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No-take zones: does behaviour matter?

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Abstract

No-Take Zones (NTZs) or strict Marine Protected Areas are being widely promoted as a powerful tool against overexploitation of fish stocks. Increased catches and sustainability of adjacent fisheries are proposed to result through two mechanisms: spillover of maturing adults, and export of larvae from spawning within the NTZ. However, the effectiveness of NTZs will depend on various factors, including the behaviour of the fish species concerned. Species with smaller territories or home ranges, such as small serranids, will show less spillover of adults than those with larger territories or home ranges, such as carangids. On the other hand, species whose home ranges are large in comparison to an NTZ will receive little protection from it. Fish, such as rabbit fish (Siganidae) or Napoleon wrasse (*Cheilinus undulatus*), that show diel or other regular movements to forage or spawn in adjacent areas, will be vulnerable to exploitation outside NTZs, unless protected areas are extended to incorporate the range of particular populations. Similarly, species such as large serranids, lutjanids and lethrinids, that show seasonal migrations to regional spawning sites, are vulnerable to being targeted, unless spawning aggregation sites are also protected. The reproductive behaviour of species, for example whether they show sex reversal in response to growth or social status, may also influence the effectiveness of management interventions. The behaviour of fish larvae can also be important in determining the extent to which they recruit to their natal area. Increasing evidence suggests that larval behaviour may be adapted to promote local recruitment, as well as wide dispersal, to a greater extent than previously supposed. The effects of protection against fishing will also depend on the trophic level of species. Both fish and invertebrates that are either prey or competitors of the principal exploited species commonly show reduced abundance within NTZs, and enhanced abundance in areas where fishing is more intense. Thus knowledge of the ranging and migratory behaviour, not only of individual species but also of specific populations, is required to inform the design of networks of NTZ; data on foraging, social and reproductive behaviour are important for predicting the effects of protective measures. Tracking individuals by telemetry can provide information critical to the conservation and sustainable management of stocks.

Introduction

In the face of declining and even collapsing marine fish stocks globally (FAO, 2003), protected areas closed to fishing, known as No-Take Zones (NTZs), or Strict Marine Protected Areas (sMPAs), have in the last few years been widely promoted as a powerful tool against overexploitation of fish stocks (Roberts and Polunin, 1991; Dugan and Davis, 1993; Rowley, 1994; Bohnsack, 1998; Roberts and Hawkins, 2000). This paper will consider the importance of the behaviour of species at different life stages with regard to the effectiveness of NTZs, primarily focusing on reef areas and coastal species. As will be illustrated, hydro-acoustic telemetry of tagged fishes provides a valuable tool for assessing the relevant behaviour of adult fish and increasingly of juveniles also.

Initially, NTZs were adopted in tropical coral reef areas as a measure to protect pristine coral reef communities for conservation purposes, or as an alternative to standard estimations of maximum sustainable yield and allocation of quotas. Determination of Total Allowable Catches (TACs) for the more than 100 species commonly present in tropical reef catches would be impracticable, and enforcement of quotas among uneducated, artisanal fishers in remote areas almost impossible. NTZs represent a simpler solution to such problems: any fisher observed within the NTZ is presumed to be in breach of regulations. In principle by assuming a degree of site fidelity among exploited species, fishing effort can be regulated by adjusting the proportional extent of NTZs in relation to fished area. With fish telemetry studies, the actual movement and location of fish can be related to areas, allowing a more practical definition of NTZs boundaries to be made.

A series of related fisheries and environmental benefits have been argued in relation to NTZs (Bohnsack, 1998). It has been anticipated that they can:

- prevent loss or extreme depletion of a stock, so safeguarding the potential for future recovery;
- protect spawning sites, or a portion of the stock, to ensure effective spawning, thus reducing the risks of recruitment-overfishing of stock;
- maintain or enhance fisheries yields in adjacent areas, by protecting fish within the NTZ until they have grown to larger size and emigrate to fished areas;
- buffer the stock against extremes, thus reducing uncertainty and variability in yield;
- protect genetic diversity if multiple NTZs can be located so as to protect portions of genetically separable populations or sub-populations;
- provide data on unexploited stock levels and on natural mortality, required to model maximum sustainable yields;
- provide reference sites for distinguishing effects of environmental change from ecosystem effects of fishing;
- protect other non-target species that may be important for ecosystem structure and function, e.g. keystone predators of echinoids.

Of the potential benefits, the most important is the anticipated gain to adjacent fisheries. The extent to which this may occur is still in dispute, and the mechanisms are the key subjects of considerable research.

The Reserve Effect

It is now widely accepted that, in regions subject to significant fishing pressure, there are positive effects of establishing a NTZ. These include an increase in fish abundance and biomass within the NTZ, and commonly an increase in mean fish length. These effects have become known as the reserve effect. Prior to the 1980s, fish population biologists tended to believe that fish recruitment was independent of spawning standing stock, and spawning standing stock would therefore not be affected by fish catch. The first evidence that a reserve effect would develop within a NTZ came from work in heavily fished tropical regions of South-east Asia (Alcala, 1988; Alcala and Russ, 1990). Among well-known examples was the observation by Russ (1985) of a four-fold increase in abundance of predatory fish in the Sumilon Island reserve, Philippines, over eight years following protection of the area. Subsequently, similar effects were described from NTZs or sMPAs in southern Africa (Buxton and Smale, 1989), Eastern Africa (McClanahan and Muthiga, 1988; Watson and Ormond, 1994), and the Caribbean (Polunin and Roberts, 1993).

To date, there have been 80 or more studies on the effect of establishing NTZs (see recent reviews by Halpern and Warner, 2002; Halpern, 2003). These studies compare fish stocks within an NTZ reserve either with those in the same area before protection, or with those in a similar adjacent area not given protection. The overwhelming majority of studies have recorded greater abundance, biomass, size and diversity of fish within the NTZ.

NTZs have also proved effective in increasing the stocks of commercially exploited invertebrates. For example, there has been an increase in the rock lobster, *Pagurus auratus,* by a factor of 5.8-8.7 inside the Leigh Marine Reserve, New Zealand (Babcock *et al*.,1999). A greater number of gray snapper above legal fishable size (>25.4 cm) have been recorded within a mangrove area set aside within the Everglades National Park to protect alligators (Faunce *et al*., 2002). This latter example is interesting as it demonstrates an effect of protection in the USA, where the authorities and sports fishermen have been very resistant to establishing any NTZ as a purely fisheries management measure.

Effects on Fish Catch

That protection usually results in an increase in fish abundance within protected areas is beyond doubt. More critical in relation to fisheries management is whether or not the establishment of NTZs can result in an increase in the same stock in adjacent areas, outside of any NTZ, and in particular whether it can result in an increase in catch from surrounding areas.

There are now some ten studies that have documented an increase in stock or catch. In perhaps the earliest well-known study, Russ and Alcala (1996) recorded a steady increase in the abundance of predatory fish immediately adjacent to the Apo Island Reserve in the Philippines. The ratio of their abundance inside versus outside the NTZ increased, as protection first influenced abundance within the reserve, and then decreased, as fish also increased their abundance outside the reserve (Fig. 1).

The most dramatic apparent benefit to fish catch from adjacent areas with which the authors are familiar occurred in the Shimoni area of the coast of Kenya (Watson and Ormond, 1994; Watson *et al.*, 1997). Here the large MPA incorporated a series of offshore reefs and islands, divided into two comparable portions. In one of these, the Mpunguti Marine Resource Area, fishing by local artisanal fishers was permitted. In the other, the

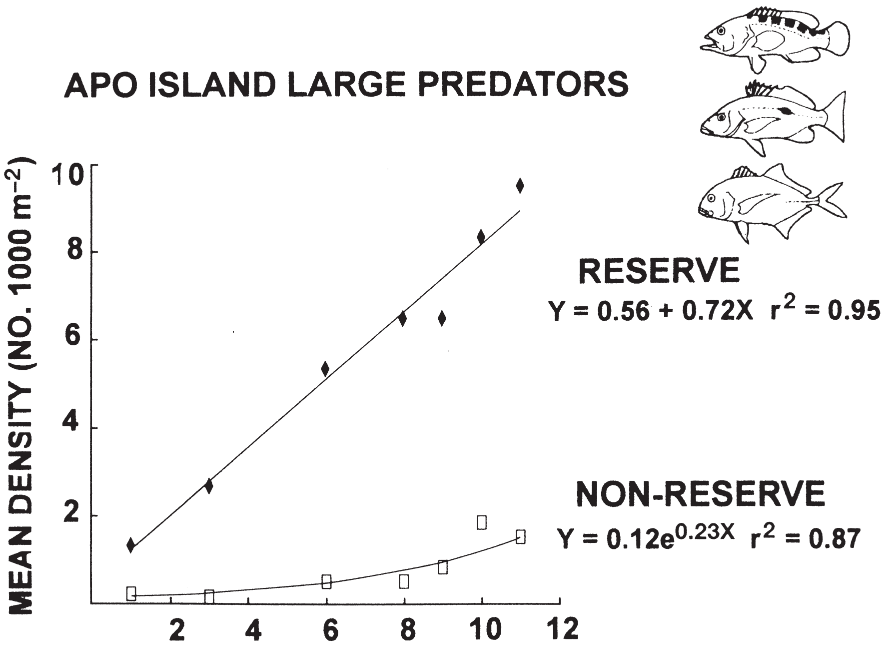

Fig. 1 – Increasing abundance of predatory reef fish both within and outside Apo Island reserve in the Philippines, with increasing time from the establishment of the protected area (from Russ and Alcala, 1996).

Kisite Marine National Park, fishing was in principle prohibited, although this prohibition was rarely enforced through the 1970s and 1980s. During the 1980s, there was a sharp decline in fish landings in the Shimoni region. Subsequently, in 1988, the Kenya Wildlife Service began enforcing the prohibition on fishing in the National Park. This was supported by a campaign of environmental education directed at local fishing communities, to persuade them of the potential benefits to the fishery of enforcing the National Park as a no-take area. By 1995, the fish stocks within the National Park area had increased to up to ten times that within the fished Mpunguti Marine Resource Area, and the fish catches from the remaining marine areas had recovered to the earlier higher level, despite a reduction in the area being fished (Fig. 2). Among more recent similar studies is a clear improvement in fish catches of between 46 and 90% within the fished areas between five small No Take Areas, established on the Caribbean island of St Lucia (Roberts *et al.*, 2001).

Mechanisms of Fisheries Enhancement

Any benefits to adjacent fisheries from the establishment of NTZs are presumed to arise through two distinct, but related, mechanisms. Firstly, if there is an increase in spawning stock within an NTZ, then an increase in the production and dispersion of larvae should result in increased 'larval export' to other areas. If stocks in neighbouring fished areas have through fishing become recruitment limited, then they may be enhanced through resulting increased

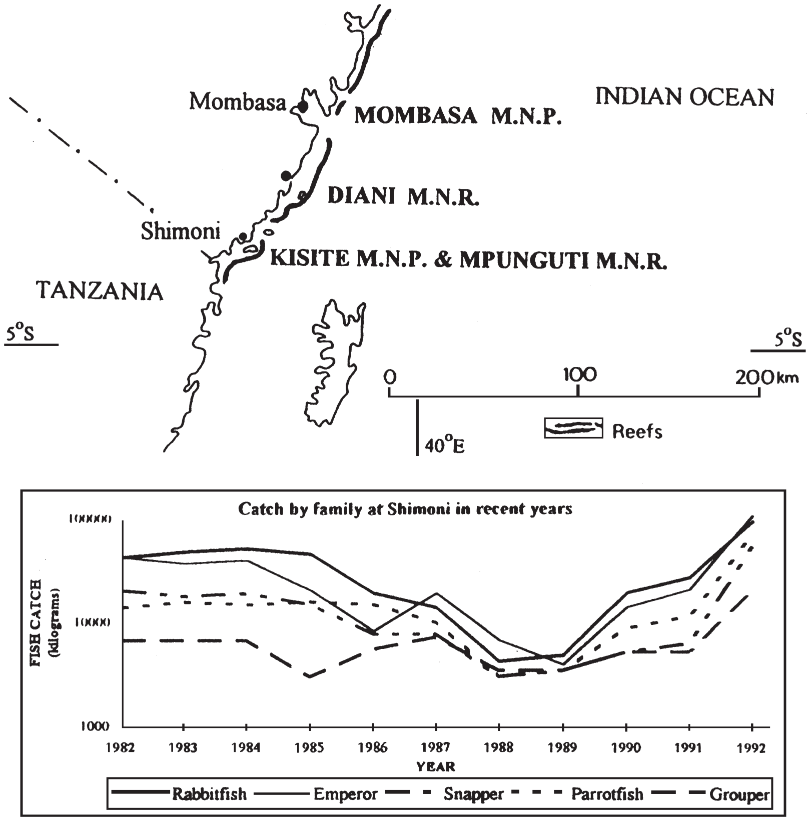

Fig. 2 – Decline and recovery in the fish catch of reef fishes in the Shimoni region of Kenya. Recovery followed enforcement from about 1990 of the fishing prohibition within the Kisite Marine National Park (from Watson *et al.*, 1997).

recruitment. Secondly, if there is an increase in abundance of adult or juvenile post-recruitment fish within the NTZ as a result of protection, then some of these fish may be expected to move out of the NTZ to surrounding areas where population densities have been depleted as a result of fishing. Even where there is no significant movement in response to a population gradient, individuals with home ranges towards the edge of an NTZ may have their home range extending over an NTZ boundary, and so may be liable to capture. The movement of post-recruitment and adult fish out of an NTZ has been termed 'spillover'.

The extent of larval export and spillover from NTZs to fished areas has become a subject of considerable topical interest. Spillover from an NTZ will clearly be influenced by the ranging and migratory behaviour of the fish. Local fishers implicitly acknowledge the occurrence of spillover by fishing close to the boundary of an NTZ, a practice often referred to as 'fishing the line'. Evidence for spillover may be relevant to local fisheries managers in seeking the support of local fishers for the establishment or maintenance of an NTZ. By contrast, it has been assumed that local fishers are less likely to experience a benefit from enhanced larval export, since fish larvae were presumed to be carried passively by ocean currents to areas a considerable distance away. This view, however, is being revised as a result of new knowledge about fish larval behaviour. We will consider the influence of fish behaviour first on spillover, and then on larval export.

Spillover and Species Mobility

The mobility of post-recruitment fish will determine the extent of spillover from an NTZ. As pointed out by Bohnsack (1996), however, the degree of protection afforded a population through the establishment of an NTZ will itself be inversely related both to species mobility, and to the size of the protected area. Thus species with large home range size, compared to the size of an NTZ, will receive relatively little protection from the enforcement of the NTZ (Holland *et al.*, 1996). In the extreme case, migrant or free-ranging species will receive no benefit from the creation of NTZs, except where critical areas, such as spawning grounds or migration bottlenecks (e.g. for tuna passing through the Straights of Messina), can be protected.

These conclusions were supported by Kramer and Chapman (1999) who modeled species mobility and spillover influence on abundance differences between NTZs and surrounding fished areas. They found that:

a) increases in abundance will be higher in reserves that are larger or have higher area to edge ratios;
b) species with low mobility will show greatest increase within the NTZ, and hence greatest potential increase in larval export;
c) species with intermediate levels of mobility will provide the greatest spillover benefit to nearby fisheries.

This latter conclusion arises because i) although fish with very high mobility will not receive protection from the creation of an NTZ, ii) fish with very low mobility will develop increased abundance in the NTZ as compared with the fished area, but will show minimal spillover. A variety of other models have sought to predict the effect of NTZs on fish catch (e.g. Polacheck, 1990; DeMartini, 1993).

Fish species that are territorial will be least mobile. In behavioural studies, a territory is defined as an area that is both exclusive to one or more individuals, and is defended against other individuals (Wilson, 1975). A high proportion of coral reef fish are territorial, though once territories have been established, individuals may show agonistic behaviour only occasionally and even appear to tolerate the presence of neighbours. Territories may be occupied and defended not only by single fish, but by bonded pairs, as in many butterflyfishes (Chaetodontidae), or by larger social units, as in many wrasse (Labridae), parrotfish (Scaridae) and groupers (Serranidae) (Reese, 1975; Robertson, 1972; Kuwamara, 1984; Van Rooij *et al.*, 1996). In many reef groupers, a dominant territorial male defends a large area within which females occupy a series of overlapping home ranges, or non-overlapping sub-territories within it (Shpigel and Fishelson, 1991). The size of territories varies considerably between species from only a metre or two, as in the some damselfishes, such as *Stegastes*, (Sadovy, 1986) to hundreds of metres in the case of the largest parrotfish (e.g. *Cetoscarus bicolor*) (unpubl. data RFGO) and grouper (e.g. *Plectropomus* spp.) (Zeller, 1997). As in other vertebrate groups, the size of territories varies inversely with food abundance, but broadly speaking the size of territory increases with the biomass of the species.

Home ranges differ from territories in being areas that are neither exclusive nor defended (Wilson, 1975). They too vary considerably in size, but usually they are larger than territories for the same or comparable species. Home range size depends on species and habitat, but is generally proportional to body size, both across species (Kramer and Chapman, 1999) and within a species, as described for coral trout, *Plectropomus leopardus* (Goeden, 1978).

Reef fish territories can be plotted by following (e.g. with SCUBA) and mapping the movements of individual fish for as little as a few hours. Where individuals can be recognised through tagging or individual variation in colour pattern, more precise plots can be obtained. By contrast, it can take much longer to plot the full extent of an individual's home range, since some parts of the range may be visited relatively infrequently. Hence acoustic tracking may be a more effective method, particularly for larger fish species with correspondingly greater home ranges. Zeller (1997) plotted the territories of coral trout, *Plectropomus leopardus,* at Lizard Island, Australia, by ultrasonic telemetry (Fig. 3). Fish were recorded for a maximum of 202 days, observed to use regular locations, moved a mean of 192 m with a maximum distance of 1122 m, and had average minimum polygon home ranges of 10458-3188 m^2, that were observed to be stable within and between tracking sessions.

An example of a study using telemetry to map the home ranges of a species within a small marine protected area (<1 km^2) was carried out on Coconut Island, Kaneohe Bay, Hawaii (Meyer *et al.* 2000). The home ranges of five Hawaiian white-saddle goatfish were determined using acoustic tags and fixed hydrophones. All of the fish remained within the reserve, but showed consistent diel behaviour patterns, refuging in holes within preferred areas by day, and foraging over extensive areas of sand and coral rubble by night. Another study at the same site illustrates how some species often assumed to be wide ranging may in fact have relatively well defined home areas. Holland and colleagues (1996) tagged blue trevally, *Caranx melampygus,* with both acoustic transmitters and plastic tags; 75.5% were recaptured or relocated within 0.5 km after 4-454 days, but the distance from site of first capture was not related to time at liberty.

Dispersion

While many reef fish species are territorial, or have fairly well defined home ranges, others may be essentially vagrant, wandering over broader regions in search of food and shelter. Some may adopt temporary home ranges on encountering suitable habitat or abundant food, before moving when conditions become less favourable. The degree of protection afforded such species by an NTZ will depend on two factors. These are the length of time that individuals typically remain in an area, and the rate at which individuals present within the area at any one time disperse over a wider region.

Information on the extent and rates of dispersion of such species has come as a by-product of mark-recapture studies using conventional tags. Of 2,932 red snapper tagged on artificial reefs in the Gulf of Mexico, approximately half were recaptured locally, while others moved a mean of 29.6 km, and a maximum of 352 km (Patterson *et al.*, 2001). Similarly, in a mark-recapture study of five temperate reef fish species, 7.4% of one species, *Petrus rupestris,* were found to have moved 200-1000 km towards distant aggregations of the same species. Among the other four species, 57-93% of individuals had not moved away, and the remain-

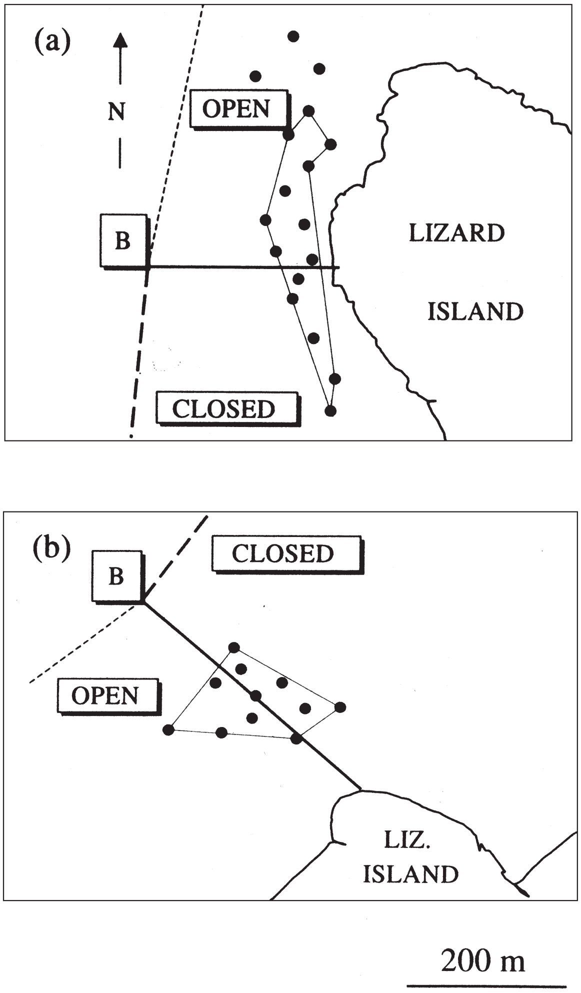

Fig. 3 – Two examples of the home ranges of coral trout, *Plectropomus leopardus,* at Lizard Island, Great Barrier Reef, as determined by ultrasonic telemetry. The polygons show the minimum area polygons for the individual fish, whose home ranges in these cases straddle the boundary between areas open and closed to fishing (from Zeller and Russ, 1998).

der had moved only short distances from the site of first capture (Griffiths and Wilke, 2002). However, it is not always easy to know how such results should be interpreted, because there are issues of fish mortality and tag loss, which can be high in reef fish (Whitelaw and Sainsbury, 1986). The behaviour of the fish recovered, or those that have been tagged, may not be representative of the population. For example, many of the fish not recovered may be those that moved out of the search area. Capture and tagging activities may provoke affected fish to move more when they might not otherwise have done.

Direct Observation of Spillover

A number of studies have been undertaken with a view to monitoring movement of fish out of a protected area. Attwood and Bennett (1994) tagged 11,022 fish over 5.5 years within the 50 km long Tsitsikama coastal reserve, South Africa. Of the 9.1% that were recaptured, 17.8% had moved outside the reserve. Other studies have used underwater observers as a means of re-recording tagged fish. Beinssen (1988) tagged 273 coral trout at Heron Island, on the Great Barrier Reef, Australia, of which 13.9% were resighted. Most of these had moved only short distances (500-1500 m), and were presumably still within their original territory; only one crossed the boundary to move out of the Heron Island reserve. Chapman and Kramer (2000) used both recapture and underwater observation to re-record fish tagged on capture in Antillean fish traps in the Barbados Marine Reserve and adjacent non-reserve. Standardised recapture distances ranged from 0 to 116 m, and weighted median re-sighting distances from 0 to 44 m, depending on the species. The greatest re-sighting distance was 538 m, and the greatest recapture distance 616 m; despite these figures no emigration from the reserve was recorded.

Hydro-acoustic telemetry is increasingly providing an alternative tool for such studies, since individuals can be relocated and tracked on a more reliable basis, and tracking can be undertaken in deeper water that is unsuitable for work using SCUBA. Eristhee and Oxenford (2001) tracked Bermuda chub by acoustic telemetry. They found consistent overlapping individual home ranges that were similar in size between reserve and non-reserve sites. Similarly, Zeller and Russ (1998) used ultrasonic telemetry and underwater observation of freeze-branded individuals to compare movement of coral trout, *Plectropomus leopardus,* in and out of NTZs at Lizard Island, Australia. The density of coral trout was 20% higher in the NTZs, but the difference was not significant: 93 of the 183 freeze-branded fish subsequently observed underwater had not crossed the NTZ boundary within the 2 month study period. Using data from ultrasonic transmitters, they found that fish with home ranges on the boundary of an NTZ crossed boundaries a mean of 15.3 times per month. Curiously, the mean distance moved by fish was greater within the NTZs than outside, when estimated by underwater observations. This difference was not evident in the telemetry data, and so was interpreted as an artefact associated with the direct observation protocol.

In principle, either direct observation (e.g. by SCUBA) or tagging (e.g. conventional tags or acoustic transmitters) could be employed to monitor movement across the boundaries of an NTZ, and so detect any net emigration or spillover. It may be difficult in practice, however, to detect any net emigration, as this would probably be hidden as a tiny fraction of the huge number of fish movements that take place every day, as a result of the normal activity of fish whose home ranges straddle the boundary. In the cases of conventional tagging or acoustic telemetry, the problem would be exacerbated by the low proportion of the fish population that is recovered or being monitored. In addition, it may be that most emigration is by sub-adult or fugitive fish that are less susceptible to capture and tagging, and less easy to observe. Thus determination of spillover from direct observation of fish movement across a boundary may prove impractical.

Density Gradients across Boundaries

As an alternative, researchers have also looked at patterns in fish abundance across NTZ boundaries to deduce evidence of spillover. If there was no net emigration of fish across the boundary of an NTZ, a sharp divide might be predicted between an area of higher fish abundance within the NTZ, and one of lower abundance in an adjacent fished area. Where instead there is net movement or spillover of fish from the NTZ, a gentler gradient in abundance would be expected from within the NTZ to within the adjacent fished zones. Such gradients in abundance have been observed across the boundaries of NTZs in several studies. Perhaps the best known case is the reduction in catch by fish traps with increasing distance from the centre of the Barbados Marine Reserve (Fig. 4), observed by Rakitin and Kramer (1996).

We too have observed similar density gradients in fish abundance across the boundaries of NTZs contained within the Marine Protected Area at Nabq, South Sinai, Egypt (Ashworth and Ormond, 2005). Within the fished portions of the MPA, fishing is permitted only to Bedouin who have traditional rights. In 1995, the Bedouin community agreed to the establishment of five NTZs, which by 2000 had resulted both in differences in fish family abundance between fished and unfished zones, and an increase in catch per unit effort (CPUE) from 0.79 to 1.31 kg unit gear^{-1}hr^{-1} within the open areas (Galal *et al*., 2002). Subsequently, we observed gradients in fish abundance on transects between one of the NTZs and the adjacent fished zones (Fig. 5). The gradients in abundance varied in slope, depending both on the species concerned and on the intensity of fishing, which was greatest on transects nearer the shore.

Other Regular Movements

The effectiveness of NTZs and the degree of spillover into a fishery will also be affected by other types of fish movement. Firstly, many species of rabbitfish (Siganidae), grunts (Haemulidae), snappers (Lutjanidae), and cardinal fish (Apogonidae) show diel or other regular foraging movements between distinct roosting and foraging areas. Normally both roosting and foraging areas would be considered as parts of the home range, but the two areas may be some distance apart. Brown surgeonfish (*Acanthurus nigrofuscus*) migrate up to 1.5 km between fore-reef and reef flats at sunrise and sunset (Mazeroll and Montgomery, 1995; 1998), with movement being triggered by ambient light levels (Myrberg *et al*.,1988).

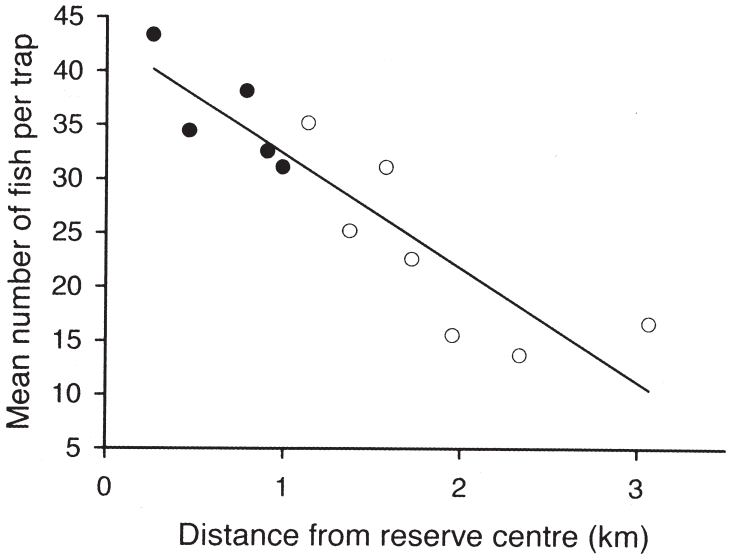

Fig. 4 – Catch per unit effort of fish traps with increasing distance from the centre of the Barbados Marine Reserve. The decline in catch with increasing distance from the centre, within (solid symbols) as well as without (open symbols) the reserve, are considered due to decreasing abundance of fish as they move out of the reserve and are caught (from Rakitin and Kramer, 1996).

Similar considerations apply to spawning movements. Many fish show movement on an occasional or daily basis to suitable spawning sites within their regular home ranges. These species have been termed resident spawners (Thresher, 1984; Domeier and Colin, 1997). They include some species of grouper such as coney, *Epinephelus fulvus,* as well as most species of wrasse (Labridae) and parrotfish (Scaridae) (Randall and Randall, 1963; Warner, 1987). Other species, termed transient spawners, migrate seasonally to locations outside their daily home range. Typically, fish are drawn from a large area and travel for days or weeks to reach local or regional spawning sites, where they remain for a period often extending over one or two lunar phases. Transient spawners include various species of grouper (Serranidae), snapper (Lutjanidae), and emperor (Lethrinidae). (Shapiro, 1987; Sadovy *et al.*, 1994).

A prime example of a transient spawner is the Nassau grouper, *Epinephelus striatus,* that migrates to spawn at specific sites at full moon, in the southern Caribbean in December and January, and in the northern Caribbean in May and June. These movements have been studied using both conventional and acoustic tags. Bolden (2000) studied the movements of Nassau grouper in central Bahamas using Floy dart tags and acoustic transmitters that enabled fish to be tracked for 24 hrs a day. Fish were observed to travel up to 220 km to reach a spawning site, where their mean stay was 46 days. Other serranid genera in the Pacific tend to travel shorter distances to more local spawning sites. Zeller (1998) studied spawning of coral trout, *Plectropomus leopardus,* at Lizard Island, Great Barrier Reef, Australia. He used ultrasonic tags to track 35 fish that used four spawning sites between 220 and 5,210 m from their home range sites. Only 31% of fish participated in spawning, which peaked at new moon; females tended to make overnight visits, but males made multiday visits to spawning sites.

Such spawning sites are very vulnerable to overexploitation by fishers. Unregulated exploitation can completely eliminate a spawning aggregation; for example, 33% of Nassau grouper spawning aggregations have disappeared from Belize

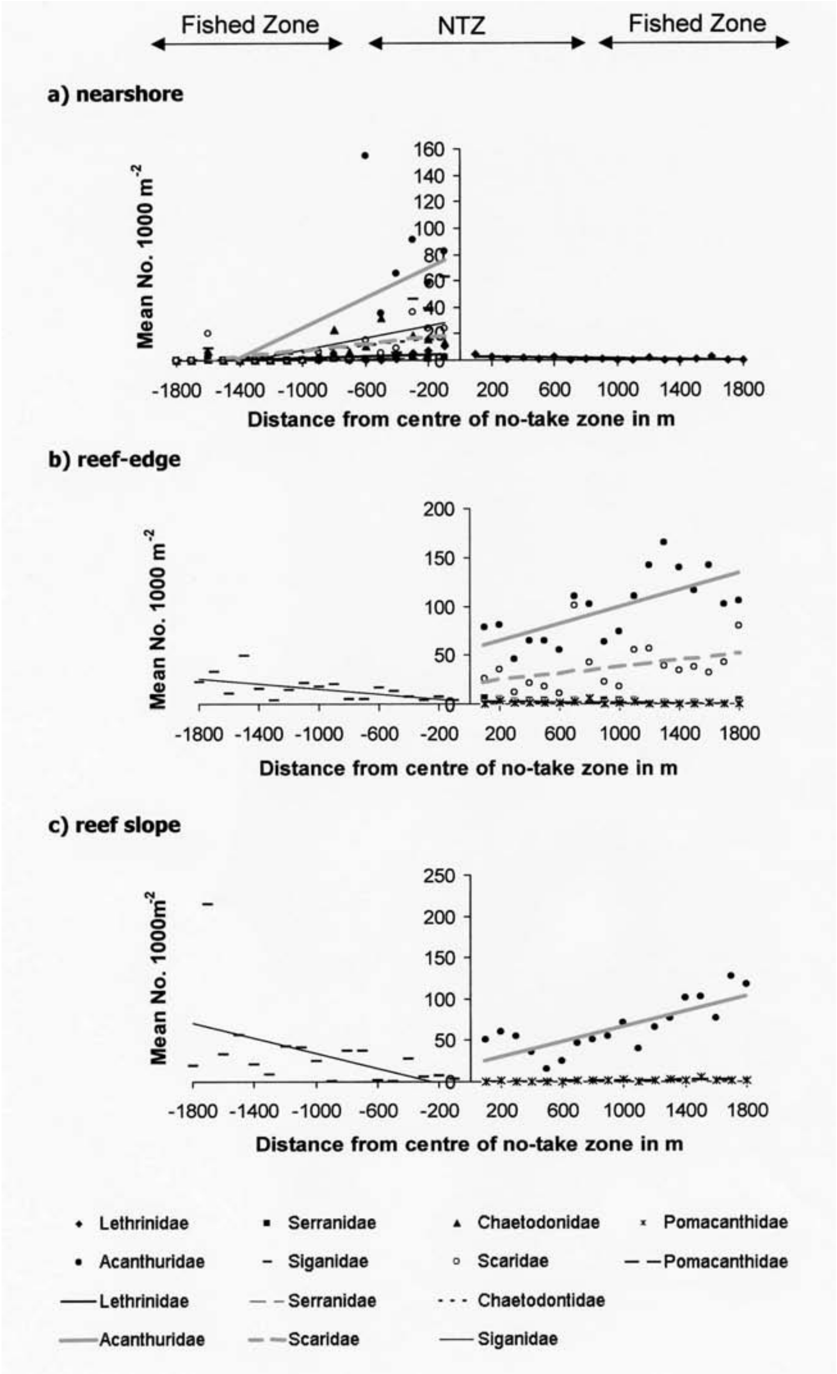

Fig. 5 – Abundance of fish as observed by underwater visual census along transects at three different depths moving from the centre of a No-Take Zone into both the adjacent fished areas within the Nabq Marine Protected Area at Nabq, South Sinai, Egypt. Only families showing a statistically significant trend are included. Nearer the shore most families show a significant decline in abundance moving out of the NTZ, but furthest from the shore some families are less abundant in the NTZ than in the fished zones (after Ashworth and Ormond, 2005).

and the Caribbean due to overfishing (Sala *et al.*, 2001). One of the largest remaining sites has been reduced from 15,000 to less than 3,000 fish within 25 years. It is therefore desirable to include major spawning aggregations within MPAs whenever possible. The ease with which seasonal aggregation sites can be overlooked is demonstrated by a recent study by Eklund and colleagues (2000). They described how a new NTZ in the Florida Keys National Marine Sanctuary was established without it being appreciated that a spawning aggregation of 96 black grouper, *Mycteroperca bonaci*, was located less than 100 metres outside of the NTZ.

The effect of heavy exploitation can be compounded in sex reversing species, which includes most groupers (Serranidae). Fishing typically results in heavier mortality of larger individuals, and in the scarcity of the larger sex (Punt *et al.*, 1993, Hunstman and Schaaf, 1994). This is especially so if sex reversal occurs at a fixed age, and less so where sex change is mediated socially (Vincent and Sadovy, 1998). Epinepheline groupers have female-biased sex ratios (Moe, 1969; Shapiro, 1987), although occasional male-biased populations have been reported. These have attributed to heavier exploitation of the smaller females, because they tend to occur nearer to shore (Johannes *et al.*, 1996). An illustration of the effects of exploiting aggregations in protogynous species is provided by Coleman and colleagues (1996), who describe how fishing reduced the proportion of males from 17% to 1% in gag, *Mycteroperca microlepis,* and from 36% to 18% in scamp, *M. phenax,* but produced no change in sex ratio in the non-aggregating red grouper, *Epinephelus morio*.

Larval Export

While the production of larvae is critical, so to is their fate. In particular the import and export of larvae may determine both fish populations within an NTZ, and the extent that these populations contribute towards replenishment of stocks in surrounding areas. Fish can remain as larvae from 3-6 weeks, depending on food availability and ambient temperature (Moloney *et al.*, 1994; Bingham, 1992). It has been presumed that larval recruitment from a spawning location occurs over a large area, encompassing hundreds to over a thousand kilometers (Boehlert, 1996; Roberts, 1997). Shanks and colleagues (2003) examined the dispersal distance of propagules of marine benthic organisms. They estimated dispersal distances for 32 taxa, and the time spent dispersing for 25 of these taxa. They found that the more time spent in water, the further the propagules were generally dispersed. The curve of frequency distribution and dispersal distance is bimodal with, however, a gap between 1 and 20 km. The model suggested that at less than 1 km distance dispersed, the larvae tend to spend less than 100 hours as plankton. If the larvae spend longer than this, then they probably remain in near-bottom waters. Larvae dispersing further than 20 km tended to spend more than 300 hours as plankton. Shanks and colleagues (2003) suggest that there may be evolutionary constraints against a mid-range dispersal strategy covering the gap between 100 and 300 hours in the plankton. From their results, they propose that marine reserves need to be large enough (at least 4-6 km diameter) to contain short-distance propagules, but far enough apart (10-20 km) that long-distance propagules can settle in an adjacent reserve.

Is Recruitment Supply Driven?

Irrespective of the distance to which larvae may be carried, two key issues have arisen in relation to the effects of larval dispersal on fish recruitment. First, is recruitment supply driven? Second, does significant retention of larvae occur on their reefs of origin? Considering the first of these issues, there are a number of factors that may drive the supply of larvae, including timing of spawning, pelagic larval duration, lunar and tidal cues, and stochastic factors including larval growth and mortality, and oceanographic processes (Valles *et al.*, 2001). Thus recruitment of damselfishes (Pomacentridae) on the Great Barrier Reef, Australia, has been found to match seasonal patterns in larval abundance (Milicich *et al*., 1992). In turn, annual variation in the abundance of adults on the Great Barrier Reef has been found to vary with recruitment (Williams, 1979; Doherty and Fowler, 1994). Consistent differences in levels of recruitment were observed between sites, however, and presumed to be related to habitat characteristics (Milicich and Doherty, 1994). By contrast, Robertson (1988a, b) found no relationship between larval abundance and adult populations in several families of Caribbean reef fish.

The relative importance of pre- and post-recruitment processes may differ between species and locations. An interesting study in this context is that by Sponaugle and Cowen (1996) who compared larval supply and juvenile recruitment in two reef fish in Barbados. One, the bicolour damselfish, *Stegastes partitus*, is a small, solitary, relatively sedentary territorial herbivore with benthic eggs, while the other, the ocean surgeon, *Acanthus bahianus,* is a larger, mobile schooling herbivore, with pelagic eggs. They found that *Stegastes* larvae were more abundant in the south, and *Acanthurus* larvae more abundant in the north, suggesting that larval supply was not simply the result of passive transport. The abundance of juvenile *Stegastes* matched that of the larvae, although it was less variable spatially. By contrast, the pattern of abundance of juvenile *Acanthurus* was the inverse of the larval supply pattern, implying that post-settlement processes were influencing juvenile abundance. More generally, it has been argued that recruitment patterns are likely to be affected by a range of ecological processes, such as predation, competition, behaviour, habitat selection, facilitation, and resource availability (Hixon, 1991; Jones, 1991; Leis, 1991; Cowen and Sponaugle, 1997).

Spatial differences in fishing pressure can result in changes in resident fish community structure (Russ, 1991; Roberts, 1995; Bohnsack and Ault, 1996). This suggests that fisheries-related differences in ecology between an NTZ and a neighbouring fished area could result in differences in rates of recruitment, or in post-settlement survival. Even without such differences, larval supply may differ between adjacent areas. Valles and colleagues (2001) compared the supply of larvae of the bicolour damselfish, *Stegastes partitus*, to a marine reserve (Anse Chastenet) with that for an adjacent fished area (Grand Caille) within the Soufriere Marine Management Area (SMAA), St Lucia, over a single autumn period. They found a consistently higher abundance and diversity of larvae arriving at the fished area, despite the proximity of the two sites. This difference was attributed to local scale variation in hydrodynamics and biological features.

Is Larval Retention Significant?

The second issue, particularly relevant to the role of NTZs, is whether significant retention of larvae occurs on their reefs of origin. As described above, it has long been presumed that most marine larvae are carried long distances by prevailing currents. Hence it was anticipated both that larval recruitment to a location is independent of local reproduction (Sale, 1991; Caley *et al*., 1996), and that a high proportion of larvae are lost after transport away from their sites of origin (Dight *et al*., 1990). Subsequently, it was suggested that recirculatory features in the lee of reefs might entrap dispersing larvae, increasing the likelihood of successful recruitment locally (Kingsford *et al*., 1991; Dight and Black, 1991). Further, hydrographic models incorporating this feature have suggested that, because most larvae that are carried away fail to survive, local recruitment could be up to 10 times more likely to occur than recruitment downstream (Black, 1993).

Direct evidence that local retention may be more important than distant recruitment is not easily obtained. Swearer and colleagues (1999), however, noted that coastal waters typically have higher concentrations of nutrients and trace elements than the open ocean, and they used differences in tissue concentrations of these chemicals to distinguish larvae that experienced these two environments. They compared chemical signatures of otoliths in juvenile bluehead wrasse (*Thalassoma bifasciatum*) from windward and leeward reefs at St Croix, (US Virgin Islands). They found that larvae on the two types of reef appeared to have experienced different larval environments. The leeward reefs recruited largely retained larvae, while windward reefs mainly received larvae that had experienced oceanic conditions. Accordingly, Swearer and colleagues (1999) argued that in the Caribbean larval dispersal processes operate at different spatial scales: between islands (>100 km) and within islands (<10 km). They suggested that reefs over time receive both locally retained and ocean-dispersed larvae, but as more than 70% of settlement was on the leeward reefs, a majority of recruits originated from locally retained larvae.

Larval Behaviour

It was also long presumed that larvae are dispersed passively by ocean currents, and are unable to affect their destination. However, increasing evidence suggests that larval behaviour is adapted to promote local recruitment as well as dispersal. Some larval fish are capable of remarkable swimming speeds. Larval fish in swimming chambers have been shown to attain speeds up to 13.5 cms^{-1}, although with a 25-fold variation in abilities between species (Stobutzki and Bellwood, 1997). In studying the swimming speed of late pelagic larvae *in situ* around Lizard Island and Rangiroa Atoll, Leis and Carson-Ewart (1997) measured the speed of 50 species in 15 families of mainly perciform fish (Fig. 6). Speeds were very high for these small fish (0.7-5.5 cm), averaging 20.6 cms^{-1} or 13.7 body-lengths s^{-1}, depending on the taxa. Apogonids and nemipterids were slowest, pomacentrids and chaetodontids speeds varied with species, and acanthurids, lethrinids and serranids were fastest. Crucially, all but apogonids and nemipterids were found to have mean speeds greater than average ambient current speed. That is, late larval fish are capable of swimming fast enough to influence their dispersal destination.

The potential effect of active swimming by late stage larval reef fish has been modeled by Armsworth (2000), distinguishing between strong and weak swimming ability, and between responsiveness to current-dependent and current-independent cues for orientation. Armsworth (2000) concluded that purely hydrodynamic effects leading to incidental recruitment or passive entrainment in re-circulatory features around reefs were less important than larval swimming abilities. Rather, the model suggested that the ability of larvae to respond to sensory cues was critical. Acanthurids have specialised larvae that are strong swimmers during their late stage, capable of directed motion and selective of their benthic habitats. Thus local currents are not likely to be a constraint for acanthurids. Armsworth (2000) suggests that for these and similar species recruitment would be relatively predictable in space and time. Larval apogonids, by contrast, are weak swimmers. Armsworth (2000) notes that they might be expected to have a shorter pelagic larval duration and employ advection avoidance mechanisms, show vertical migration, and exploit the benthic boundary layer, making it more likely that they would be retained near to a reef. The idea that larval fish may home towards suitable reefs from considerable distances has been given strong support by recent evidence both that larvae are sensitive to ocean sounds, and that they will recruit preferentially to locations fitted with loudspeakers emitting characteristic reef sounds (Tolimieri *et al*., 2000; Leis *et al*., 2003). If larvae can respond to current-independent auditory stimuli, such as the sounds of wave action and currents on reefs, and swim against moderate currents to reach source reefs, then larval recruitment may be very far from the passive process hitherto imagined.

Trophic Effects

A final aspect of behaviour that may influence the response of fish stocks to the establishment of No-Take Zones is the feeding ecology and trophic role of the species concerned. The review by Halpern (Halpern and Warner, 2002; Halpern, 2003) of some 80 studies into the effects of NTZ establishment included consideration of the effects on the

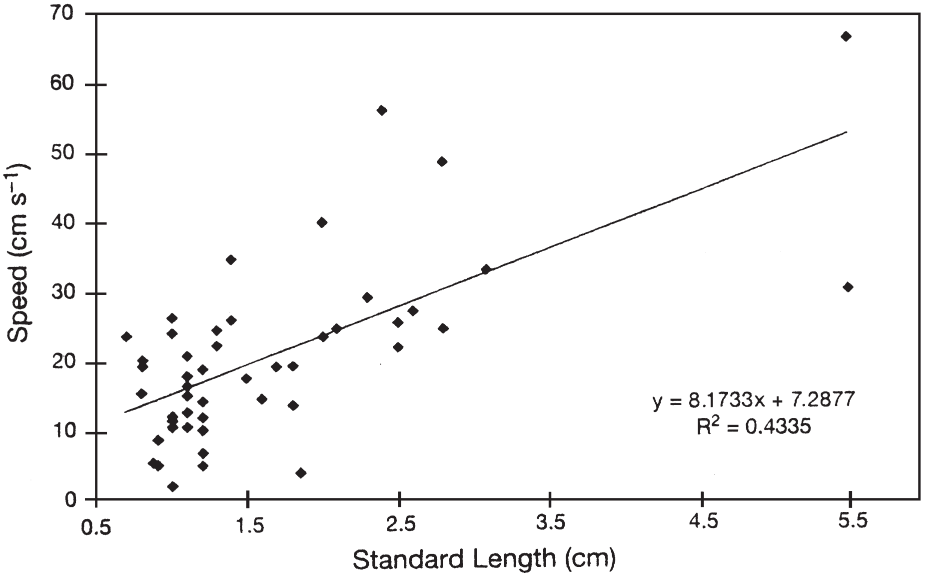

Fig. 6 – Relationship of mean swimming speed to mean size (standard length) in late stage larvae of 53 species of coral reef fish (from Leis and Carson-Ewart, 1997).

density, biomass, organism size of lower trophic groups. They concluded that the abundances of herbivorous fishes and invertebrates in NTZs is usually lower than, or similar to, that in adjacent fished areas. However, a number of studies have reported a decrease within NTZs in some fish that are either herbivores (Roberts and Polunin, 1991; 1992) or competitively inferior predators (Watson and Ormond, 1994; Sluka *et al.*, 1998; Chiappone *et al.*, 2000). Such effects seem likely to be the result of a decrease in the predation or competition due to preferentially exploited species such as larger grouper (Russ, 1985). It has also been suggested that mortality of juveniles may be higher in reserves than outside, as a result of competition or predation (Dufour *et al.*, 1995). Similar effects have also been reported for invertebrates, notably for echinoids (McClanahan and Shafir, 1990; Watson and Ormond, 1994; McClanahan *et al.*, 1999; Ruttenberg, 2001, Ashworth *et al.*, 2004), and smaller molluscs (McClanahan, 2002; Ashworth *et al.*, 2004). Again it seems most likely that these effects are due to an increase in abundance of fish predators. Thus some species may show a reduced abundance within NTZs. This will clearly have implications for conservation plans designed to sustain species abundance and maximise diversity.

A recent study in which we have participated (Ashworth and Ormond, 2005) suggests an explanation for the variable response of herbivore and invertebrate populations to NTZ establishment. As described above, five NTZs were established in 1995 at Nabq, Egypt, within which there have been significant increases in the abundance of some fish families (Galal *et al.*, 2002). A more detailed study of one of these areas has shown that the response of fish stocks varies with fishing effort. Nearer the shore where fishing effort is greatest, 9 out of 10 families were more abundant in the NTZ (Fig. 5). With increasing distance from the shore, fewer families showed this response. Furthest from the shore, fishing pressure was least and only two herbivore families (Acanthuridae and Siganidae) showed significant differences between the fished areas and the NTZ, with both being more abundant in the fished areas. The explanation for this effect must be that whereas more intense fishing using non-selective gear reduces the abundances of all families, relatively light fishing using more selective gear may reduce the numbers only of some families. If this light fishing only reduces the numbers of larger predatory fish, the numbers of some prey families may increase as a result of reduced predation pressure. If a large variety of predatory species is being exploited, but only a few prey species being released from predation, the change in abundance of these prey species may be greater than that of any predator species. Thus the response of fish populations to NTZ establishment will depend on both trophic status and fishing pressure.

Conclusions

The idea that overfishing can be regulated by protecting portions of the marine environment is easy to grasp. However, the extent to which species abundance increases within a No-Take Zone (NTZ), and the extent to which this increases fish catch in adjacent fished areas, depends on a number of factors. The ranging and migratory behaviour of species is critical in determining both the extent to which fish within an NTZ are protected from exploitation, and the extent to which spillover of denser populations within the NTZ will supplement stocks and enhance fisheries in adjacent fished areas. Species vagility may be influenced by, among other factors, the social and reproductive behaviour of species. Also key is the patterns of larval export from an NTZ. These will be greatly influenced by fish larval behaviour, specifically the extent to which larvae can be entrained with circulatory features nearshore, or detect and swim against the current towards suitable benthic habitat. Finally, the trophic and competitive status of a species may influence its response to cessation of fishing. Where fishing pressure is less intense, species that are prey, or inferior competitors of exploited predatory species, may actually increase in abundance as a result of the removal of their principal predators. Hydro-acoustic tagging of adults and chemical profiling of larvae are methods offering the possibility of monitoring spillover and export of adults and larvae respectively, so as to assess the effectiveness of NTZs.

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