aggregated into family or trophic groups, clear examples of prey release have not been documented (Russ & Alcala 1989, 1998; Jennings *et al.* 1995; Jennings & Polunin 1997). For example, Graham *et al.* (2003) studied prey release in 9 species of pomacentrids, labrids and scarids, selected from gut analysis work on the coral trout, *Plectropomus leopardus*, between fished and protected areas on the Great Barrier Reef. There are significantly more prey in fished than protected areas and the relationship is significant when the prey are summed together (Fig. 5). Conversely, even though piscivorous fishes decline in abundance across fishing grounds in Fiji, no significant increase in abundance occurs in families such as Cheatodontidae, Mullidae or Labridae, or in trophic groups such as herbivorous and invertebrate feeding fishes (Jennings & Polunin 1997)(Fig. 6). These two studies suggest that prey release may be happening at the species level but, because species are idiosyncratic, not at the aggregated level.

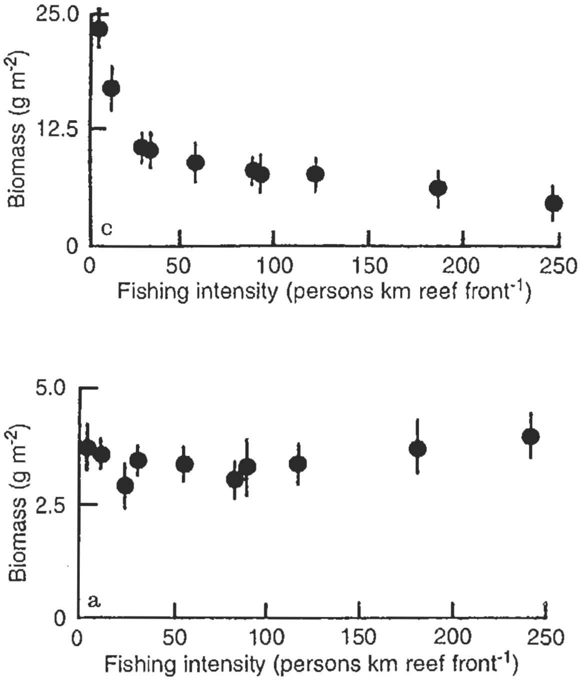


Figure 6. Piscivorous fishes > 30cm against fishing intensity in ten Fijian fishing grounds (top graph). Herbivorous and invertebrate feeding fishes <15 cm against fishing intensity at the same ten grounds (bottom graph)(From Jennings & Polunin 1997).

e. Spawning aggregations

Many reef fishes, including species of serranids, lutjanids, labrids, siganids, scarids and acanthurids, aggregate in large numbers at specific times and locations in order to spawn (Domeier & Colin 1997; Sala *et al.* 2001). A spawning aggregation can be defined as a gathering of conspecific fish, at densities significantly greater than normally occurring during the non-reproductive period, for the purpose of spawning (Domeier & Colin 1997). Spawning aggregations can be resident or transient depending on factors such as frequency, duration, site specificity and distance travelled to the site (Domeier & Colin 1997). Spawning aggregations also occur in temperate and deep water species, often subject to overfishing (Clark *et al.* 2000; Robichaud & Rose 2003). Indeed, the ease of fishing stocks that form spawning aggregations is a conservation concern (Johannes 1998; Burton 2002; Rhodes & Sadovy 2002). Spawning aggregations of the Nassau grouper, for example, have been reduced to about one-third of their original number in the Caribbean, with one of the last viable aggregations decreasing from 15,000 to less than 3,000 in the last 25 years (Sala *et al.* 2001). The Nassau grouper is a large species, and its LH traits further exacerbate its vulnerability to fishing pressure (Chiappone *et al.* 2000). The recovery of stocks that reproduce in spawning aggregations can be hindered by the effects of depensation (see box 2). Another major concern in fishing spawning aggregations is that in fishes that display hermaphroditic sexual patterns, heavily skewed sex ratios can result and may cause reproductive failure (Sadovy & Vincent 2002). The most obvious and effective management measure to protect species that form spawning aggregations is the use of closed seasons when the spawning occurs (Johannes 1998; Sala *et al.* 2001; Rhodes & Sadovy 2002). Compliance with these regulations in many resource limited situations is often poor (Rhodes & Sadovy 2002). Conversely, the use of closed seasons in some locations, such as Palau, has been pioneered by the fishers themselves based on their traditional management techniques (Johannes 1998). MPAs are again an important management technique here; however, it is important that the location of significant spawning aggregations are documented so the reserve boundaries can encompass them (Johannes 1998; Chiappone *et al.* 2000).

f. Specialisation

A major cause of rarity and risk of extinction in terrestrial and marine species is specialisation in habitat or feeding (McKinney 1997; Pyron 1999; Roberts & Hawkins 1999; Jones *et al.* 2002; Dulvy *et al.* 2003). Ecological specialisation accounts for 28% of known marine extinctions (large body size being the most prevalent extinction correlate accounting for 57% of the cases)(Dulvy *et al.* 2003). Of the average geographical range of coral reef fishes only 0.34% actually consists of coral reefs and the area of suitable habitat for individual species will likely be much less (Roberts & Hawkins 1999). Some species may specialise on very specific habitats, such as certain coral gobies that inhabit only one or two species of *Acropora*, whereas other species may have very specialised feeding habits, such as *Chaetodon trifascialis* which feeds on plating corals (Jones et al. 2002). Loss of those habitats or food sources will obviously present serious problems for those species. Perhaps the most worrying recent development on coral reefs, particularly in relation to specialists, is the increasing occurrence and severity of coral bleaching events. Six major episodes of coral bleaching occurred between 1979 and 1999, with the associated coral mortality affecting reefs in every part of the world (Hoegh-Guldberg, 1999). The mass coral bleaching event of 1998 is considered to be the most severe on record, with bleaching affecting every geographical coral-reef realm (Hoegh-Guldberg, 1999). An increase of 1-2°C in seawater temperature is expected by 2100 in response to enhanced concentrations of atmospheric greenhouse gases. This is expected to result in most regions experiencing bleaching conditions every year within 30-50 years and by approximately 2050, sea temperatures in tropical oceans will experience anomalies every year that will be several times those seen in 1998 (Hoegh-Guldberg, 1999). The resulting coral mortality is likely to significantly alter the makeup of present-day coral reef ecosystems (Lough, 2000). This large-scale coral habitat loss could cause a large number of extinctions (Reynolds *et al.* 2002) and specialists are likely to be worst affected. From a management point of view not a lot can be done, other than monitoring those species that are highly specialised to certain habitats and so most at risk and trying to reduce the multi-stressors in the regions where the species are most abundant. Species that are both locally endemic and specialised will be at greatest risk and should be identified and protected where possible.

III. Implications for sustainability

III.I Threats to large species

Clearly larger species tend to be more vulnerable to fishing effects; they tend to yield less per unit of biomass, to be more rapidly depleted by the same amount of fishing and to recover more slowly when fishing mortality is reduced or eliminated. There are cases for concern amongst smaller species, but the indication is that large species demand attention across the board in ecosystem-based fishery management both because of their own individual value, but also because of the possible ecosystem consequences of their decline. This is really the domain of conventional fisheries management, but because of disillusionment with this management, there is strong interest in the potential role of MPAs.

If the fishing mortality on a stock is reduced or removed altogether as it is in effective MPAs, numerical abundance should increase, and with greater survivorship, fish average body size should increase and with it biomass of the stock. However, world-wide, the median size of MPAs is 5km^2, much of this area is not reef and thus the median area of reef protected in MPAs is a mere 2.5km^2 (E.P. Green *et al.*, pers. comm. 2003). In this context the mobility of target species is important; at a location where fishing is otherwise intensive, sedentary target species may increase quite rapidly in abundance in small MPAs (e.g. Mosqueira *et al.* 2000; review in Russ 2002). In reality, many species do not necessarily show such MPA effects even when sedentary, and increase in MPAs is best detected when the species-level data are aggregated into families or trophic groups (e.g. Polunin & Roberts 1993; Williams & Polunin 2000) and increase is inherently unlikely in species that are mobile at large scales relative to MPA areas (overview in Polunin 2002). Large individuals are more likely to be more abundant in MPAs than outside (Mosqueira *et al.* 2000), but this is probably more to do with their sampling characteristics and vulnerability to exploitation than speed of biomass build-up (greater *r*); in fact large species are expected to recover more slowly than small species (e.g. Jennings 2001).

The mobility of fishes is rather poorly known; on the one hand some quite sedentary reef species prove to be rather mobile, while some apparently mobile species can be surprisingly site attached (e.g. Holland *et al.* 1993, 1996). The prevailing view is that mobility in most reef fishes is limited to distances of ~1km or less (Chapman & Kramer 2000; Russ 2002). Low mobility is conducive to biomass build-up in MPAs, which is essential to any increase in egg output as a basis for greater recruitment to exploited areas (Russ 2002). Low mobility also limits the distance over which 'spillover' occurs from MPAs into fishing grounds; most of the increase in abundance of large predatory fish at Apo Island (Philippines) after some 8 years of protection occurred within 500m of the MPA boundary (Russ & Alcala 1996b). There are implications that responsiveness of species to protection in MPAs is linked to LH characters, for example in differences among families in their relative abundance in MPAs (e.g. Mosqueira *et al.* 2000), and this is an area that warrants a closer look (Jennings 2001). However, *r* is not all that is involved; many increases in abundance in newly-created MPAs are too rapid to be accounted for by recruitment alone (Jennings 2001; Russ 2002).

In lagoonal habitats and in deeper waters surrounding reefs, even less is known about fish movements, but it is likely that the mobility of target species is far greater (e.g. Horwood *et al.* 1998) and for these, very large MPAs would be essential for stock recovery in areas where they were extensively depleted (FSBI 2001). The potential role of MPAs in increasing actual fisheries yield is widely debated. MPAs represent a relatively simple means to protect fish stocks and ecosystems from harmful exploitation, but other questions (including competing uses, social impacts, intensification of fishing outside and stock migrations) beg scientific questions about specific objectives. Thus use of MPAs as hedges for part of the spawning stock against management failure (Lauck *et al.* 1998) requires understanding of what area would be necessary, especially where other uses or negative consequences of closure are involved and there is mobility within the stock; for many continental shelf fishery-target species the area will have to be very large (e.g. 1000s km^2) (Guénette *et al.* 1998). In general, the good evidence needed for wide and sensitive application of MPAs in conventional management remains poor, but they have clearly helped increase local abundances of many site-attached species and this can be of great value where such animals are valued for reasons other than exploitation such as diving (Jennings *et al.* 2001a; Polunin 2002; Russ 2002).

III.II Ecosystem effects of exploitation

Whereas in oceanic systems, the overarching paradigm has been that ecosystem processes are driven by the primary productivity of phytoplankton and thus inputs of nutrients ('bottom-up control'), there is strong evidence that in reef ecosystems large carnivores play a significant role in determining the abundance of species and thus overall ecosystem structure ('top-down control')(for review see Pinnegar *et al.* 2000) and views of oceanic systems are changing (for review see Verity *et al.* 2002). Large-scale ecological data have been most influential in identifying the contrast in current understanding, but because of the limitations in the scientific approach the understanding remains rather shallow (Table 1).

Box 3 Two concepts of indirect effect in reef ecosystems

Keystone predation
Involves (1) two or more trophic levels (2) competition among organisms at the prey level and (3) predator control of a dominant prey species, and thus (4) changes in the keystone predator can lead to dramatic shifts in the abundance of species below it

Trophic cascade
Involves (1) three or more trophic levels and (2) abundance of each prey controlled by its predator and thus (3) changes in abundance of a top predator can have dramatic effects on the species composition at the bottom of the food web

There are many forms of possible indirect effects in ecosystems (Menge 1995), but at the ecosystem level, widely-discussed concepts are those of keystone predation and trophic cascades (Box 3). Candidates for keystone status are triggerfish such as *Balistapus undulatus*, the latter feeding on urchins in Kenya which control algae and these algae are thought to outcompete hard corals for space (McClanahan *et al.* 2002). The trumpet triton *Charonia tritonis* and the humphead wrasse *Cheilinus* *undulatus* probably help to control abundances of crown-of-thorns starfish *Acanthaster planci* which feed on hard corals and are also plausible keystone species, their depletion with that of the triggerfish probably helping to convert coral to algal cover in areas such as Fiji (e.g. Dulvy *et al.* 2002). These likely keystones are vulnerable to direct exploitation (Jennings & Lock 1996), implying that there is a direct link between fishery exploitation of particular species and ecosystem state. However, the keystone status relies on both predation and competition, and the extent and impacts of these processes are poorly known, the basis for predicting keystone species is poorly developed. Sea urchins, crown-of-thorns starfish and thick-shelled gastropods such as the coral-feeding *Drupella* (McClanahan 1994b) are also prominent in proposed trophic cascades of reefs (Pinnegar *et al.* 2000, Table 1).

If large predators and ecosystem state are strongly linked, then MPAs which are effective in increasing abundance of these predators can be expected to have consequences for the ecosystem as a whole. On the one hand, at Caribbean reef sites <10m depth where the grazing urchin *Diadema* was formerly abundant and the coral-to-algal shift has been quite well documented (review in McClanahan *et al.* 2002), there is little evidence that reef state has yet been affected by MPA status (ID Williams, pers. comm.). However in the 12-15m depth zone where *Diadema* was never common, a large-scale correlation between grazing fish and fleshy macroalgal cover suggests a connection between fishing and reef state (Williams & Polunin 2001). Large-scale fishing-gradient work in Fiji also suggests that fishing reduces the abundances of herbivorous and carnivorous fishes, both being conducive to an algal reef state through loss of grazing and loss of coral cover, respectively (Dulvy *et al.* 2002, NK Dulvy pers. comm.). The scientific foundations of such data are in a sense imperfect, but just as in fisheries science so in that of 'ecosystem management' the context demands some compromise with scientific rigour (Table 1).

An ecological basis for predicting the strength of trophic cascades scarcely exists (Shurin *et al.* 2002). While the concept of top-down control appears clear, there are many other processes such as recruitment contributing to changes in abundance and omnivory (e.g. species feeding across two trophic levels) having a balancing effect on such changes (e.g. Polis 1998). Food webs tend to be reticulate in nature, implying that predators tend to be generalists; thus the role of one predator removed by fishing may be replaced by that of another species. Food webs may be viewed as networks through which effects of predator depletion may be only patchily transmitted; as yet it is unclear what distinguishes the 'hubs' from the other 'nodes' of the network. In terms of systemic effects of predation, a species would be more likely to constitute a cascade hub if it were controlled by a single predator, relatively uninfluenced by other forms of mortality and recruitment variability and itself substantially controlling certain prey. Evidence for more linear feeding relationships comes from assemblages of carnivores in temperate waters, where predator-prey relationships are determined more by size than taxonomy (Jennings *et al.* 2001b) but it is unclear whether such rules might pertain to tropical reef ecosystems.

III.III Ecosystem-based fishery management (EBFM)

There are some classic cases of fisheries management extending beyond a single-species focus (Jennings *et al.* 2001a) and these include that of the Cape fur-seal/fishery interaction where culling of the predator was expected to produce benefits for the fishery. However a complex food-web model indicates that such a cull would probably reduce fishery yield (Yodzis 1998). The science of EBFM is in its infancy (Link 2002).

Reference points and control rules for EBFM have yet to be developed in the same way as they have for overexploitation of single stocks of bottomfish, pelagic fish and crustaceans (WPRFMC 2002) where overfishing is defined in terms of the reduction of biomass to a set fraction of the biomass at MSY, a reference point beyond which rebuilding action must be taken. How might EBFM be realistically regulated in terms of reference points and trajectories? A possible departure from conventional fisheries management in EBFM is that while fisheries management can use data gathered through landings and exploratory fishing data, many considerations that might be part of EBFM (e.g. coral cover, non-target

Box 4. Size spectra analysis for EBFM

Size spectra analysis can be used to describe a fish community by looking just at the size of individuals across the community, regardless of taxonomy. A regression of the community size frequency distribution gives values for both the slope and the intercept. Steepening of the slope and raising of the intercept value can be a result of either a decrease in the number of large fish, or an increase in the number of small fish, or both, and this can be elucidated with simple statistics. This simple technique to assess community structure has been applied in various demersal fisheries, both tropical and temperate (e.g. Rice & Gislason 1996; Gislason & Rice 1998; Bianchi *et al.* 2000), but until recently no attempt has been made to apply the technique to coral reef fish assemblages. Future use of this simple ecosystem-level approach should be developed to compare coral reef fish communities through time, across fishing gradients and between MPAs and adjacent fisheries.

species) would not be routinely monitorable. There is a large range of potential community measures such as diversity indices, size spectra, trophic level, and a variety of food web structural features, concepts and fluxes. Which is used will depend on objectives of EBFM, resources and what is feasible. The objective here is to discern approaches which might be accessible for tropical reefs given further research. Simple surveys of the size of the fish assemblage to conduct size spectra analysis is one obvious possibility (Box 4).

IV. Research needs

The three main approaches scientists use to study fishing effects on communities all have weaknesses (see Table 1). An inherent challenge in recommending types of research in support of EBFM is spatial scale. Large-scale comparative studies are most representative of the natural environment. Rigorous experimental work is conducted only at small scale (1-100s m^2), whereas the scale of any fishing and fisheries management is far greater (1-1000s km^2). The opportunities for scale-relevant work to inform EBFM are in fact very few. They include studies of long-term change (e.g. Jennings *et al.* 1999b, 2001a), of large-scale differences in community structure (e.g. Dulvy *et al.* 2002) and modelling (e.g. Grigg *et al.* 1984). The first requires long-term sets of data that for life-history studies would really need to be broken down to species level; appropriate detail and time spans appear not to exist for tropical waters, although this needs checking. The second needs large-scale differences in fishing pressure, such as those found between along fishing gradients or between effectively enforced MPAs and fished areas. The third needs to become more proactive in incorporating 'real' data.

Table 1. The three main approaches to investigating fishing effects on communities in the marine environment and the major challenge faced by each approach.

Approach	**Challenge**
Experimental	Small spatial scales used make it difficult to convincingly relate to the natural environment
Comparative (large scale)	Difficult to control for variables so results may be confounded by habitat, recruitment effects or other effects
Modelling	Mostly theoretical so comes under criticism for not using real data

First we will discuss some general research needs relevant to the various chapters above. Then the two key issues of how fishery depletion or recovery can be predicted in vulnerable species and how metrics to inform managers of ecosystem-level change can be developed will be explored. Finally two areas of feasible research much needed at the present time will be discussed

LH traits and capture fisheries

Although influences such as high value and rarity must be considered, many workers advocate the use of maximum size as a predictor of species vulnerability to exploitation (e.g. Jennings *et al.* 1998, 1999a; Dulvy *et al.* 2000, 2003; Frisk *et al.* 2001, 2002; Reynolds *et al.* 2001; Denny *et al.* 2002). Maximum observed size may thus be used to identify those species that are likely to be most at risk and thus most in need of monitoring, reducing labour intensity. An exciting management possibility involves use of maximum size and a standardised method for assessing fishing intensity as predictive tools to assess how different species will respond to the exploitation (Jennings *et al.* 1999a). Further development of the method (e.g. specific factors such as habitat degradation and recruitment variations need to be addressed) would enable species at particular risk to be identified region by region and appropriate management methods to be employed, taking into account the local situation. Continued collation of LH traits of different species, and investigation of suitable surrogates will be useful, provided this is at a fishery-relevant scale. Further use of the comparative method will ensure phylogenetic relatedness of species is accounted for.

Coral reef specific issues

More research is needed at the species level for the most heavily exploited fish in the live reef trade for both food and aquaria. However, as with conventional reef fisheries, the resources are not available to do this at a large scale. Studies on maximum sizes of the species involved may be one avenue worth exploring, however the strength of such techniques when looking at such small species as those exploited for the aquarium trade needs to be assessed. Data on particularly vulnerable or heavily fished species will be important and continued trade monitoring of these is essential as is the further development of databases such as GMAD.

Malthusian overfishing occurs as a result of poverty and human population growth. The use of fishing intensity gradients (see below) are a means of assessing the impact of increasing human populations based on the fishing techniques of local users.

Maximum size data may also be useful in assessing the vulnerability of non-target species to fishing pressure when they are affected as bycatch, however research on this is needed. Previous studies have documented evidence of prey release and species outbreak at the species level, but not when species data are aggregated. Future work at the intermediate level, trying to elucidate LH traits that result in fish and invertebrate species outbreaking or declining when predators and competitors are removed, is much needed. Also, innovative ways of looking at the system, such as through size spectra analysis may be fruitful avenues to explore. The importance of large-scale spatial and temporal data collection techniques should again be highlighted here, resulting in fishery-relevant results.

Knowledge of location and timing of spawning aggregations is necessary to enable these vulnerable occurrences to be protected within MPAs or closed seasons. Further studies of the effects of fishing spawning aggregations on the sex ratios of the exploited populations should be carried out to assess the effect of different fisheries, such as the live food fish trade when this targets smaller individuals.

Identification of species that are highly specialised, particularly those that are also endemics, will be important to enable management measures for their protection to be developed.

Sustainability issues

More research on the effectiveness of MPAs in building up stock biomass is badly needed. In particular this should address species with different LH traits to assess how this specifically relates to speed of recovery when fishing mortality is removed. Further studies on mobility of both bottom dwelling and pelagic species should be a priority, as it has implications for which species will benefit from MPAs and on the size of the area that should be protected. Tag and release, sonic tracking and natural marking techniques (such as through stable isotope analysis) will be useful in investigating such movement patterns. Current understanding is that many species display large intra-reefal movement, but little movement across channels between reefs (Davies 1995). Clearly, a marine reserve encompassing a section of a reef or island would be preferable to a whole reef or island if spillover of adult biomass is a primary objective (Graham 2003). Concern over adequate protection of species such as coral trout that move large distances within reefs would have to be considered in this case (Davies 1995; Kramer & Chapman 1999). However, increases in predator densities and biomass can occur within MPAs which only protect part of a reef (Russ & Alcala 1989, 1996a; Williamson 1999). Furthermore, work on the coral trout *P. leopardus* has demonstrated that although home range size may be large, there is often a preference for a number of smaller locations within that range (Zeller 1997). Further research on this topic is needed. However, as adult spillover is typically local to the reserve boundary (Russ & Alcala 1996b), perhaps the most pertinent issue for the advocacy of MPAs as fishery enhancement tools at present is the degree of openness of larval dispersal of coral reef fish, as the evidence for increases due to larval export is still inconclusive (Nowlis & Roberts 1999; Crowder *et al.* 2000; Russ 2002). Traditionally thought of as open populations with wide dispersal, several studies are suggesting a high degree of self recruitment to natal reefs (Box 1). This important topic is inherently difficult to research, however new techniques are being developed to quantify the amount of self recruitment versus dispersal to other reefs.

Ecosystem effects of fishing and MPAs should receive high research priority. The increasing number of multistressors on reefs, including coral bleaching, may result in phase shifts in reef communities becoming more widespread. Identification of keystone species and hubs in food webs will likely be advantageous in understanding such perturbations.

Key questions that need to be explored include:

How can fishery depletion or recovery be predicted across assemblages of reef species?

Marine tenure systems in parts of the South Pacific provide an opportunity to assess large-scale effects of fishing on reefs. For example, customary fishing rights areas (CFRAs) or *qoliqoli* in Fiji provide an exciting opportunity because they represent a gradient of fishing intensities at large scale. As a set number of people have fishing rights to each area, reliable estimates of fishing intensity can be established (Jennings *et al.* 1999a). Other marine tenure systems and effective MPAs also provide an opportunity to study ecosystem effects of fishing at large spatial scales (Russ & Alcala 1999, Graham *et al.* 2003). Many tropical regions have heavily-impacted reefs (e.g. South East Asia and the Caribbean), but in the South Pacific many reefs remain in a relatively pristine condition (Dalzell et al. 1996) permitting studies of the effects of fishing with the onset and development of exploitation. Use of these fishing gradients and MPAs to further study the effects of fishing and protection on vulnerable species and validate use of LH data to elucidate trends will be an important avenue for future research.

Estimation of *r* from spawner-recruit relationships at small stock size and relating this to LH data or suitable surrogates will assist in developing simple techniques for predicting both vulnerability and rebound potential and thus for management. Specific studies of different sized stocks could address the issue of depensation, although this is a complicated topic, particularly with the high variability in recruitment and the current debate over the openness of fish stocks.

Refinement of visual and video techniques for estimating abundance of large infrequent species is needed. Behavioural responses of some species to SCUBA divers can result in unreliable estimates through underwater visual census (UVC) (Willis & Babcock 2000). Furthermore, rarer species may not occur in great enough densities to be picked up by UVC (Dulvy *et al.* in prep) and thus alternative techniques to assess their abundances are required. Other techniques such as hook and line fishing and baited underwater video (BUV) can be useful alternatives to UVC for carnivorous reef fishes (Willis & Babcock 2000). Surveys of local fishers can also be useful to establish the distribution of large rare species (Dulvy *et al.* in prep). The general consensus at present is that different survey techniques may be necessary depending on the species of interest and that a combination of techniques may be necessary to survey multispecies assemblages (Willis & Babcock 2000; Willis *et al.* 2000).

How can metrics be developed to inform managers about ecosystem-level change?

EBFM reference points will require development of appropriate ecosystem-level metrics. Further development of databases of LH variables for reef species which can be made widely available to managers will assist them in making informed management decisions. Research to date is advocating maximum size compared to the nearest relative as a useful and reliable indicator of which species in a community will decline more rapidly than others. Continued corroboration of these kinds of simple indicators with the work outlined above will enable managers to use the technique with some confidence.

Stable isotope analysis can be used to assess the trophic level of individuals and thus make comparisons between areas of differing fishing intensity. Furthermore, a recent study in the North Sea has demonstrated that size, regardless of taxonomy, is a good predictor of trophic level in a mostly carnivorous fish community enabling linear feeding relationships to be analysed (Jennings *et al.* 2001b). Repeating this work on coral reefs to see if the same relationship is apparent would facilitate simple trophic modelling (e.g. Ecopath, Ecosim) of fishing and assessment of its ecosystem effects.

Size spectra analysis is one simple technique that has proved useful in demersal fisheries and could easily be applied to the coral reef fishery environment (Box 4). Species richness and diversity indices of various kinds also provide combined measures of the number of species present and the distribution of individuals among them.

Large-scale ecology enables correlations to be made, for example between grazers and corals, or predators and grazers. With further development of these correlations it may be possible to detect thresholds over which a shift in the community structure or a likely phase shift will occur. A recent study across a fishing intensity gradient in Fiji, for example, has demonstrated a threshold linked to predator depletion over which crown-of-thorns starfish outbreak and will likely lead to a phase shift in the community (Dulvy *et al.* in review). Assessing the likelihood of such phase shifts through indexes of fishing pressure and simple assessments of predator density could be a means for marine management.

Specific research suggestions

Development of suitable reference points for EBFM will require new metrics to be developed. Two projects are recommended in this regard.

1) *Cross-species changes.* This project would begin with a feasibility study to establish what current long-term data sets, and/or locations with fishing gradients could be utilised to assess effects on ecosystems. The project would then test the predictive model outlined in Jennings *et al.* (1999a) which uses a standardised measure of fishing intensity and maximum size data to establish a quantitative relationship between effort measures and abundance trends. A similar index of fishing pressure as used in previous work in Fiji could be applied to test the model elsewhere if resource users in the area are reliant on the reefs for their protein at a subsistence level, but not commercially (Jennings *et al.* 1999a). However, a more accurate measure of fishing effort is required using the number and size of boats, number of fishers, area of reef and commercial output. Once established the technique could be tested by making predictions of abundance trends in a new region from the fishing pressures exerted there and then ground-truth these predictions with underwater visual census. If a reliable predictive method could be developed it would greatly reduce the management effort and resources needed to assess coral reef fishery stocks in a wide range of situations and locations.

2) *Ecosystem-level changes.* An interesting way to look at the ecosystem effects of fishing is through indirect effects such as predator-prey relationships. If there were much redundancy, ecosystem structure would tend to be maintained when many species were removed (Naeem 1998), while keystone species constitute hubs among the nodes of ecosystem networks (Jain & Krishna 2002), their removal resulting indirectly in outbreak and/or 'dropout' of other species in the system. In reality species are likely to vary in their importance for ecosystem structure and consequences of large-scale species removal and recovery will only be understood if rules governing these roles are elucidated. The characteristics that may render some species relative to others more vulnerable to outbreaking, or declining, have yet to be identified in marine systems, but modelling and observation suggest a range of possibilities, including in particular vulnerability to predation, and biological characteristics that are conducive to it (e.g. for insects Hunter 1991). Understanding these characteristics would have substantial implications for the way relatively pristine communities are managed, the trajectory of systems recovering from impacts, and the fundamental understanding of the relationships between the whole and its biological parts.

The fishing gradients available in areas of the Pacific offer an opportunity to investigate these questions in relatively pristine habitats away from other anthropogenic impacts. Densities of fishery-target fish and non-target fish and mobile invertebrates would be determined by focusing on diurnally active non-cryptic species in underwater visual counts (Jennings & Polunin 1997). Selecting which species to include would involve a two-stage process. Firstly, a database of candidate species would be drawn up to highlight ecological contrasts, based on published data including FishBase (www.fishbase.org). Secondly, during an initial field work phase, this database would be matched with abundances of species in the field. High replication together with the species focus would increase the power to detect small differences in abundance at large scale (Graham *et al.* 2003).

A derived response variable of species to differences in predation pressure would be related to life history (e.g. growth, reproduction, body size) and ecological (e.g. trophic or behavioural attributes) factors. Many biological attributes may be linked to predator vulnerability, and these would be categorically assigned, including feeding location (off-reef vs. on-reef), shoaling behaviour (shoaling vs. solitary/small groups), mobility (territorial vs. home ranging), body size (L_{max} large vs. small), trophic level (high vs. low) and defence against predators (e.g. mimicry, opercular spines, body spines, poisonous/non-poisonous spines, crypsis and eye spots, inflation, toxic skin). From a statistical analysis of relationships between the corrected response variable values and life-history/ecological characters, a model could be derived of how these characters are associated with the response of the non-target invertebrates and fishes to the removal of large consumers.

Other ways to asses changes across whole communities are through diversity measurements and size spectra analysis (Box 4). Unpublished size spectra from coral reef fisheries in Fiji provide evidence of prey release towards the lower end of the size range, but as yet the smallest size classes and species have not been investigated. Simple underwater surveys of the whole assemblage by size alone could be used to assess changes in community structure across gradients of fishing pressure, between fished and protected areas and ultimately through time. Size spectra and diversity data are synoptic measures of change which seem particularly good candidates as the basis for EBFM reference points, but these clearly need further research.

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