



Patterns and prediction of population recovery in marine reserves

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Abstract

Marine reserves (no-take zones) are widely recommended as conservation and fishery management tools. One potential benefit of marine reserves is that they can reduce fishing mortality. This can lead to increases in the abundance of spawners, providing insurance against recruitment failure and maintaining or enhancing yields in fished areas. This paper considers the factors that influence recovery following marine reserve protection, describes patterns of recovery in numbers and biomass, and suggests how recovery rates can be predicted. Population recovery is determined by initial population size, the intrinsic rate of population increase r , and the degree of compensation (increases in recruits per spawner as spawner abundance falls) or depensation (lower than expected recruitment at low abundance, Allee effect) in the spawner-recruit relationship. Within a reserve, theoretical recovery rates are further modified by metapopulation structure and the success of individual recruitment events. Recovery also depends on the extent of reductions in fishing mortality (F) as determined by the relationship between patterns of movement, migration, and density-dependent habitat use (buffer effect) in relation to the size, shape and location of the reserve. The effects of reductions in F on population abundance have been calculated using a variety of models that incorporate transfer rates between the reserve and fished areas, fishing mortality outside the reserve and life history parameters of the population. These models give useful indications of increases in production and biomass (as yield per recruit and spawners per recruit respectively) due to protection, but do not address recruitment. Many reserves are very small in relation to the geographical range of fish or invertebrate populations. In these reserves it may be impossible to distinguish recovery due to population growth from that due to redistribution. Mean rates of recovery can be predicted from r , but the methods are data intensive. This

is ironic when marine reserves are often favoured for management or conservation in data-poor situations where conventional stock assessment is impossible. In these data-poor situations, it may be possible to predict recovery rates from very low population sizes by using maximum body size or age at maturity as simple correlates of the intrinsic rate of natural increase.

Introduction

Most marine reserves¹ are small (1–20 km²), and were established on an *ad-hoc* basis to provide general conservation benefits rather than to meet specified and verifiable management objectives. However, in recent years, following concerns about the deleterious impacts of intensive fishing on target species and the marine environment (e.g. Dayton et al., 1995; Jennings and Kaiser, 1998; Hall, 1999; Kaiser and de Groot, 2000), marine reserves have increasingly been proposed as tools for fisheries management and conservation (e.g. Davis, 1981; Polunin, 1984; Bohnsack, 1990, 1998; Roberts and Polunin, 1991, 1993; Daan, 1993; Dugan and Davis, 1993; Quinn et al., 1993; Rowley, 1994; Auster and Shackell, 1997; Allison et al., 1998; Guénette et al., 1998; Lauck et al., 1998; Sladek-Nowlis and Roberts, 1999). One objective of marine reserve management in this respect is to increase the abundance of spawners. This may provide insurance against recruitment failure and maintain or enhance yields in fished areas (Bohnsack, 1998). Since marine reserve management is often implemented when populations of fished species are at perilously low levels, population recovery is critical to building spawning stock biomass. Most of the evidence for population recovery in marine reserves comes from empirical studies. These show that the abundance (biomass or number of individuals) of some species is higher in reserves than adjacent fished areas, or that abundance in a reserve has increased following protection (Bell, 1983; Russ, 1985; Alcala, 1988; Samoilys, 1988; Buxton and Smale, 1989; Clark et al., 1989; Alcala and Russ, 1990; Bohnsack, 1990; García-Rubies and Zabala, 1990; Bennett and Attwood, 1991; Francour, 1991; Roberts and Polunin, 1992; Polunin and Roberts, 1993; Watson and Ormond, 1994; Dufour et al., 1995; Roberts, 1995; Jennings et al., 1996; McClanahan and Kaunda-Arara, 1996; Letourner, 1996; Rakitin and Kramer, 1996; Russ and Alcala, 1996, 1988 a,b; Wantiez et al., 1997; Chapman and Kramer, 1999; Mosquera et al., 2000). However, in those studies that compare

abundance in and outside reserves, it is not always easy to distinguish differences in abundance due to recovery from those due to habitat effects. With a few exceptions, areas chosen as marine reserves have not been studied in detail before protection and studies of recovery are not based on BACI (before-after control-impact) designs.

Population recovery is an increase in the biomass and numbers of individuals when fishing mortality is reduced. In the present context, recovery means an increase in abundance from historically low population levels that is sustained for a period of years. Recovery depends on the reduction in fishing mortality (F) that results from reserve protection, the size of the remaining population and its intrinsic rate of increase (r). The relative reduction in F , and hence the rate of biomass increase, depends on rates of movement and migration between the reserve and fished areas, density dependent habitat use (buffer effect), and whether the protected ecosystem provides adequate food for fish or invertebrate populations to grow. For species that spend part of their time outside the reserve, F may not fall very much, particularly if overall fishing effort remains the same and fishers are simply displaced to the reserve boundary (e.g. De Martini, 1993; Horwood et al., 1998; Horwood, 2000). If spawner biomass and egg production do increase, then (mean) recruitment will also increase because mean recruitment success at low abundance is positively correlated with egg production (e.g. Myers et al., 1995a, b).

The effects of reductions in F following marine reserve protection have been assessed using a variety of models. In most cases, these have predicted changes in yield per recruit (Y/R) or spawners per recruit (S/R) using a dynamic pool approach that incorporates transfer rates between the reserve and fished areas and fishing mortality outside the reserve (Beverton and Holt, 1957; Polacheck, 1990; Die and Watson, 1992; Russ et al., 1992; De Martini, 1993). Typically, these models suggest that reserves increase S/R but have limited effects on Y/R in adjacent fished areas unless fishing mortality is high and the area closed is large. Gains in S/R are greater when transfer rates are low,

so reserves function most effectively as a conservation tool for sedentary species.

Per-recruit models give a useful indication of changes in production (Y/R) and biomass (S/R) following protection, but do not address the recruitment process itself. Fishery benefits are more likely to accrue from increased egg production by spawners, and export of eggs and larvae to adjacent fished areas, than from the movements of older individuals. Models of these processes suggest that marine reserves can reduce the risk of stock collapse at high F because they help maintain spawner biomass (e.g. Guénette and Pitcher, 1999).

Population recovery is determined by initial population size, the intrinsic rate of increase (r), and the degree of compensation or depensation (Allee effect) in the spawner-recruit relationship. Theoretical rates of increase are further influenced by meta-population structure and the success of individual recruitment events. Successful recruitment is fundamental for population persistence and recovery when spawners have been reduced to very low abundance. For example, a reduction in F may not promote recovery if the spawner-recruit relationship results in lower than expected recruitment at low population levels (depensation), because the remaining individuals are too isolated to reproduce successfully. Per-recruit models neglect one of the most important components of recovery, namely how R/S changes in response to population size.

In this review I consider the factors that influence recovery rates and ways to predict them. I concentrate on recovery from very low population abundance, since one justification for the use of marine reserves is to rebuild stocks. Fished stocks can be significantly depleted. In heavily fished areas outside marine reserves, for example, abundance is often <10% of that in the reserve (Roberts and Polunin, 1991) and, at the time of collapse, the biomass of collapsed stocks has been <1% of their maximum (Beverton, 1990). As well as looking at theory, I draw on empirical examples from marine reserves and collapsed fisheries where total fishing bans have been implemented. In the latter part of the review, I consider how recovery rates can be predicted. Mean recovery rates can be predicted from the intrinsic rate of natural increase, but many of the methods are data intensive. Taking this into account I also look at ways of predicting recovery rates in data-poor situations.

Factors affecting recovery rates

Intrinsic rates of natural increase

The intrinsic rate of natural increase (r) is a measure of the potential growth rate of a population. The intrinsic rate of natural increase can be calculated using the demographic interpretation of the Euler-Lotka equation (Stearns, 1992)

$$\sum_{x=\alpha}^{\omega} e^{-rx} l_x m_x = 1 \quad (1)$$

where α is age at maturity, ω is maximum reproductive age, l_x is survivorship (the proportion of the cohort surviving to age x) and m_x is age-specific fecundity per surviving individual. Equation 1 has to be solved numerically rather than analytically. The equation has usefully been modified in various ways to provide estimates of r for fish populations and to determine their ability to recover when fishing is stopped. The approaches used have depended on the quantity of relevant data available. The intrinsic rate of natural increase is correlated with other life history parameters such as age and size at maturity, growth rate and asymptotic size. Later in this review we see that easily measured life history parameters may provide surrogates of r .

Compensation and depensation

Population growth rates at low abundance determine how fast recovery can occur. Spawner-recruit relationships reflect the potential for population growth as they describe the average number of recruits (R) produced per spawner (S) at different levels of population abundance. The intrinsic rate of population increase is a function of the slope of the spawner-recruit relationship at low spawner abundance (e.g. Myers et al., 1997). Spawner-recruit relationships show compensation because the number of recruits per spawner (R/S) increases at low population abundance (e.g. Ricker, 1954; Beverton and Holt, 1957; Shepherd, 1982). Thus the 'per capita' rate of population growth will rise when a population is depleted. Depensation leads to a lower than expected R/S (per capita rate of increase) at low abundance (Figure 1). Thus even if a severely depleted population is protected from fishing by a marine reserve, depensation may condemn it to extinction.

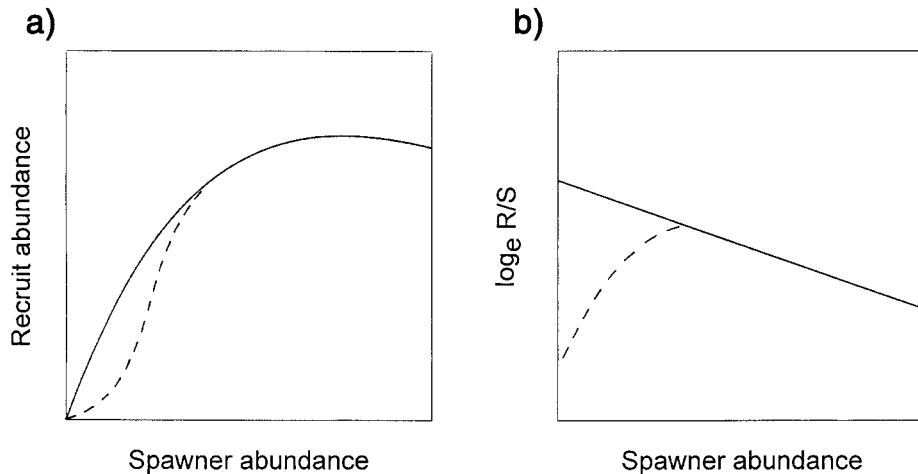


Figure 1. A Ricker spawner-recruit relationship (continuous line) (a) shows compensation because R/S increases with decreasing S (b). If there is depensation in the relationship (broken line), then the per capita rate of increase is lower than predicted by the model (a) and R/S falls at the lowest stock sizes (b).

There are a number of reasons why depensation may exist. For example, depensation would also occur if some females failed to find mates when stock size was low or if the fertilisation rates of broadcast spawners were dependent upon sperm concentration. Moreover, some bivalve species and sea-urchins have lower survival if they cannot settle among conspecific adults (Orensanz and Jamieson, 1998). This is most likely in invertebrate and non-shoaling fish populations and I will consider this in detail. Depensation is also referred to as the Allee effect (Allee, 1931, Stephens et al., 1999).

If depensation exists, the rate of population recovery following marine reserve protection will be slower or, in the worst case, there will be no recovery. Unfortunately, it is not easy to see whether depensation exists in spawner-recruit relationships because there are usually very few data points at low population abundance and variability about the mean spawner-recruit relationship is high. Moreover, depensation and hypercompensation (compensation greater than that predicted by a specified model) may balance and produce a spawner-recruit relationship that obscures either effect (Levitan, 1991). Depensation is a process that should not be overlooked by fishery managers, since, when a stock is depleted, it can lead to a dramatic collapse in yield for a very small increase in effort (e.g. Bannister and Addison, 1986).

Liermann and Hilborn (1997) developed a depensatory parameter q and estimated the likelihood of depensation in a range of fish populations. This

parameter describes deviation from the Beverton and Holt (1957) spawner-recruit relationship

$$R = \frac{aS}{b+S} \quad (2)$$

where R is recruit abundance, S is spawner abundance, a is maximum abundance of recruits and b is abundance of spawners that gives mean recruitment of $a/2$. To describe the level of depensation, the parameter d can be added to equation (2)

$$R = \frac{aS^d}{b^d + S^d} \quad (3)$$

If $d = 1$, equation (3) is a Beverton and Holt spawner-recruit relationship but when $d > 1$ there is depensation and when $d < 1$ there is hypercompensation. However, in equation (3), the degree of depensation for a given d depends on the values of the other parameters and thus d cannot be used for making comparisons among populations. Liermann and Hilborn (1997) reparameterised the Beverton and Holt model and developed an alternate depensation parameter q

$$q = \frac{\left(\frac{a(0.1S^*)^d}{b^d + (0.1S^*)^d}\right)}{\left(\frac{a'(0.1S^*)}{b' + (0.1S^*)}\right)} \quad (4)$$

where S^* is the maximum observed spawner abundance and a' and b' are the parameters from equation (3) when the model agrees with the depensatory model

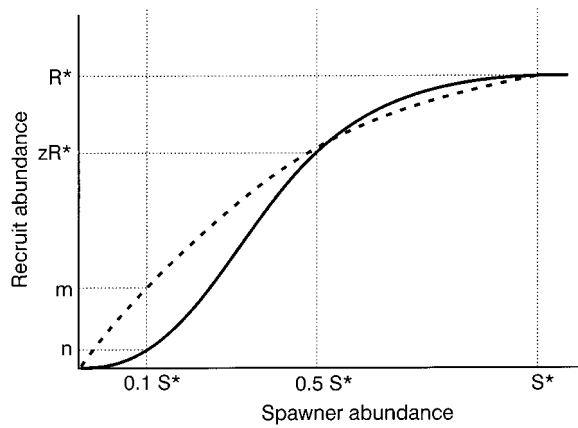


Figure 2. The graphical definition of R^* , z and q where $q = n/m$. The broken line shows a Beverton-Holt spawner-recruit relationship and the continuous line shows the relationship with depensation. Redrawn from Liermann and Hilborn (1997) with permission.

at $0.5S^*$ and S^* . The models agree when R^* , the recruitment at S^* , and z are the same for each curve where

$$z = \frac{\left(\frac{a(0.5S^*)^d}{b^d + (0.5S^*)^d} \right)}{R^*} \quad (5)$$

The full derivation is shown in Liermann and Hilborn (1997) and summarised graphically in Figure 2. q is effectively the ratio of recruitment in the depensatory model to that in the standard model at $0.1S^*$ (n/m in Figure 2). When $q < 1$ there is depensation and when $q > 1$ there is hypercompensation.

Liermann and Hilborn (1997) calculated values of q for a number of stocks, and combined the information using hierarchical modelling to produce distributions showing variability of q within orders of fishes. Their approach emphasised the uncertainty about the existence of depensation in populations where it had previously been disregarded, and indicated the relative likelihood of competing hypotheses (depensation vs hypercompensation).

For the Pleuronectiformes, the modal value of q was < 1 (Figure 3). This suggested that depensation may occur and that some flatfish populations pushed to low levels may not recover. Certainly, for these stocks, it would be wrong to assume that depensation does not exist on the basis of the analysis presented (Liermann and Hilborn, 1997). For Clupeiform and Gadiform populations, the modal values of q exceeded 1, suggesting there was less likelihood of depensation.

Invertebrate populations are more likely to show depensation than fishes, because the adults may have little or no mobility and cannot necessarily

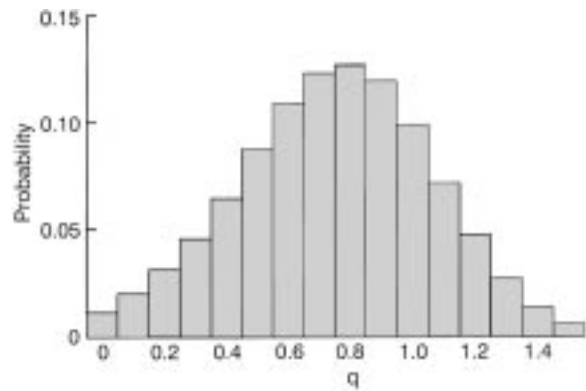


Figure 3. Distribution showing the variability of the depensation parameter q for the Pleuronectiformes. The distribution was obtained by combining information for separate stocks using a Bayesian hierarchical modelling technique. Redrawn from Liermann and Hilborn (1997) with permission.

aggregate to reproduce (Orensanz and Jamieson, 1998). Depensation is possible when the number of eggs fertilised (by copulation) or fertilisation rate (broadcast spawning) are positive functions of density (Leviton et al., 1992; Quinn et al., 1993; Levitan, 1995; Appeldoorn, 1995; Levitan and Sewell, 1998; Babcock and Keesing, 1999). For broadcast spawners, sperm concentration falls rapidly as sperm are diluted, and fertilisation success can fall to almost zero when individuals are separated by more than a few metres (Pennington, 1985; Levitan et al., 1992). Pennington (1985), for example, showed that when sea urchins (*Strongylocentrotus purpuratus*) were separated by more than one metre, fertilisation rates were $< 10\%$ and Babcock and Keesing (1999) showed that fertilisation rates of greenlip abalone (*Haliotis laevis*) eggs fell to $< 20\%$ at 10 m. High fertilisation rates are observed in unfished invertebrate populations because individuals show aggregative settlement (larvae settle with conspecifics) or aggregate after settlement. However, since fishers make the highest catch rates in aggregations, fishing tends to make abundance distributions more uniform. This can prevent recovery when fishing is stopped by marine reserve protection. For example, bans on fishing for white abalone (*Haliotis sorenseni*) have not led to appreciable population recovery (Tegner et al., 1996).

Depensation occurs at low density because it may be impossible for individuals to aggregate. The greenlip abalone, (*Haliotis laevis*), for example, has to aggregate to reproduce successfully (Shepherd, 1986). Shepherd and Brown (1993) studied the aggregative behaviour of this species in South

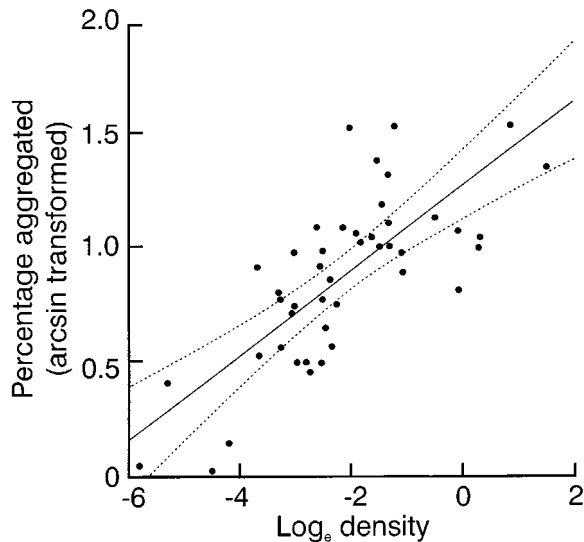


Figure 4. The relationship between the proportion of the abalone *Haliotis laevis* that are in aggregations and their density at Waterloo Bay, South Australia. 95% confidence limits for the fitted regression are shown. Redrawn from Shepherd and Brown (1993) with permission.

Australia. At 20 study sites in Waterloo Bay, the proportion of adults that aggregated for spawning was lower when total abundance was lower (Figure 4). Adults were taken to be aggregated when three or more adult (>110 mm shell length) abalone were less than 1 m apart. Shepherd and Brown (1993) considered the depensation that followed fishing and poor recruitment had contributed to recruitment failure in this stock. At a site near West Island, Shepherd and Brown (1993) observed that the proportion of greenlip abalone adults that aggregated declined from 67% to 16% over a 7 year period when density fell from 1.8 to 0.7 m⁻². Since adults could not aggregate at very low densities, they would fail to reproduce successfully. Even a closure of this fishery would be unlikely to promote recovery, unless managers transplanted abalone to the region and placed them in aggregations.

Recruitment variation

Measures of recruits per spawner (R/S) at low abundance are means, but actual recruitment fluctuates strongly in space and time. Variance around a fitted spawner-recruit relationship is assumed to be lognormally distributed (e.g. Hilborn and Walters, 1992; Myers et al., 1995). Variability is driven by the biological and physical variability of the environment (e.g. Cushing, 1996; Chambers and Trippel, 1997) and by

the fecundity of spawners (Koslow, 1992; Rickman et al., 2000).

Recruitment variation is largely unpredictable, but explains the patterns of recovery that are seen in practice. Because reserves tend to be small, and rarely protect whole populations, it is difficult to distinguish 'recovery' due to increases in total population size from recovery due to the relocation of individuals. However, total fishery closure following stock collapse may provide a situation comparable with the use of a very large marine reserve, and allows us to look directly at the relationships between r and recovery rates from very low population size. In reality, a reserve would only be expected to reduce F to zero for an entire population in exceptional circumstances. One example would be a reserve around an isolated oceanic atoll, where the populations of reef fishes are predominantly self-recruiting. In many cases, small reserves will only effect a fractional reduction in F because fish are accessible to fishers as soon as they cross the reserve boundary.

There have been several fishery closures following stock collapse, and the approach has been used to promote recovery in depleted herring (*Clupea harengus*) (e.g. Jakobsson, 1980; Bailey, 1991), capelin (*Mallotus villosus*) (e.g. ICES, 1990, 1994a) and cod (*Gadus morhua*) (e.g. Shelton and Healey, 1999) populations. Abundance and recruitment data for the Icelandic spring spawning herring and the Barents Sea capelin stocks provide examples of population recovery. On the basis of their relatively early age at maturity, fast growth and high fecundity, these stocks are expected to have high intrinsic rates of natural increase. For both stocks recovery was rapid, with some years of good recruitment at low stock sizes (Figures 5–6). Both collapse and recovery were influenced by climatic and multispecies effects as well as changes in F , but these cases highlight the potentially rapid rates of recovery for stocks with high r .

Spawning and total stock biomass levels of the Icelandic herring were very low when fishing was stopped, but high recruitment in the absence of fishing mortality during 1988 and 1989 led to increases in numerical abundance that translated to significant increases in total and spawning stock biomass (SSB) by 1990 (Figure 5). After 5 years of no fishing, SSB exceeded the levels 5 years before the fishery was closed (Jakobsson, 1980). Unfortunately, in 1992, the year the fishery reopened, recruitment was extremely poor (Figure 5) and fishing soon led to further reductions in biomass. Recovery of the Barents Sea capelin

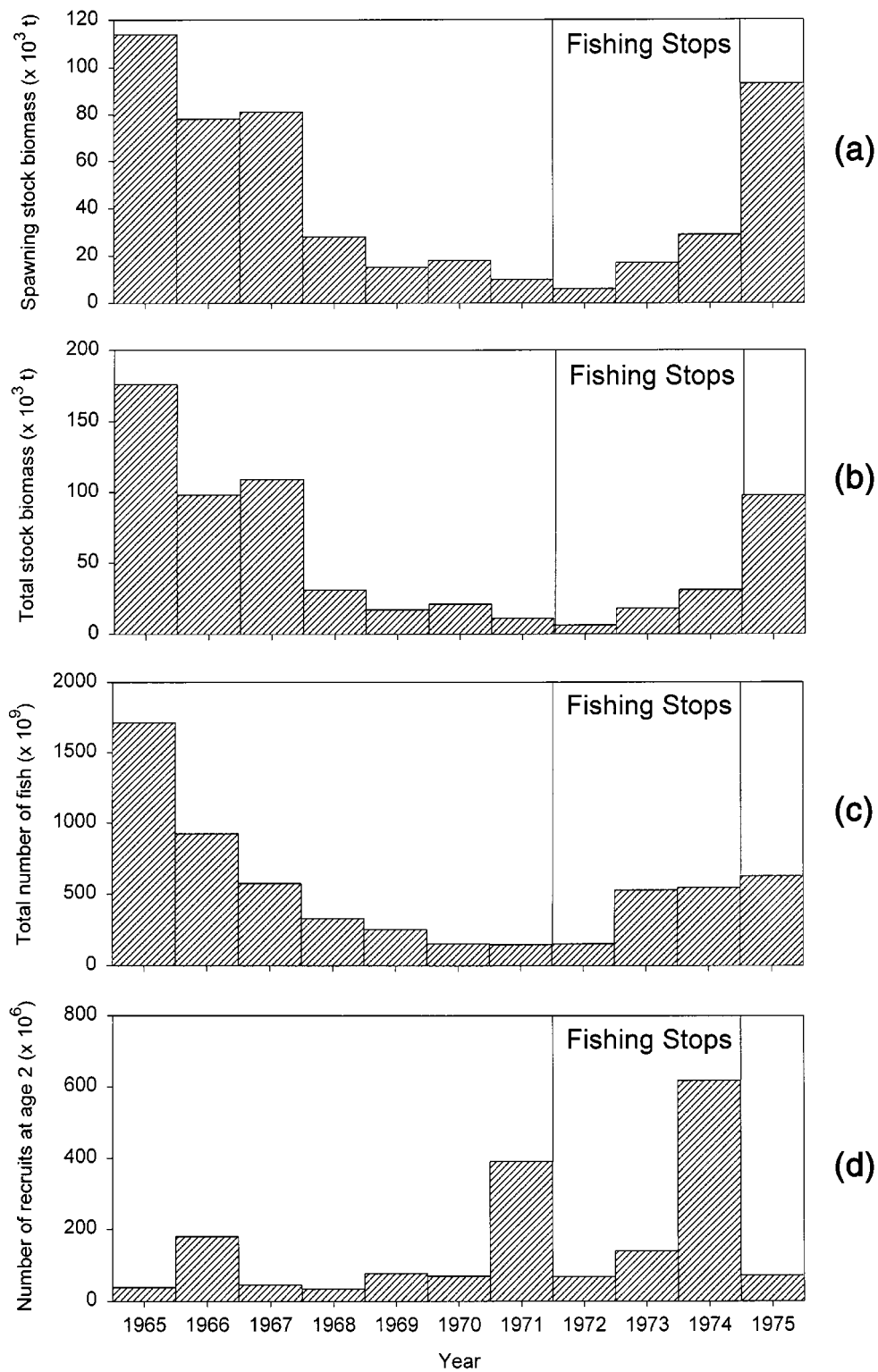


Figure 5. Collapse and recovery of (a) spawning stock biomass, (b) total stock biomass, (c) total stock number and (d) recruitment of the Icelandic summer spawning herring. The fishery was closed from 1972 to 1974 inclusive. Data from Jakobbson (1980).

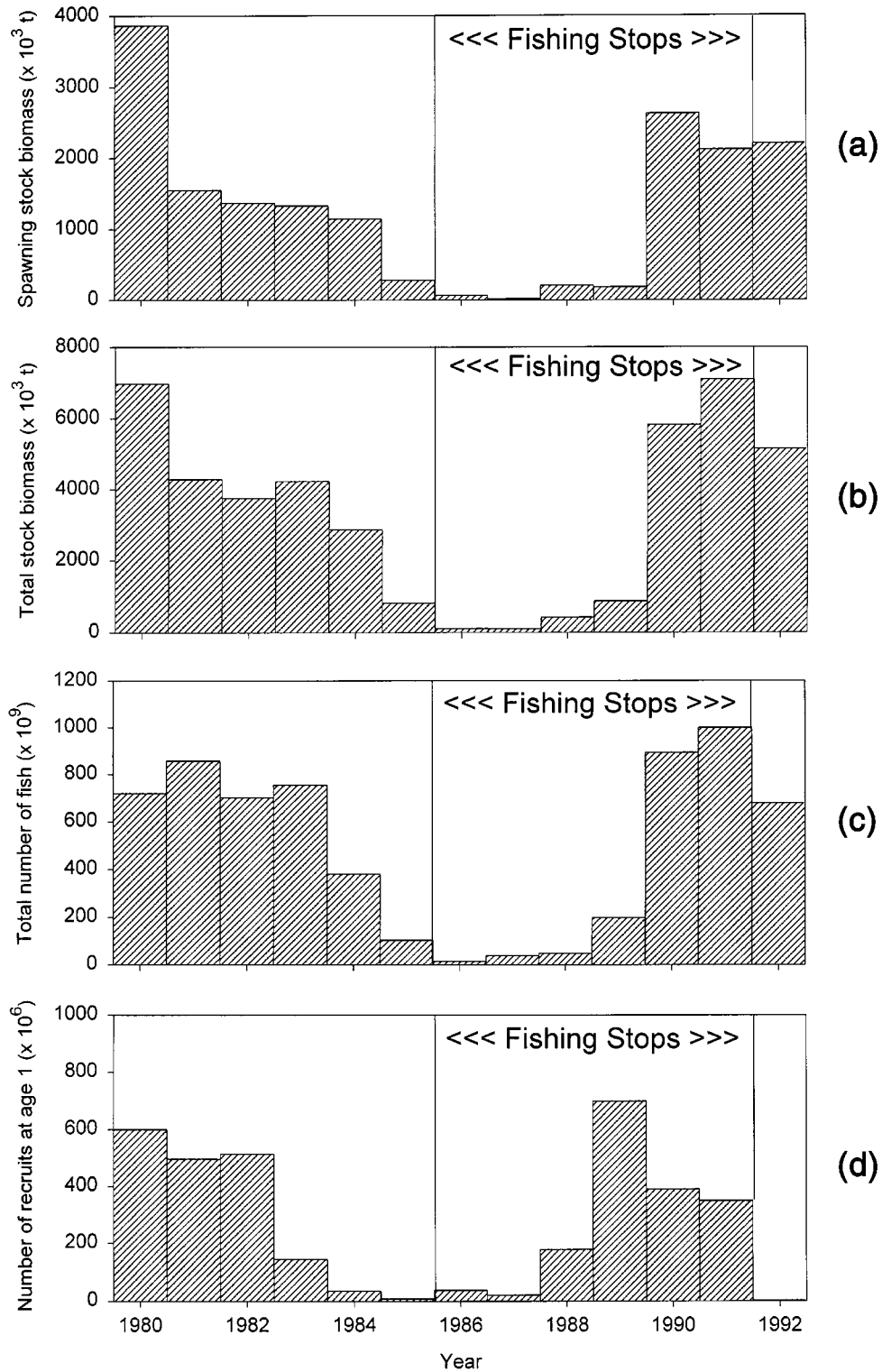


Figure 6. Collapse and recovery of (a) spawning stock biomass, (b) total stock biomass, (c) total stock number and (d) recruitment of the Barents Sea capelin. The fishery was closed from 1986 to 1991 inclusive. Data from ICES (1990, 1994a).

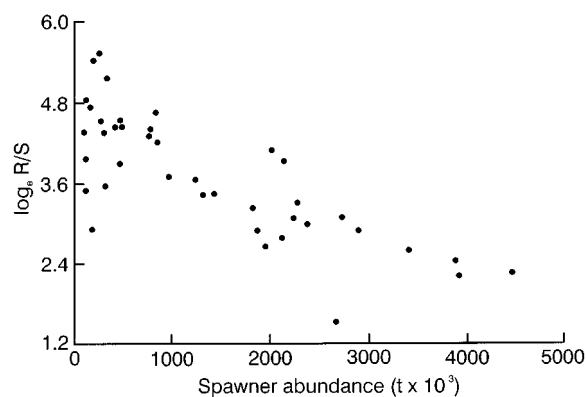


Figure 7. Compensation in the relationship between recruits per spawner (R/S) and spawner abundance for the North Sea herring. Based on Bailey (1991).

followed a fishing ban initiated in 1972 and was boosted by good recruitment in 1971 and in 1974 (ICES, 1990, 1994a). The 1971 recruitment led to increased stock biomass in 1973 and 1974 and the excellent year class in 1974 led to a higher SSB in 1975 than was present 5 years before closure (Figure 6).

The Icelandic herring and Barents Sea capelin both showed compensation in the spawner-recruit relationship and R/S remained high at low abundance. Fishery closure met the management objective of rebuilding SSB, and proved to be a simple and effective, albeit reactive, management technique. Similarly, closure of the North Sea herring fishery following collapse in the mid 1970s, when biomass was <1% of the historical (late 1940s) average (Beverton, 1990), resulted in a rapid recovery of SSB. The North Sea herring also showed compensation, with consistently high R/S when abundance was low and no sign of depensation (Figure 7, Bailey, 1991). This might be expected in a species that continues to form shoals as abundance is reduced.

The northern cod (*Gadus morhua*) has a slower life history than the herring or capelin, with later maturity and slower growth. This stock collapsed to historically low levels in 1992 (Hutchings and Myers, 1994) and the fishery was shut in July 1992. However, seven years later, there was no sign of recovery (Shelton and Healey, 1999). This may, in part, be due to the low intrinsic rate of increase for a stock with a slow life history (Myers et al., 1997), but depensation cannot be discounted (Shelton and Healey, 1999). In addition, it is difficult to monitor changes in stock size at low abundance, and small increases in abundance

may not be detected by groundfish surveys. Hutchings (1999) has also suggested that the slow recovery may not be unexpected given natural stochastic variation in the life history variables that directly influence r .

Metapopulation structure

The successful recruitment and settlement of fish and invertebrate larvae to reserves is essential for population recovery, and the failure of populations to recover following marine reserve protection has been attributed to the absence of source populations. For example, in 1977, the mainland coast of southern California from Palos Verdes Point to Dana point was closed to abalone fisheries because stocks had collapsed (Tegner, 1993). Pink (*Haliotis corrugata*) and green (*H. fulgens*) abalone were historically abundant in this region, and yet they did not recover. There were substantial stocks of the same species on nearby islands. Studies with drifters, that were used to indicate patterns of larval dispersal, suggested that only a tiny proportion of the planktonic larvae produced by green abalone were transported more than a few kilometres during their lifespan, and that recovery in the reserve would not be fueled by inputs of larvae from the islands. Rather, some form of artificial stock enhancement in the reserve would be needed. The limited larval dispersal that helps abalone recruit in close proximity and thus to aggregate and reproduce at maturity, also limits their capacity to colonise isolated reserves where stocks have been depleted.

Most marine invertebrates and some relatively site-attached fishes, such as those on coral reefs, exist as metapopulations, sedentary or relatively sedentary subpopulations connected by dispersing larval stages (Hanski, 1991; Botsford et al., 1994). Metapopulations take various forms, from total connectance, where all populations act as sources and sinks for the dispersing larvae, to near-zero connectance, where individual components are almost entirely self sustaining. More frequently, there is simply unbalanced connectance, where components act as sources and sinks to various degrees. Patterns of connectance are often stable, since populations may persist in the same locations for many years (Botsford et al., 1998; Orensanz and Jamieson, 1998).

Patterns of connectance will determine rates of recovery in marine reserves (Carr and Read, 1993; Allison et al., 1998). Consider, for example, some possible patterns of connectance between two fished

populations and a population protected by a reserve (Figure 8). When there is total connectance (Figure 8a), the population in the reserve can recover because it receives recruits from the fished areas as well as itself. The population in the reserve is also self-sustaining if stocks in the fished areas collapse. In Figure 8b, the population in the reserve is potentially self-sustaining and will recover if the population remaining in the reserve at the time of protection can reproduce successfully (i.e. there is no depensation). When recovered, the population in the reserve would be a source of larvae to the populations in the fished areas, which are known as sink populations because they are sustained by the recruitment of larvae from an external source (in this case the reserve). From a fisheries viewpoint this is significant because sink populations can be fished intensively without affecting other populations (Botsford et al., 1998). There are examples of fisheries based on sink populations, such as those for northern shrimp (*Pandalus borealis*) in some fjords (Parsons and Frechette, 1989) and Pacific oysters (*Crassostrea gigas*) at sites in British Columbia (Jamieson and Francis, 1986), and the need to identify and conserve source populations is well known amongst invertebrate-fishery managers (Fogarty, 1998). When there is no connectance (Figure 8c), the populations are self-sustaining and the reserve will provide conservation benefits but will not have any effect on the fished populations. If the reserve is a sink population (Figure 8d), successful recruitment to the reserve will depend on the persistence of the fished populations. This is undesirable!

These simple examples show that an understanding of metapopulation structure is crucial to siting marine reserves and predicting patterns of recovery. For many invertebrate species, the limited larval dispersal means that networks of closely-spaced small reserves may be needed to ensure connectance (e.g. Shepherd and Brown, 1993). Larval life of the abalone, for example, is relatively short compared with fishes (e.g. Brothers et al., 1983; Victor, 1986; Wellington and Victor, 1989) and other invertebrates such as sea urchins, so dispersal is limited and dependent on local hydrography (e.g. Shepherd et al., 1992). While there must be some long range dispersal that allows new habitats to be colonised, this appears to be very rare. Thus some populations of the blacklip abalone (*Haliotis rubra*) that were separated by 1.5 km of unsuitable (marine!) habitat were genetically different (Brown, 1991) and most recruitment is highly localised (Prince et al., 1987, 1988). Larvae of the greenlip abalone

(*Haliotis laevis*) of southern Australia were transported 100s of metres and recruitment was focused in areas where hydrographic phenomena would lead to the concentration of larvae (Shepherd et al., 1992). Shepherd and Brown (1993) suggested that greenlip abalone populations in northern Waterloo Bay on the Eyre Peninsula, South Australia, collapsed because they were sinks for larvae from southern populations in the same Bay. Serious overfishing of southern populations would prevent any recovery in the north. When natural sources of invertebrate larvae do not provide recruits to a marine reserve, transplants of adults may be needed to ensure recovery (Tegner, 1992).

An understanding of metapopulation structure is also fundamental to ensuring the recovery and persistence of fish populations in reserves (Tuck and Possingham, 2000). In extreme cases, depletion of source populations may lead to total recruitment failure in a downstream marine reserve, and no recovery will occur. For example, Munro and Watson (1999) reported recruitment failure in Jamaica where source populations were absent. Only larvae with long life spans, that were transported long distances, could recruit to this area.

Man et al. (1995) used a metapopulation model to investigate changes in the total abundance of a fish population when marine reserves protected different components of the population from fishing. The model could be used to estimate recovery rate for different levels of marine reserve protection where, for example, a reef fish metapopulation inhabits a series of patch reefs isolated by sand or deeper water. The model defined patches that could be open to fishing or a marine reserve, and the patches had two states, namely those that contained fishes recruited to the fishery and those that did not (Man et al., 1995). Closing patches to create reserves helped to sustain the total population when the local extinction rate (loss of recruited fishes) became large and this was because the reserves provided recruits to fished areas. The abundance of the exploited population was maximal when half of all patches were occupied (Man et al., 1995). Therefore, if recovery were taken as the management objective, the manager would aim to ensure that half of all the patches were occupied by recruits at any time. If occupancy were suboptimal, the occupancy of patches could be increased by increasing the number of reserves. This would be an unusual approach to management, but it might be realistic provided that the assumptions of the model were approximated.

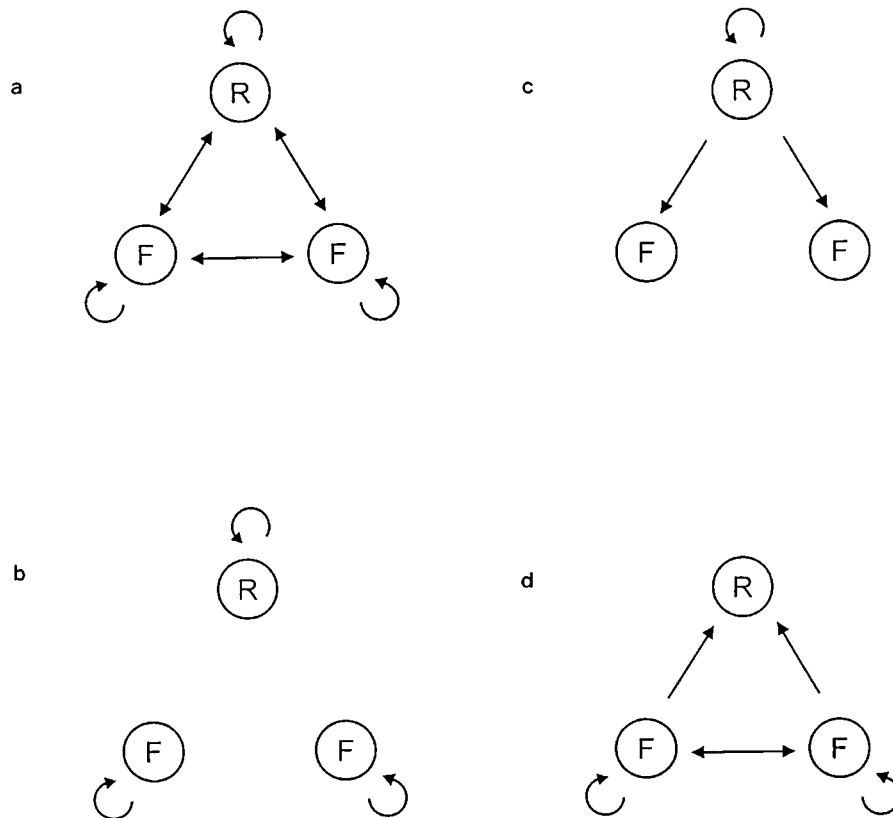


Figure 8. Potential patterns of connectance between 2 fished populations (F) and a population subject to marine reserve protection (R).

Movement, migration and density dependent habitat use

Most fished species are very mobile. Some movements are local and linked to short term activities contributing to growth, survival and reproduction, while others are longer and encompass new environments. Movements have an important impact on population recovery as they can take individuals out of a reserve and in to fished areas. The smallest scale movements that affect recovery are foraging movements, such as the diel commuting of goatfishes (*Mulloides flavolineatus*) between coral reefs and other habitats (Holland et al., 1993). There are also territorial movements and ranging movements where an area is explored (Waldner and Robertson, 1980). On a larger scale, fish migrate. Migrations are persistent movements of greater duration and more consistent direction than foraging movements. Responses to local resources may be temporarily suppressed during migration (Dingle, 1996).

Rates of movement between reserves and fished areas (transfer rates) are incorporated in most per-recruit type models of population recovery in reserves (e.g. Beverton and Holt, 1957; Die and Watson, 1992; De Martini, 1993) because they determine the change in F that follows marine reserve protection. Transfer rates may be estimated, or based on studies that describe actual movements of individuals across reserve boundaries (e.g. Holland et al., 1993, 1996; Kramer and Chapman, 1999; Chapman and Kramer, 2000). Not surprisingly, models show that rates of recovery decrease as transfer rates increase, when other parameters are fixed. Empirical studies also show that rates of recovery are faster for relatively site-attached species (Russ and Alcala, 1998b) and the greatest rates of recovery are expected when species have relatively small home ranges and are non-migratory (Kramer and Chapman, 1999). For many reef species, movements are closely related to habitat, and natural boundaries, such as large areas of sand adjacent to a reef reserve, may limit movement (Chapman and Kramer, 2000). Faster recovery

is expected when (i) the area of the reserve increases in relation to the length of the boundary and (ii) the boundary follows a natural barrier to movement.

Many bird and mammal species show density-dependent habitat use, where increases in abundance are associated with increases in range (Sutherland, 1996). The ranges occupied by many fish populations also change in response to their abundance (Crecco and Overholtz 1990; MacCall, 1990; Hutchings, 1996; Atkinson et al., 1997; Bowering et al., 1997; Brodie et al., 1998). The northern anchovy (*Engraulis mordax*), for example, is found at high densities in a few 'hot spots' (areas of greatest habitat suitability) when abundance is low but begins to occupy a wider range of habitats at lower density when abundance increases (MacCall, 1990). The cod (*Gadus morhua*) also exhibits density-dependent habitat use (Hutchings, 1996), with high densities of cod remaining in a few hot spots across a range of population sizes, and other areas being occupied at low and medium density when overall population abundance is high.

Most marine reserves are small, and only protect a fraction of the area occupied by a population. For populations that show density-dependent habitat use, the location of a reserve in relation to the distribution of a population will determine observed patterns of recovery or decline. Moreover, as abundance in the reserve increases, species showing density-dependent habitat use may emigrate from the reserve to surrounding fished areas, slowing the apparent rate of recovery in the reserve and adding to fishery yields. Of course, density-dependent habitat use has important implications for fishers and stock assessments too (e.g. Myers and Stokes, 1989; Winters and Wheeler, 1985). For example, fishers can continue to make large catches from hot spots when overall population abundance is very low. This is one reason why it can be difficult to persuade fishers that a population has been reduced by fishing; only those fishers who fish on the periphery of the populations range will observe large declines in catch rates as population abundance falls.

Theories that individuals tend to adopt specific distributions in response to habitat suitability or the behaviour of conspecifics, provide a basis for predicting density-dependent habitat use. For example, as the abundance of a population increases, individuals could pack more tightly into favoured habitats or disperse to colonise new areas. Initially, individuals are expected to occupy areas where feeding opportunities or habitat structure are best

(highest suitability). However, as more individuals gather in these areas, competition for food or space may begin to reduce their suitability. Individuals would now be expected to move to previously unoccupied habitats, where the quality of resources is lower but the lower levels of competition lead to higher realised suitability. If individuals are free to move between habitats, then their distribution will tend to the 'ideal free distribution' (IFD) where realised suitability is assumed to be equal in all habitats and no individual can go to a better habitat (Fretwell, 1972; Fretwell and Lucas, 1970). The distribution is called the ideal free because individuals are assumed to be 'ideal' in their judgement of suitability and 'free' to move between chosen locations (Sutherland, 1996).

The IFD would not apply to species that are territorial or have dominance hierarchies, since individuals are not free to move (Sutherland, 1996). Rather, they are predicted to adopt an 'ideal despotic distribution' (IDD) (Fretwell, 1969), where the realised suitability will be different in different habitats because the areas of highest suitability are occupied by the strongest competitors. The IDD may apply to some reef fishes and Kramer and Chapman (1999) give examples of territorial fishes relocating to areas that have been cleared of competitors. The net effect of the IFD and IDD is that many fish populations will occupy a larger area as they increase in abundance. This applies particularly to temperate 'groundfish' species such as pleuronectids and gadoids which show very strong density-dependent habitat use, but less so to those reef fishes that remain close to settlement sites throughout their lifespan. It is notable that the IFD can be substantially modified if depensation is accounted for. Realised habitat suitability still declines when more competitors are present, but suitability is also low when few competitors are present (e.g. Sutherland, 1996).

Rakitin and Kramer (1996) made one of few tests of density-dependent habitat use on a tropical reef reserve, looking at patterns of abundance across a reserve boundary in Barbados. The abundance of many species was higher in the reserve and decreased with distance from the boundary (Rakitin and Kramer, 1996). However, there were no clear signs of emigration. This may be due to habitat boundaries, such as areas of sand, that stop fish dispersing as predicted by the IFD or IDD. Chapman and Kramer (1999) improved on this analysis by controlling for habitat type and showed that density was still significantly

higher in the reserve, but that the mobility of species was not correlated with the relative difference in density between reserve and non reserve. The evidence for spillover (emigration of exploitable stages from protected to fished areas) was quite weak for these reef fishes. One would expect a very different result for groundfish species where strong density dependent habitat use has already been demonstrated.

For a mobile stock showing density-dependent habitat use, the location of a reserve in relation to the areas of highest habitat suitability will have a key effect on the observed patterns of recovery. Most marine reserves protect a very small proportion of the total area occupied by a population. If that population is relatively mobile, and fishing effort excluded from the marine reserve is employed elsewhere, then reductions in F are likely to be small (e.g. Beverton and Holt, 1957; Horwood et al., 1998).

Consider three marine reserves (A, B and C) sited in different parts of the range that can be occupied by a population. One is sited in a hot spot, an area of high habitat suitability where the density of fish is high at low (total) population levels (A, Figure 9), while the others are sited towards the periphery of the range (B and C, Figure 9). At time = 1, when population abundance is low (Figure 10), the density of fish is high in the hot spot reserve, but low in the others. As the population abundance increases to a maximum at time = 3, there is little change in the abundance of fish in reserve A because it is already sited in a hot spot and the range of the fish is increasing rather than their density. However, in reserve B, rapid recovery is clearly observed because fish are moving to occupy this area. Reserve C, on the periphery of the range, only witnesses 'recovery' when total population abundance is very high. Patterns of abundance in this reserve will be driven almost exclusively by changes in the overall size of the population and will not result from this reserve influencing F .

This simple example suggests that a reserve should be sited in the hot spot (A) to maximise reductions in F . The hot spot is where fishers are likely to want to fish as well. Reserves at B and C will have minimal effects on total population size and observed patterns of abundance are simply governed by variable dynamics and fishing pressure affecting the total population. Even when a population is severely depleted by fishing, abundance in the hot spots can remain high, because fish move into these areas as total abundance falls. For example, as the northern cod stock collapsed, catch-per-unit-effort was still high

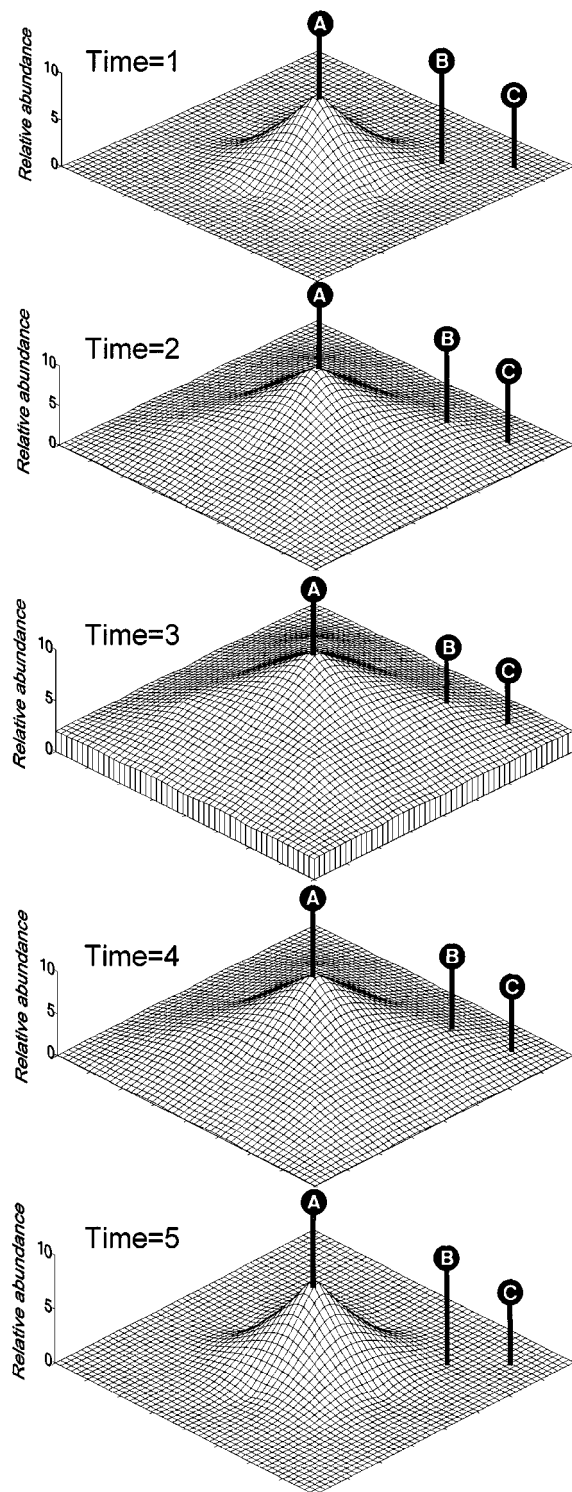


Figure 9. Hypothetical changes in the distribution and local abundance of a fish population showing strong density dependent habitat use. Total abundance changes with time as shown in Figure 10. A, B and C indicate the locations of 3 small marine reserves.

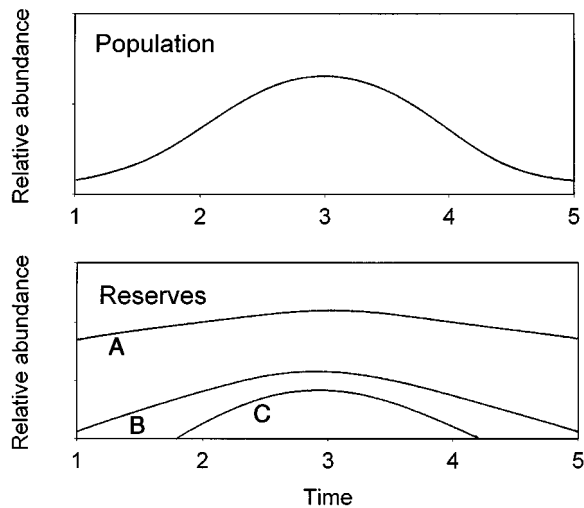


Figure 10. Relationships between changes in total population abundance (a) and changes in local abundance (b) of fish at marine reserves A, B and C (Figure 9) when the population shows strong density dependent habitat use.

in a few areas of high habitat suitability (Hutchings, 1996).

For fish conservation, reserves are better sited in hot spots than in habitats that are 'representative' of the marine environment. Hot spots can often be identified with ease from existing fishery or survey data, but reserves may be difficult to establish there because fishers will tend to retreat to them as total stock abundance falls. The probability of density increases following protection is lower in these 'ideal' reserve sites than in adjacent areas. This is because the habitat may be fully utilised unless the stock is in a perilous state. For a stock showing strong density-dependent habitat use, abundance increases will result in export to adjacent fished areas rather than an increase in abundance within the reserve.

The 'plaice box' provides an interesting example of the effects of large-scale movements of a fish population on the extent of population recovery in a marine reserve. The plaice box is a 38 000 km² area in the eastern North Sea that was closed seasonally from 1989, and for the whole year since 1995, in an attempt to reduce mortality on juvenile plaice, increase SSB and enhance fishery yields (ICES, 1994b, 1999; Piet and Rijnsdorp, 1998). The plaice box is not a true no-take zone as a few smaller vessels are allowed to fish there, but fishing effort is dramatically reduced. An ICES (1994b) model, that assumed fixed patterns of plaice distribution and fishing effort, and

estimated changes in the number of survivors using a time step of one quarter year, suggested that full closure (as implemented in 1995) would increase the SSB and yields. Early assessments were in accordance with model outputs and the abundance of plaice increased. However, the recovery was short-lived and contrary to expectation, yield and SSB decreased after total closure in 1995 (ICES, 1999). Formerly, plaice smaller than the minimum landing size (27 cm) were abundant in the box, but after 1995 their distribution changed, with more found on the western periphery. This meant that they were caught by beam trawlers targeting adult plaice around the edges of the box and suffered high discard mortality. Revised model outputs suggest that the recent emigration of plaice has reduced the potential fishery benefits of the box. Various reasons have been proposed to account for the emigration of plaice from the box, and they are based on the premise that the habitat suitability in the box has fallen below that in other parts of the North Sea. One possibility is that the lack of beam trawling disturbance inside the plaice box has reduced food supply, since trawling disturbance in shallow sandy habitats is known to favour the proliferation of fast growing, productive and opportunistic benthic species (e.g. Kaiser and Spencer 1996; Lindeboom and de Groot, 1998) that may be consumed by plaice. Indeed, increases in benthic productivity due to trawling in the southern North Sea were predicted to have led to increases in growth of sole and plaice (Rijnsdorp and van Leeuwen, 1996). Conditions for feeding and growth may now be better in the heavily trawled areas outside the plaice box and plaice appear to have relocated to these areas. Of course, there are other possibilities, specifically that movements were related to changes in temperature, but this large marine reserve may no longer be promoting population recovery and providing appreciable fisheries benefits (ICES, 1999).

Phase shifts

Models of population growth, and hence recovery, are based on the assumption that a population returns to its former state along a specified growth trajectory. In other words, we assume fishing effects are reversible (Jennings and Polunin, 1996). However, since the real environment fluctuates, growth and recruitment rates are variable and the 'former' state is never constant. As such, recovery is sporadic, with large gains in abundance when recruitment and growth are successful and minimal gains when they are not.

Intensive fishing may cause long-term changes to the environment that hinder population recovery. For example, on tropical reefs where herbivorous and invertebrate-feeding fishes are reduced by intensive fishing, the reef may shift from an algal and coral to sea-urchin dominated community (e.g. Done, 1992; Knowlton, 1992; Hughes, 1994). The reduction in invertebrate feeders reduces predation mortality on urchins and allows them to proliferate. Moreover, once established, urchins can tolerate low algal biomass because they have low consumption and respiration rates. This allows them to outcompete herbivorous fishes and reach maximum biomass levels an order of magnitude higher than previously (McClanahan, 1992). Since the herbivorous fishes are poor competitors, they cannot recover when fishing stops (McClanahan, 1994, 1995). Unless natural failures of urchin recruitment or disease lead to a collapse of urchin populations, other intervention is needed to promote recovery. This has been attempted on small scales by deliberate removal of urchins. McClanahan et al. (1996) attempted such removal in Kenyan reef lagoons. When they removed urchins from unfished experimental plots there were significant increases in algal cover, fish abundance and fish species richness within one year. However, on fished reefs, where the biomass of herbivorous fishes was low, algae became very abundant and overgrew corals. Their results suggested that the removal of urchins in recently established marine reserves would shift the ecosystem to a state that promotes recovery of fish populations. The ecosystem shifts observed in their manipulative studies were similar to those observed in the Caribbean when there was mass urchin mortality following disease (e.g. Lessios et al., 1985; Carpenter, 1988).

Predicting recovery rate

Rates of natural increase

Estimates of the intrinsic rate of natural increase (r) provide the basis for predicting recovery rate. However, direct use of the Euler-Lotka equation (1) to estimate r (e.g. Hutchings and Myers, 1994) is data intensive and is only appropriate for a few commercially-important stocks where age-specific survival and fecundity schedules are available. Perhaps the most powerful approach for measuring potential recovery at very low population sizes (i.e. when density dependence has a minimal impact on

population growth rate) is based on the premise that r is reflected in the initial slope of a spawner-recruit relationship. This requires a well-established spawner-recruit relationship, and thus limits the application of the method to populations that have been studied for some years.

Myers et al. (1997) developed an expression for r based on the initial slope of a Ricker spawner-recruit relationship

$$R = aSe^{-bS} \quad (6)$$

where R is the abundance of recruits, S is the abundance of spawners, a is the slope of the relationship at the origin (recruits per spawner at low stock sizes) and b captures the density dependence of the relationship by describing how fast the number of recruits per spawner falls as S increases. Myers et al. (1997) showed how a could be standardised to give the number of spawners produced by each spawner per year. The following is from Myers et al. (1997).

In a general spawner recruit relationship, the relationship between a and \hat{a} , the mean biomass of spawners produced during the lifetime of a spawner, is

$$\hat{a} = a.SPR_{F=0} \quad (7)$$

where $SPR_{F=0}$ is the spawning biomass resulting from each recruit in the absence of fishing mortality.

If adult survival is p_S , then \hat{a} is related to \tilde{a} , the number of spawners produced by each spawner per year after the age of maturity

$$\hat{a} = \sum_{x=1}^{\infty} (p_S)^x \tilde{a} \quad (8)$$

Summing the geometric series and rearranging

$$\tilde{a} = \hat{a}(1 - p_S) \quad (9)$$

Returning to the Euler-Lotka equation (1), and assuming (i) that $m_x = m_0$ for fish of age α and (ii) that when $x \geq \alpha$ then $l_x = l_\alpha p_S^{x-\alpha}$ where l_α is the proportion of juveniles that survive from age zero to maturity, it follows that

$$l_\alpha m_0 \sum_{x=\alpha}^{\infty} p_S^{x-\alpha} e^{-rx} = 1 \quad (10)$$

With some rearrangement and summing of the geometric series, Myers et al. (1997) expressed this as

$$\frac{l_\alpha m_0 e^{-r\alpha}}{1 - p_S e^{-r}} = 1 \quad (11)$$

Since m_0 is the number of eggs produced by each spawner and l_α is the fraction of age zero fish surviving to maturity, $m_0 l_\alpha$ must equal \tilde{a} and equation (11) can be expressed as

$$(e^r)^\alpha - p_S(e^r)^{\alpha-1} - \tilde{a} = 0 \quad (12)$$

Myers et al. (1997) solved this equation using data for North Atlantic cod stocks to estimate their potential for recovery if protected from fishing. Estimates of r ranged from 0.15 to 1.03 with an average of less than 0.2 for stocks in colder areas such as the southern Gulf of St Lawrence and greater than 0.5 for stocks such as those in the warmer North and Irish Seas. For $r = 0.2$ and 0.5, the mean population doubling times (given by $\log_e(2)/r$) are approximately 3.5 and 1.4 years respectively. Clearly, given that some of these cod stocks have been dramatically reduced by fishing, often to 5% or less of their biomass at times of high abundance, recovery could take decades if fishing were stopped.

For northern cod, protected since 1992 by a moratorium, Myers et al. (1997) estimated r as 0.26 (corrected value cited in Hutchings, 1999). This suggests a doubling time of 2.7 years. However, no recovery of this population had been detected by 1999. Hutchings (1999) showed that the lack of recovery could be due to natural stochastic variation in life history variables. He used an age-structured life history model to determine how changes in age at maturity, pre- and postreproductive mortality and postreproductive growth rate affected estimates of r at low population size. Relatively small increases in pre- and post-reproductive mortality reduced r . For example, if postreproductive mortality rose from 0.20 to 0.45, the increase in r translated to increases in doubling time from 4.1 to 7.1 years for cod maturing at age 4, and from 5.2 to 8.8 years for cod maturing at age 7. There is some empirical evidence for increases in the natural mortality of cod since the fishery closure. Hutchings (1999) approach allowed him to estimate the effects of age-specific changes in survival and growth on r . This is not possible when r is estimated from spawner-recruit relationships. Unfortunately, the extensive data requirements will usually preclude application of his approach.

Assessment of r based on spawner-recruit relationships requires many years' data, and spawner-recruit data at low population levels are often very scarce. This leads to many concerns about the adequacy of the fitted model and the evidence for strong compensation. The elasmobranchs are one group thought to be particularly endangered by fishing and yet knowl-

edge of their population dynamics is relatively poor. Smith et al. (1998) estimated the ability of shark populations to recover following the cessation of fishing, by assuming density-dependent compensation occurs before the age at maturity and that the populations have a stable age composition when subject to fixed levels of mortality. This is not true, but is probably a more reasonable assumption for elasmobranchs than for species with more variable dynamics.

Smith et al (1998) wrote an expression for l_x in terms of survival to age at 50% maturity α

$$l_x = l_\alpha e^{-M(x-\alpha)} \quad (13)$$

where M is the instantaneous rate of natural mortality. The Euler-Lotka equation (1) can then be modified and rearranged

$$l_\alpha \sum_{x=\alpha}^{\omega} e^{-M(x-\alpha)} e^{-rx} m_x = 1 \quad (14)$$

where ω is maximum age. Smith et al. (1998) now took m_x as a constant β because the proportion breeding and age specific fecundity were not known for these shark species. β was the mean number of female offspring produced by all females older than α . The resultant equation is a less data-intensive form of the Euler-Lotka equation

$$e^{-(M+r)} + l_\alpha \beta e^{-r\alpha} [1 - e^{(-M+r)(\omega-\alpha+1)}] = 1 \quad (15)$$

This allows r to be estimated from the basic life history parameters α , ω , M , β and l_α , and the method is thus applicable to many populations for which relatively limited life history data are available.

Smith et al. (1998) estimated survival to the age at maturity, l_α , when fishing mortality F was equal to M . This level of fishing was assumed to be sustainable. If assumptions about population stability are made, this level of pre-adult survival reduces the population to approximately half the 'virgin' size. Compensatory density-dependent changes in survival are assumed to occur only in l_α . If the population is fished until $F = M$, then total adult mortality increases from M to Z and this decreases adult population size and reproductive output. The expected decrease in r (as defined by Smith et al.) is then compensated for by an increase in l_α .

It is possible to solve for l_α when $Z = F + M(l_{\alpha,z})$ by making the assumption that fishing is sustainable when $F = M$ and that $r = 0$. Equation 15 then becomes

$$e^{-Z} + l_{\alpha,z} \beta [1 - e^{-z(\omega-\alpha+1)}] = 1 \quad (16)$$

The rebound level of r for each population can now be calculated by reducing F to 0. To do this, the reduced population is assumed to maintain exploitation compensated l_α . Smith et al. (1998) designated the rebound level of r the intrinsic rebound potential r_{2M} , and this allowed the recovery rates of a range of shark species to be compared. The late-maturing species were predicted to have particularly low rebound potentials. For example, r_{2M} for the gray reef (*Carcharhinus amblyrhynchos*) that matures at age 7 was 0.054, while r_{2M} for the closely related dusky shark (*C. obscurus*) that matures at age 21 was 0.020. These values of r_{2M} equate to doubling times of 13 years and 35 years respectively and would result in very slow recovery following protection. Rates of recovery would be even slower if, as is likely, any reserve used for protection only affected a partial reduction in F .

Estimating increases in biomass

Recovery in biomass following marine reserve protection can be the simple consequence of reduced mortality rates and greater survivorship at age. This is the process that has been addressed when 'per-recruit' type models have been used to assess the fishery benefits of marine reserve protection (Beverton and Holt, 1957; Die and Watson, 1992; Russ et al., 1992; De Martini, 1993; Horwood et al., 1998; Attwood and Bennett, 1995). A key parameter in these models is transfer rate. This will differ between species and with ontogeny. The best estimates of transfer rate come from detailed size-based assessments of actual movements from tagging and tracking studies and are appropriate for high value resource species that can be tagged, such as coral trout (*Plectropomus leopardus*) (Zeller and Russ, 1998). Data storage tags that record depth, light levels and temperature allow tracks to be reconstructed, and are providing vast datasets on the movements of species such as plaice (*Pleuronectes platessa*) (Metcalf and Arnold, 1997). These data should allow individual behaviour-based models of migration to be parameterised and provide a basis for predicting density dependent habitat use.

However, species for which useful information on transfer rates can be obtained by tagging are a small proportion of those considered for marine reserve protection. Probably the most constructive approach is to seek life history correlates of transfer rates. Previous models have assumed that species with fast life histories (early maturity, fast growth, small

maximum size) have lower transfer rates than those with slower life histories (e.g. De Martini, 1993). Moreover, Kramer and Chapman (1999) have shown a significant cross-species relationship between home range length and body size, though they did not test whether this was still significant after accounting for phylogenetic relatedness between species (Harvey and Pagel, 1991). For closely reef-associated species, home range size and body size may be correlated because of the fractal properties of benthic shelter (De Martini, 1998). There is considerable scope for further investigation of the links between life histories and transfer rates. If such links exist, they will vastly improve our capacity to parameterise models and to assess the effects of reserve protection on recovery rates. They will also provide a basis for optimising the size and shape of reserves to achieve specified fishery or conservation benefits.

Predicting recovery with limited data

Many of the models needed to assess the conservation benefits of marine reserves are as complex as those used for conventional fishery analysis and cannot realistically be applied to most fish and invertebrate populations that are threatened by fishing in 'data-poor' environments. Indeed, one of the advantages of reserves is that they simplify management and reduce enforcement costs when there are few resources for scientific research and policing. In these circumstances, it would be useful if recovery rates could be predicted using methods that require minimal data. One approach is to establish relationships between measures of population recovery, such as the intrinsic rate of natural increase, and life history parameters that are more easily measured.

Studies of fish life histories have revealed close relationships between maturation and growth parameters (Alm, 1959; Beverton and Holt, 1959; Beverton, 1963, 1987, 1992; Leggett and Carscadden, 1978; Pauly, 1980; Jennings and Beverton, 1991; Sadovy, 1996). These relationships result from tradeoffs among life history allocations (Stearns, 1976; Beverton, 1987; Roff, 1992; Charnov, 1993). Species with short lifespans, high natural mortality, early maturity, fast growth and small body size have faster rates of population growth than long-lived, slow growing, late maturity, low natural mortality, large body size species with low reproductive output. Maximum size, usually measured using the parameter L_∞ of the von Bertalanffy growth equation,

is closely related to observed maximum size, and is negatively correlated with growth, age at maturity, reproductive output and natural mortality (Beverton, 1963, 1987; Charnov, 1993; Sadovy, 1996). These correlations suggest that a parameter as well known as maximum size may be a useful surrogate for a species' life history and may therefore be used to predict vulnerability to fishing. Indeed, gross estimates of vulnerability for temperate and tropical reef fishes can be made from knowledge of their maximum size and phylogenetic relationships (Jennings et al., 1998, 1999). The potential rate of population increase is inversely related to vulnerability, so we can reasonably expect life history correlates of r .

The studies of Myers et al. (1997) and Smith et al. (1998) suggest that indices of the intrinsic rate of natural increase may be predicted from life history parameters such as age at maturity. Cross-stock and cross-species analyses by Myers et al. (1997) and Smith et al. (1998), respectively, suggest that their indices of r are closely correlated with age at maturity, although it would be useful to support the cross-species analysis with a phylogenetic comparative approach that accounts for non-independence of the data (Harvey and Pagel, 1991). There is considerable scope for developing approaches that provide estimates of r from limited data. An initial approach may be to use the slope at the origin of a spawner-recruit relationship as a measure of r (e.g. Myers et al., 1997), and to relate this to life histories with some of the extensive datasets that have already been compiled (e.g. Myers et al., 1995).

Linking theoretical and empirical studies

Empirical assessments of recovery rates in marine reserves are often based on pooled data for groups of species or families (especially on tropical reefs). Since the component species have different r , transfer rates and life histories they will recover at different speeds, and we can only generalise about recovery rates because the numerically-dominant species in some families share similar life histories.

One of the most comprehensive studies of population recovery in marine reserves was conducted by Russ and Alcala (1996). At Apo reserve, Philippines, fish abundance was measured 7 times during an 11 year period of effective protection from 1983 to 1993. Target groups were dominated by a few species with similar life histories (Russ and Alcala, 1998b) and

abundance trends in the reserve were compared with those in the fished area. The density of large predators increased 7.1 times over 11 years and the increase showed no sign of slowing at the time of the last census. These data suggest that the population of large predators had a doubling time of approximately 4 years. This would give $r = 0.17$, a relatively low value consistent with the slow life histories of these predators (Russ and Alcala, 1998b).

A consideration of likely doubling times suggests that some of the 'recovery' observed in marine reserves is due to immigration or to the fortuitous appearance of a successfully recruited year class into the size range that is counted during visual census work. White (1988), for example, recorded significant increases in density of serranids and lutjanids after just one year of protection in the Pamilacan and Balicasag marine reserves in Philippines, increases that are unlikely to be due to true population growth. Similarly, Bohnsack (1990) recorded doubling times of approximately 2 years and 1 year for lutjanids and haemulids in the Looe Key National Marine Sanctuary, Florida Keys. These doubling times imply unrealistically high values of $r = 0.35$ and $r = 0.7$ for lutjanids and haemulids respectively and lend credence to Bohnsack's (1990) suggestion that part of the observed recovery was due to decreased avoidance of divers in an area that was spearfished prior to reserve protection.

Bennett and Attwood (1991) made a detailed study of recovery rates of individual species at the De Hoop Marine Reserve on the southern coast of South Africa. This is a relatively large reserve, protecting 46 km of coastline. They used catch-per-unit-effort (CPUE) as an index of abundance and looked at changes in abundance over 4.5 years of protection. Galjoen (*Coracinus capensis*) and Dassie (*Diplodus sargus*) were the most abundant species in the reserve and accounted for 57.8% and 33.9% of total catch (in numbers) respectively, from the central Koppie Alleen site where the study was conducted. Both species were not very mobile and resident in small areas (a few km²) for long periods. The mean CPUE (number of fish 100 h⁻¹) of both species increased by a factor of >4 from the period before protection to a 29 month period after 29 months of protection. Some of the early increase in abundance was not thought to be due to population recovery, but after 29 months an analysis of size distributions for *Diplodus sargus* suggested that new abundant cohorts had appeared. Bennett and Attwood (1991) discussed some of the potential problems when using CPUE data for the assessment of recovery, in

particular that competition among anglers may have led to reduced catches by the experimental group in the period before protection.

When looking at empirical studies of recovery in small reserves, short-term gains in abundance will come from redistribution and increased survival (due to reduced F) of year classes that have already recruited. As SSB increases, increases in recruitment (usually measured at settlement stage for most reef fishes) may not impact the egg production of species with slow life histories for at least 3–4 years. The general difficulties with making empirical assessments of population recovery in reserves are (i) that the individuals in the reserve are a small proportion of the total population, (ii) that census methods are biased by changes in behaviour that follow the removal of fishing pressure and (iii) that population growth cannot readily be distinguished from population movement or redistribution (e.g. Cole et al., 1990; Kulbicki, 1998, Willis et al., 2000).

Conclusions

Population recovery in marine reserves may result from increased survival due to reduced fishing mortality and from increased egg production that leads to increased (mean) recruitment. The basic measure of population growth rate is the intrinsic rate of natural increase and this is reflected in the ratio R/S at low stock sizes. The degree of compensation or depensation at low stock sizes has a key effect on population growth. Depensation may occur in some fish populations and does occur in many invertebrate populations where fertilisation rates fall rapidly with falling density of spawners. Recovery is strongly dependent on the supply of recruits to a reserve, and, if local populations are depleted, a new reserve may not be recolonised by species with limited larval duration. In this case, reserves may have to be artificially stocked to promote recovery. Long-term recovery is most likely in a reserve where the population is self-sustaining, and the reserve may benefit fisheries if it also acts as a source of larvae to surrounding areas. Movement is a key determinant of the reduction in F effected by a reserve, and thus determines recovery rates. For species showing density dependent habitat use, reserves should be sited in hot spots if they are to provide the greatest conservation benefits. Patterns of abundance in small reserves may be driven by the spatial dynamics of the total population rather than the

effects of the reserve on F . Thus unrealistically rapid responses of species with ‘slow’ life histories in small reserves are likely to provide spurious evidence for the effects of protection.

Recovery rates can be predicted from modified fishery assessment models and estimates of r . Phase shifts in the ecosystem can prevent any recovery. Estimates of reductions in F following reserve protection require estimates of transfer rates between the reserve and adjacent fished areas. Methods of calculating transfer rates and r are usually data-intensive, and not applicable in data poor situations where reserves are often favoured for management. There is considerable scope to identify simple life history correlates of transfer rates and r for use in data poor situations.

Empirical measures of recovery rates are scarce. Most marine reserves protect a fraction of the total population and it is hard to distinguish real population growth from changes in distribution. Moreover, census techniques may provide biased data when changes in behaviour of fishes take place after protection. Stronger experimental designs are needed to look at recovery. At present, BACI designs or those that account for habitat differences between marine reserves and adjacent areas are the exception rather than the rule.

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Note

1. In this paper, the term ‘marine reserve’ is taken to be synonymous with ‘no-take zone’: an area in which there is no fishing.

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