



Benefits beyond boundaries: the fishery effects of marine reserves

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Marine reserves are areas of the sea where fishing is not allowed. They provide refuges where populations of exploited species can recover and habitats modified by fishing can regenerate. In some places, closed areas have been used for fisheries management for centuries [1] and, until recently, natural refugia also existed, inaccessible through depth, distance or adverse conditions. Developments in technology have left few areas of fishing interest beyond our reach. Recently, the idea of marine reserves as fisheries management tools has re-emerged with developing interest in ecosystem-based management, and observations of incidental fisheries benefits from reserves established for conservation. In light of new evidence, we argue that, by integrating large-scale networks of marine reserves into fishery management, we could reverse global fishery declines and provide urgently needed protection for marine species and their habitats.

Marine reserves are predicted to benefit adjacent fisheries through two mechanisms: net emigration of adults and juveniles across borders, termed 'spillover', and export of pelagic eggs and larvae. Inside reserves, populations increase in size, and individuals live longer, grow larger and develop increased reproductive potential [2]. Enhanced production of eggs and larvae inside reserves is predicted to lead to net export and increased settlement of juvenile animals outside the boundaries.

Using marine reserves for fisheries management is controversial. Critics argue that most commercial species are too mobile to benefit, that marine reserves are only appropriate in very specific cases (usually small-scale tropical fisheries) and that it is too risky to implement them on a larger scale until we have more and stronger experimental proof of their efficacy (Box 1). Fishers worry that reducing fishing grounds will decrease catches and increase travelling time. They are also cynical about the levels of compliance to closed-area regulations that can realistically be expected.

Until recently, most insights into reserve function came from theoretical research. However, empirical evidence is increasing and demonstrations of effects outside reserve boundaries are emerging from a wide range of habitats and fisheries. Here, we examine this new body of evidence, and ask what we can expect of well managed reserves. To do

this, we focus on reserves that have been effectively enforced for at least five years, and draw upon studies of more limited fisheries closures that provide insight into

Box 1. Improving studies of marine reserves

Some scientists question many of the findings that we discuss here. They point out, rightly, that most studies of reserves employ designs that cannot unequivocally deliver a verdict on whether they work. Many compare a single reserve with one or more control sites. Because in some cases (but certainly not all), reserves were chosen because they have good quality habitats, this leaves open the possibility that differences detected are habitat rather than protection effects. Similarly, changes over time in measures of reserve performance might be due to habitat or background environmental changes.

The strongest study design for reserves research is considered to be before-after-control-impact-pairs analysis (BACIP) [48]. Here, three or more reserves are paired with several control locations, and data collected at intervals before (ideally three or more times) and after protection. In this way, the effects of protection can be separated from those of habitat. Sites adjacent to reserves might receive spillover and will not be adequate controls. So, to settle questions of spillover, we need several sets of reserve-adjacent area-control site triplets. Our difficulties do not end there. Reserves can potentially export larvae tens of kilometres away, so sites within that supply envelope might also be affected by the reserve and will not represent true controls. Conditions and habitats in control and reserve sites must be matched closely, but as distance between them increases conditions might diverge. Good controls are very difficult to find.

There are also human problems. Few funding organizations will support collection of several years of pre-protection data. Scientists also find it hard to maintain control over the design of reserve experiments. Management plans are often modified, reserve boundaries changed and protection poorly implemented. It is hardly surprising then that few studies have achieved this level of design sophistication. Furthermore, very few collect data on fishing effort, without which it is impossible to know whether absence of an effect is because reserves do not work or is just due to lack of protection.

Some people suggest that fishers' resistance to reserves will diminish or disappear when scientists produce better quality statistical evidence, but we doubt this. Fishers are most often convinced of the usefulness of reserves through the experience of other fishers. This makes an all-round picture of how reserves have affected fishing, the wider community and the ecosystems, of more relevance than statistical tests. However, sceptical fishery managers and decision makers might be won over by stronger science. That said, we find it paradoxical that many managers place more faith in management tools whose performance has not been subject to the level of critical scrutiny that they demand of reserves. This is not to say that seeking such a high standard of proof is not necessary for reserves. The next generation of studies must strive for it. But we should also demand the same evidence of efficacy for other fishery management tools. The poor state of the world's fisheries suggests that these tools are not performing as intended.

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how fully protected reserves can work (Gell and Roberts [3] provide a more detailed analysis and 16 case studies). We find that well enforced marine reserves have great potential to maintain or enhance fishery catches and increase sustainability. They should be used much more widely and with more confidence in their function.

Magnitude of build-up of spawning stocks in marine reserves

There is currently a vigorous debate over the quality of reserves research (Box 1). However, our confidence that reserves work increases with consistent, repeated demonstrations that uphold predictions about their effects. We believe that, taken together, this body of evidence from a wide range of ecosystems shows that reserves promote large, rapid and sustained build-up of biomass of commercially important species within their boundaries. In the Tsitsikamma National Park in South Africa (established in 1964, making it one of the oldest reserves in the world) densities of a commercially important sparid fish, *Chrysolephus laticeps*, were an estimated 42 times higher than in nearby fishing grounds [4]. A more recent study in the park found that experimental catch per unit effort (CPUE) for four shorefish species was 5–21 times greater than in exploited areas [5].

In the Scandola Nature Reserve in Corsica, densities of 11 fish species were five times higher in reserve than in fished sites after 13 years of protection [6]. Experimental CPUE for lobsters inside the Columbretes Island Marine Reserve in Spain were 6–58 times greater than those from fished sites [7]. Also in Spain, pen shells *Pinna nobilis* are now 12 times more abundant in the 100-ha no fishing zone of the Tabarca Marine Reserve (est. 1986) than in nearby fished areas*. Russ and Alcalá [8] reported a sevenfold increase of larger predatory reef fish after coral reefs were protected for 11 years at Apo Island in the Philippines.

Dramatic increases in body size have also been reported inside reserves. In three temperate rocky reef reserves of New Zealand, protected for between five and 20 years, snapper *Pagrus auratus* larger than the minimum legal size were 14 times more abundant than in fished areas [9]. After five years of protection, 35% of blue cod *Paraperca colias* inside New Zealand's Long Island-Kokomohua reserve were > 33 cm long, compared with < 1% in nearby fished areas [10]. In the Maria Island Reserve in Tasmania, large fish (> 32.5 cm) became more than three times more common after six years of protection [11]. In the Everglades National Park in Florida, USA, (est. 1985) the modal size of grey snapper *Lutjanus griseus* was 25–30 cm compared with 15–20 cm in exploited areas [12].

Increases in animal abundance and size in marine reserves translate into increased reproductive potential. In New Zealand reserves, egg production of lobster *Jasus edwardsii* at deep-water sites increased by 9.1% per year of protection [13], and for snappers was 18 times higher than in fished areas [9]. After > 20 years of protection in the Edmunds Underwater Park in Washington State, USA,

lingcod *Ophiodon elongatus* produced 20 times more eggs than they did in adjacent fished areas, and copper rockfish *Sebastes caurinus* 100 times more [14]. Rodwell *et al.* [15] estimated that 70% of the biomass of fish in Kenya's Mombasa Marine National Park was reproductively active compared with just 20% in nearby fishing grounds.

Box 2. Success for large-scale closures in Atlantic fishing grounds

Georges Bank in the Gulf of Maine, USA, once ranked among the most productive fishing grounds in the world. However, intensive exploitation since World War II resulted in the decline and collapse of the fisheries. In 1994, in response to severe fishery depletion, three areas totaling 17 000 km² were closed to fishing for groundfish (bottom-dwelling fish) [19]. They were also closed to all gears that might catch groundfish incidentally, or damage their habitats (e.g. scallop dredges). Some forms of fishing were still permitted, such as longlining, so the areas were not completely no-take, but they still offer important insights into how fully protected areas might work at this scale.

Five years later, the Georges Bank closures, together with a package of cuts in fishing effort introduced at the same time, were hailed as a success for fisheries management [19]. Closed areas significantly reduced fishing mortality of groundfish species, and stocks of haddock *Melanogrammus aeglefinus*, yellowtail *Limanda ferruginea* and witch flounders *Glyptocephalus cynoglossus* have increased in particular. Although many key fishery species are still at low densities compared with historical levels, the trends have turned upwards after many years of decline. Cod *Gadus morhua* have responded more slowly to protection, perhaps because they are more mobile or had been driven down farthest, but there are signs that their biomass is also rebuilding [56,57]. Fishers are beginning to report improvements in catches. One Cape Cod fisherman reported that he now travels less than half the distance and catches nearly twice as much cod as he did before the closures [3].

The most dramatic effect has been on scallops *Placopecten magellanicus*, which, before the closures, had been heavily depleted. After five years of protection, densities of legal-sized scallops reached 9–14 times those in fished areas [19]. Satellite monitoring showed scallop-fishing vessels clustering around the edge of the closed areas. Areas of high fishing effort corresponded with the places that biophysical models suggest would have received most scallop larvae exported from closed areas*. Those models suggest that, with a 40-day larval duration, currents can take larvae from closed areas to large regions of the bank as well as back into closed areas to replenish protected stocks†.

The closures are also enabling benthic habitats to recover. Protection from trawling has led to significant increases in the density, biomass, species richness and production of benthic animals, such as echinoderms, hydroids and seafans [58], and these effects are likely to be enhancing production of commercial species such as haddock and flounders, leading to long-term sustained benefits.

* Lewis, C.V.W. *et al.* (2001) Effects of area closures on Georges Bank bivalves: larval transport and population dynamics. http://www-nml.dartmouth.edu/Publications/internal_reports/NML-00-2/. For simulation model, see: <http://www.seascallop.com/currents.html>; Rago, P. and McSherry, M. (2002) Spatial distribution of fishing effort for sea scallops: 1998–2000. Appendix G in Northeast Region Essential Fish Habitat Steering Committee, Workshop on the Effects of Fishing Gear on Marine Habitats off the Northeastern United States. October 23–25, 2001, Boston, Massachusetts. NOAA, Woods Hole, Massachusetts. <http://www.nefsc.nmfs.gov/nefsc/publications/crd/crd0201/index.htm>.

† Lewis, C.V.W. (1999) Biological-physical modeling of sea scallop fishery closures. <http://www.cbl.umces.edu/fogarty/usglobec/misc/field.notes-3.html>.

* Sánchez Lizaso, J.L. *et al.* (2001) *Biological and Socio-Economical Effects of the Marine Reserve of Tabarca* (Spanish Mediterranean). VALFEZ internet conference: http://www.valfez.org/internet_conf/Tabarca/sld001.htm.

Box 3. Communities return to traditional closed areas in Fiji

Fiji has a long history of using closed areas for fisheries management [59]. Communities are now returning to this traditional technique to deal with contemporary issues of overexploitation and diminishing marine resources. In the early 1990s, residents of Ucunivanua village consulted with the University of the South Pacific (USP) and the Biodiversity Conservation Network (BCN) for advice on management of their declining catches. Together, they put in place several management strategies: replanting mangroves, banning mangrove cutting, coral extraction and poison fishing, obtaining alternative income from a bioprospecting enterprise and setting up a species-specific fishery closure for one of their main fisheries species, the *Anadara* clam [59].

The clam closure began in 1997 and was applied to a 24-ha area of seagrass and mudflat directly in front of the village. The community liaised with scientists to design a sampling programme and have monitored clams inside and outside the closed area since 1997. Results show a dramatic increase in the numbers and size of clams in the closed area after three years of protection, and an increase in the number of smaller clams recruiting to fished areas (Fig. 1). Clams reached sizes bigger than had been seen for generations. After three and a quarter years of management, clams had increased in abundance by 13 times in the closed areas and by five times in the fished area. Catch per unit effort increased and people reported catching clams twice as quickly as before the closure [20,59]. Data collected in 2002 show that, after five years of protection, there have been further increases in clam abundance. Clams are now 19 times more abundant in the closed area and seven times more abundant in the fished area (Ucunivanua community and A. Tawake, unpublished data).

The community reported other positive effects, including improvements in the seagrass habitat and the return of species that had disappeared from the area, such as seahares and stingrays. In response to the effects that they were observing, and aware of the temptation for fishers seeking other species to take clams from the closed area, the community decided to make the area completely no-take. The success of the Ucunivanua project for fisheries replenishment, and the high level of community involvement have led to similar projects developing throughout Fiji

Increases in protected populations are often rapid, frequently doubling or tripling in two to five years (Boxes 2,3). Stocks of five families of exploited reef fish tripled in biomass inside reserves within five years of protection in St Lucia [16]. Experimental fishing CPUE in the De Hoop Marine Reserve in South Africa was an order of magnitude higher than from sites outside after seven years of protection [17]. In the Florida Keys, densities of yellowtail snapper *Ocyurus chrysurus* increased by more than 15 times in the fully protected Sanctuary Preservation Areas over four years [18]. Increases can be sustained well beyond the first few years of protection. Russ and Alcalá [8] reported a continuous linear increase in densities of large predatory fish in the Apo Island Reserve, Philippines, over 11 years of protection. Kelly *et al.*'s [13] findings of sustained rates of spiny lobster increase in New Zealand included data from reserves up to 21 years old. In Merritt Island National Wildlife Refuge in Florida, reserve effects have built up over four decades as long-lived fish have grown (Box 4).

Which species and habitats benefit from reserve protection?

Species that respond most rapidly to protection are often relatively sedentary and spend much of their life in

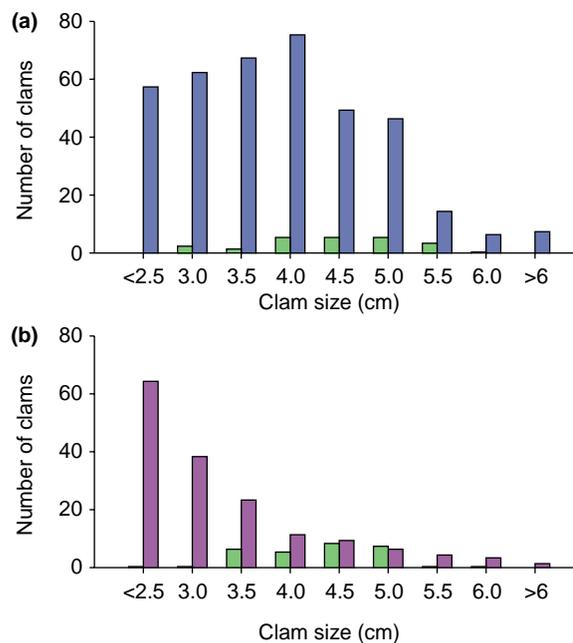


Fig. 1. The number of clams counted in 50 1-m² quadrats in each size class in the closed area (a) and in the adjacent fished area (b) in April 1997 (green bars) when the closed area was established and in 2000 (August 2000, blue bars; September 2000, purple bars) after 3.3 years of protection, in Ucunivanua, Fiji. Data collected by the Ucunivanua community monitoring team [20]. Reproduced, with permission, from [20].

[20,59]. Communities are returning to their traditional practice of *tabuor* closed areas, combining centuries of local knowledge with the latest developments in marine ecology.

reserves, including invertebrates, such as scallops *Placopecten magellanicus* on Georges Bank [19] (Box 2) and *Anadara* clams in Fiji [20] (Box 3). Many coral reef fish are also relatively sedentary and have benefited rapidly from protection [8,16,21]. In temperate waters, less mobile fish, such as flounder, have responded strongly to fishery closures [19] (Box 2).

Evidence is also increasing for the role of marine reserves in protecting more mobile animals. For example, many species of lobster have seasonal movements on scales that might be expected to preclude them from protection in small reserves. However, there is now convincing evidence from the Mediterranean [22], New Zealand [13], Australia [11], the Bahamas [23] and Canada [24] that lobster stocks do build up in reserves and that, for some species, a proportion of the population show high levels of site fidelity [24,25].

Fish capable of moving long distances are not expected to benefit from protection. However, tagging studies that reveal intra-species differences in movement behaviour are forcing us to rethink our expectations of reserve performance. They help explain unexpected beneficiaries from reserves seen in field studies [26]. Just like lobsters, in many fish species a proportion of the population might remain within a relatively small area, whilst others

Box 4. World record catches cluster around Cape Canaveral reserves

The Merritt Island National Wildlife Refuge at Cape Canaveral, Florida, USA contains two areas (totaling 40 km²) that have been closed to human access and fishing since 1962 for the security of the nearby Kennedy Space Center [60]. An additional 60-km² area was closed to motorized vessels in 1990, further reducing fishing pressure in the area. Before protection, there was intensive recreational fishing.

Johnson *et al.* [60] experimentally fished closed areas after 24–28 years of protection and found more abundant and bigger fish compared with nearby exploited areas. Overall catch per unit effort for black drum *Pogonias cromis* was 12.8 times higher in unfished than in fished areas, red drum *Sciaenops ocellatus* 6.3 times higher, common snook *Centropomus undecimalis* 5.3 times higher, and spotted sea trout *Cynoscion nebulosus* 2.3 times higher. Red drum, spotted sea trout and black drum were all significantly larger in size inside the reserves than they were in fished areas.

Bohnsack (in [16]) looked at the effect of these reserves on the adjacent recreational fishery. He found that a much higher percentage of world-record-size fish were caught close to the reserves than were caught farther away. Within a 200-km stretch of coast around the reserves (just 13% of the Florida coast), anglers caught 62% of record-breaking black drum, 54% of record-breaking red drum and 50% of record-breaking spotted sea trout, but only 2% of record common snook. The first three game fish are year-round residents of the refuge, whereas snook is at its northern range limit and leaves in winter [60]. The rate at which each species responded to protection corresponded closely to their longevity (Fig. 1). For spotted sea trout (longevity 15 years), there was a post-protection lag in appearance of record fish of nine years, for red drum (longevity 35 years) 27 years, and for black drum (longevity 70 years) 31 years.

By the end of the 1980s, the rate of accumulation of new records in spotted sea trout slowed, but continued to accumulate for the longer lived drum species (Fig. 1). Since the mid-1980s most Florida records for both these species have been recorded close to the refuge. Captures of record fish around the refuge indicate that spillover is occurring. A tagging study at the site showed that common snook moved, on average, 148.0 km, red drum 47.6 km, black drum 47.7 km, and spotted sea trout 10.0 km [61].

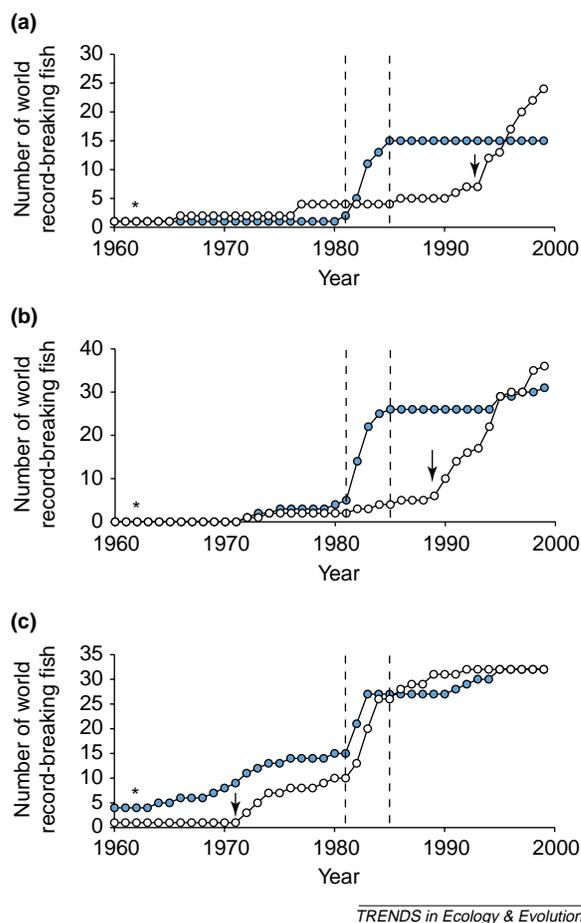


Fig. 1. Cumulative world records for black drum (a), red drum (b) and spotted sea trout (c) in the 200-km coastal section adjoining the Merritt Island refuge (open circles) and records from rest of Florida (filled circles). Asterisks show when protection began. Dashed lines show period following introduction of new size class regulations and the arrow shows when there was a rapid increase in accumulation of new records for each species. Reproduced, with permission, from [16].

undertake significant movements. The resident population enables build-up of biomass and reproductive capacity within a reserve. The more mobile animals ensure that benefits are exported beyond the boundaries. For example, a fraction of the snappers around marine reserves in New Zealand show strong site fidelity and respond swiftly to protection, whereas the remainder make longer seasonal movements that take them into fishing grounds [9]. A similar pattern has been observed in at least five commercially important South African shore fish. For these species, ~67–93% of individuals were recaptured within 1 km of their original tagging site, whilst the rest moved greater distances of tens or even hundreds of kilometres [27]. Reef fish tagged in the Discovery Bay Marine Reserve, Jamaica, show contrasting movement patterns within species, with some individuals repeatedly caught at the same place within the reserve, whilst others were recaptured up to tens of kilometres away [28].

For species with even larger scales of movement, marine reserves can still be valuable, offering protection at vulnerable stages. Many migratory species aggregate or pass through migration bottlenecks, where they become particularly vulnerable to fisheries [29]. Throughout the world, overfishing is eliminating spawning aggregations of snappers and groupers [30]. In the US Virgin Islands, protecting a spawning aggregation site for the grouper *Epinephelus guttatus* led to swift increases in average fish size and in the numbers of males in this hermaphroditic species [31], in spite of covering just 1.5% of the fishing grounds [32]. There is new evidence that highly mobile species, such as cod *Gadus morhua*, might home to specific coastal spawning sites and would benefit from reserve protection in a similar way [33,34]. Even highly migratory species, such as sharks, tuna and billfish, could benefit from reserves targeted to places where they are highly vulnerable, such as nursery grounds, spawning sites or aggregation sites such as seamounts [35]. Marine reserves

could also protect migration routes. In the case of blue crabs *Callinectes sapidus* in Chesapeake Bay, USA, only their spawning area is currently protected. However, including within the reserve a deep-water spawning migration route for females could improve sustainability of the fishery [36].

Research into marine reserves is also revealing how pervasive the effects of fishing are on marine ecosystems. Since the 19th century, fisheries scientists have known that exploitation reduces populations, decreases average body size, contracts population age structures and alters species composition. But the degree to which marine ecosystems have been transformed by fishing is surprising [37,38]. Rebounding populations in reserves make it clear that fishing has greatly depressed densities and sizes of exploited species. A recent study [39] shows for a range of fisheries worldwide that biomass of large predatory commercial fish has declined to 10% or less of pre-exploitation levels. With such depressed biomass levels now the norm, it is easier to understand the rapid rebound of exploited species seen in marine reserves. In Fiji, clams in closed areas have reached sizes not seen for three generations [20] (Box 3). Around Merritt Island National Wildlife Refuge, black drum *Pogonias cromis* are reaching sizes previously seen only in faded photographs from early last century (Box 4). Furthermore, reserves are showing how entire habitats have been transformed by fishing. In New Zealand and Tasmanian reserves, populations of sea urchins have declined as their predators (fish and lobsters) have grown, transforming overgrazed urchin barrens into kelp forest [11,40,41]. Similar effects have been observed in Californian reserves [42]. In Chile, the recovery of a predatory gastropod *Concholepas concholepas* in closed areas reduced densities of their prey species, causing mussel-dominated rocky shores to be transformed into seaweed and barnacle systems [43]. Refuges from fishing are therefore increasing seascape diversity.

What are the magnitudes and scales of fishery benefits from reserves?

There is good evidence that fisheries have benefited through spillover of juveniles and adults, and export of eggs and larvae. Tagging data demonstrate, for example, that crabs in the Sea of Japan [44], lobsters in Newfoundland [24] and New Zealand [25], bream in New Zealand [45] and reef fish in Kenya [46] all moved between protected and fished areas.

The first sign that reserves are increasing catches in adjacent fishing grounds is often people fishing close to reserve boundaries. Eight years after the Mombasa Marine National Park in Kenya became fully protected, catches nearby reached three times more than those further away and senior fishers claimed these fishing spots for themselves [46,47] (L. Rodwell, PhD thesis, University of York, 2001). Marker buoys for lobster pots ring the boundaries of the Leigh Marine Reserve in New Zealand, the Bicheno Reserve in Tasmania and the Anacapa reserve in California's Channel Islands [3]. Bohnsack and Ault [18] found lobster pots set preferentially close to the boundaries of the Sambos Ecological Reserve in the Florida Keys. However, not all studies suggest spillover

occurs. Experimental fishing CPUE of blue cod within New Zealand's Long Island-Kokomohua reserve increased four-fold after seven years of protection, but remained the same in control sites 1–5 km away [10].

Potential scales of spillover vary across species and ecosystems. Fish tagging and movement data from coral reefs suggest spillover will typically extend a few hundreds of metres to a few kilometres from reserves [48]. By contrast, studies quoted above suggest spillover can reach tens to hundreds of kilometres for more mobile species in systems such as estuaries, rocky reefs and continental shelves.

There is less direct evidence for larval export from reserves to fishing grounds but some of the best examples come from stocks that were severely depleted before reserve establishment. In Chile, a three-year closure of the squat lobster *Pleuroncodes monodon* fishery led to a dramatic increase in biomass, and re-expansion of the species by >50 km into areas previously depleted by fishing [49]. This was probably driven by larval dispersal, as was the recovery of clams in fishing grounds in Fiji [20] (Box 3) and of scallop populations around closed areas on Georges Bank [19] (Box 2). Until recently, it was thought that ocean currents would transport most offspring spawned in reserves far beyond their boundaries. A broad array of new evidence (biogeographical, genetic, chemical, behavioural and oceanographical; reviewed in [50]) suggests that many larvae could be delivered close to reserves, as near as a few hundred metres for Fijian clams, and a few tens of kilometres for Georges Bank scallops. If, as it seems, local retention is common, both spillover and larval export could enhance local fisheries and ensure that protected populations are self sustaining. Emerging evidence on scales of larval dispersal suggests that reserves should be relatively closely spaced in networks, from a few to a few tens of kilometres apart [51].

Some studies have directly examined changes in catches adjacent to reserves. Roberts *et al.* [16] found that, in five years, CPUE of fish traps increased by 46–90% in fishing grounds around a network of reserves in St Lucia. A similar effect was reported from Nabq, Egypt, where CPUE from the trammel net fishery increased by 66% after five years' protection of a series of reserves [21]. In the Philippines, CPUE of the line fishery around the 0.74-km² Apo Island Reserve increased tenfold over 20 years of protection [52]. Fishers in Fiji reported a doubling in catch per unit effort for clams outside their closed area [20] (Box 3). Kelly *et al.* [53] found that lobster catches close to the Leigh Marine Reserve in New Zealand were more variable than those from areas further away, but large catches were more common. Closures on Georges Bank have brought the scallop fishery back from the verge of collapse and show that reserves can work at large scales and for industrial fisheries (Box 2).

How large should reserves be?

Examples discussed here show that reserves and closed areas work well across a size range spanning <1 km² to >5000 km². The key to success is matching reserve size to the scales of movements of the organisms that they are designed to protect. For sedentary animals living on coral

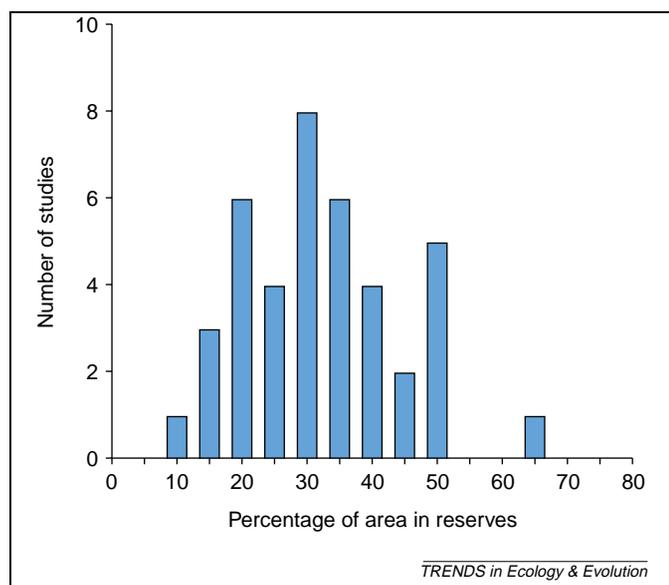


Fig. 1. Frequency distribution of the fraction of fishing grounds recommended to be included in marine reserves, based on 40 studies (mainly theoretical) that examine the question of how much area should be protected from fishing. Data points were derived by first obtaining the range of estimates over which some measure or measures of reserve performance were maximized/optimized/achieved and then taking either the mid-point or, where this was different, the point of greatest benefit from within that range. Literature included in the survey is available on request from the authors.

reefs, reserves of <1 km across have augmented local fisheries, especially where established in networks [16,21,52]. For more mobile estuarine fish, reserves in Florida (16 and 24 km²) have sustained spillover to local recreational fisheries for decades (Box 4). Three closures totaling 17 000 km² on Georges Bank have helped turn around long-term declines of several important exploited species (Box 2).

The overall scale of protection is as important as the size of reserve units. Although closed areas in Newfoundland produced local benefits to lobster catches, at just 2% of fishing grounds, they have had a trivial effect on overall landings [54]. More than 40 theoretical and modeling studies have addressed the question of how much of the sea should be protected from fishing (reviewed in [26]). Depending on the fishery and conditions being considered, they conclude that fisheries benefits require closures of between 10 and 80% of fishing grounds. Most predict maximum benefits with closures of 20–40% (Fig. 1). Intriguingly, the most convincing demonstrations of fishery benefits to date are mainly from places where coverage of protected areas falls into this approximate range: Apo Island (10%), Merritt Island (22%), Georges Bank (25%) Nabq (33%) and St Lucia (35%). For the three locations where data are available to make a judgment, Apo, Georges Bank and St Lucia, the ‘gold standard’ of higher overall catches with reserves than without, in spite of a reduced fishing area, appears to have been achieved (to date, for scallops only at Georges Bank). These bold initiatives uphold theoretical predictions that fishers will see improved catches where reserves of sufficient size are introduced to heavily exploited fisheries [2], and prove that effective enforcement is possible over a wide range of both

reserve sizes and management sophistication. Of course, reserves on their own will not deliver sustainable fisheries. We must complement them with reduced effort, decreased reliance on destructive fishing methods and clearer allocations of fishing rights and responsibilities. But by protecting and restoring the productive capacity of marine ecosystems, reserves can provide the bedrock on which other tools can build towards success.

Conclusions

Rapidly increasing evidence shows that reserves and fishery closures benefit species as diverse as molluscs [19,20] (Boxes 2,3), crustaceans [13,24,25] and fish of a wide variety of sizes, life histories and mobilities [3] (Boxes 2,4). Benefits develop within two to five years of establishment and continue to build for decades. The examples we describe here show that reserves work in habitats as different as coral reefs, kelp forests, temperate continental shelves, estuaries, seagrass beds, rocky shores and mangroves [3].

Research on reserves is revealing the profound degree to which people have modified marine ecosystems by fishing. Nature conservation in the oceans cannot be achieved without marine reserves, neither, we would contend, can the world’s fisheries be made sustainable. Fortunately, the evidence available suggests that we can design effective reserves for any habitat that is fished. At the World Summit on Sustainable Development in 2002, countries agreed ambitious targets for creating national networks of marine protected areas by 2012 and rebuilding overexploited fisheries by 2015[†]. Marine reserves offer a means to deliver on the first and contribute to the second promise.

Acknowledgements

We thank WWF-US and The Pew Charitable Trusts for support. Alifereti Tawake (University of the South Pacific) and Rato Pio Radikedike and other residents of Ucuivanua village in Fiji generously shared their latest findings with us. We could not have written this paper without the enthusiastic support of all the researchers and reserve managers who responded to our requests for information. Julie Hawkins and four anonymous referees provided numerous helpful comments.

References

- Johannes, R.E. (1978) Traditional marine conservation methods in Oceania and their demise. *Annu. Rev. Ecol. Syst.* 9, 349–364
- Bohnsack, J.A. (1998) Application of marine reserves to reef fisheries management. *Aust. J. Ecol.* 23, 298–304
- Gell, F.R. and Roberts, C.M. (2003) *The Fishery Effects of Marine Reserves and Fishery Closures*, WWF-US (http://www.worldwildlife.org/oceans/fishery_effects.pdf)
- Buxton, C.D. and Smale, M.J. (1989) Abundance and distribution patterns of three temperate marine reef fish (Teleostei: Sparidae) in exploited and unexploited areas off the southern cape coast. *J. Appl. Ecol.* 26, 441–451
- Cowley, P.D. *et al.* (2002) The role of the Tsitsikamma National Park in the management of four shore-angling fish along the south-eastern cape coast of South Africa. *S. Afr. J. Mar. Sci.* 24, 27–36
- Francour, P. (1991) The effect of protection level on a coastal fish community at Scandola. *Corsica. Rev. Ecol. Terre Vie* 46, 65–81
- Goñi, R. *et al.* (2001) Effects of protection on the abundance and distribution of red lobster (*Palinurus elephas*, Fabricius, 1787) in the

[†] United Nations (2002) *World Summit on Sustainable Development: Plan of Implementation*: http://www.johannesburgsummit.org/html/documents/summit_docs/2309_planfinal.htm.

- marine reserve of Columbretes Islands (Western Mediterraneo) and surrounding areas. In *First International Workshop in Marine Reserves, Murcia, Spain 1999*, pp. 117–133, Ministerio de Agricultura, Pesca y Alimentación, Spain
- 8 Russ, G.R. and Alcala, A.C. (1996) Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecol. Appl.* 6, 947–961
 - 9 Willis, T.J. *et al.* (2003) Protection of exploited fishes in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *J. Appl. Ecol.* 40, 214–227
 - 10 Davidson, R.J. (2001) Changes in population parameters and behaviour of blue cod (*Paraperis colias*; Pinguipedidae) in Long Island – Lokomohua Marine Reserve, Marlborough Sounds, New Zealand. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 11, 417–435
 - 11 Edgar, G.J. and Barrett, N.S. (1999) Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *J. Exp. Mar. Biol. Ecol.* 242, 107–144
 - 12 Faunce, C.H. *et al.* (2002) Size structure of gray snapper (*Lutjanus griseus*) within a mangrove ‘no-take’ sanctuary. *Bull. Mar. Sci.* 70, 211–216
 - 13 Kelly, S. *et al.* (2000) Spiny lobster, *Jasus edwardsii* recovery in New Zealand marine reserves. *Biol. Conserv.* 92, 359–369
 - 14 Palsson, W.A. and Pacunski, R.E. (1995) *The Response of Rocky Reef Fishes to Harvest Refugia in Puget Sound*. Proceedings, Vol. 1: Puget Sound Research '95. Puget Sound Water Quality Authority
 - 15 Rodwell, L.D. *et al.* (2002) A model of tropical marine reserve-fishery linkages. *Nat. Res. Mod.* 15, 453–486
 - 16 Roberts, C.M. *et al.* (2001) Effects of marine reserves on adjacent fisheries. *Science* 294, 1920–1923
 - 17 Bennett, B.A. and Attwood, C.G. (1993) Shore-angling catches in the De Hoop Reserve and further evidence for the protective value of marine reserves. *S. Afr. J. Mar. Sci.* 13, 213–222
 - 18 Bohnsack, J.A. and Ault, J.A. (2002) *Reef Fish Community Dynamics and Linkages with Florida Bay*, 2002 Annual Progress Report for South Florida Ecosystem Restoration Program. NOAA/NMFS/SEFSC/Protected Resources Division PRD/01/02-06
 - 19 Murawski, S.A. *et al.* (2000) Large-scale closed areas as a fisheries management tool in temperate marine systems: the Georges Bank experience. *Bull. Mar. Sci.* 66, 775–798
 - 20 Tawake, A. *et al.* (2001) Harvesting clams and data: involving local communities in monitoring: a case in Fiji. *Conserv. Biol. Pract.* 2, 32–35
 - 21 Galal, N. *et al.* (2002) Effect of a network of no-take reserves in increasing exploited reef fish stocks and catch per unit effort at Nabq. *South Sinai, Egypt. Mar. Freshw. Res.* 53, 199–205
 - 22 Goñi, R. *et al.* (2001) Dynamics of a protected Western Mediterranean population of the European spiny lobster *Palinurus elephas* (Fabricius, 1787) assessed by trap surveys. *Mar. Freshw. Res.* 52, 1577–1587
 - 23 Lipcius, R.N. *et al.* (2001) Marine reserves for Caribbean spiny lobster: empirical evaluation and theoretical metapopulation recruitment dynamics. *Mar. Freshw. Res.* 52, 1589–1598
 - 24 Rowe, S. (2001) Movement and harvesting mortality of American lobsters (*Homarus americanus*) tagged inside and outside no-take reserves in Bonavista Bay, Newfoundland. *Can. J. Fish. Aquat. Sci.* 58, 1336–1346
 - 25 Kelly, S. (2001) Temporal variation in the movement of the spiny lobster, *Jasus edwardsii*. *Mar. Freshw. Res.* 52, 323–331
 - 26 Roberts, C.M. and Hawkins, J.P. (2000) *Fully-protected Marine Reserves: A Guide*, WWF Endangered Seas Campaign, Washington, DC and University of York. (www.panda.org/resources/publications/water/mpreserves/mar_dwld.htm)
 - 27 Griffiths, M.H. and Wilke, C.G. (2002) Long-term movement patterns of five temperate-reef fishes (Pisces: Sparidae): implications for marine reserves. *Mar. Freshw. Res.* 53, 233–244
 - 28 Munro, J.L. (2000) Outmigration and movement of tagged coral reef fish in a marine fishery reserve in Jamaica. *Proc. Gulf Carib. Fish. Inst.* 51, 557–568
 - 29 Roberts, C.M. and Sargent, H. (2002) The fishery benefits of fully protected marine reserves: why habitat and behaviour are important. *Nat. Res. Mod.* 15, 487–507
 - 30 Johannes, R.E. (1998) The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends Ecol. Evol.* 13, 243–246
 - 31 Beets, J. and Friedlander, A. (1999) Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus*, in the US Virgin Islands. *Environ. Biol. Fish.* 55, 91–98
 - 32 Bohnsack, J.A. (2000) A comparison of the short-term impacts of no-take marine reserves and minimum size limits. *Bull. Mar. Sci.* 66, 635–650
 - 33 Begg, G.A. and Marteinsdottir, G. (2000) Spawning origins of pelagic juvenile cod *Gadus morhua* inferred from spatially explicit age distributions: potential influences on year-class strength and recruitment. *Mar. Ecol. Prog. Ser.* 202, 193–217
 - 34 Robichaud, D. and Rose, G.A. (2001) Multiyear homing of Atlantic cod to a spawning ground. *Can. J. Fish. Aquat. Sci.* 58, 2325–2329
 - 35 Norse, E.A. Marine reserves for large pelagic fishes. In *Marine Conservation Biology: the Science of Maintaining the Sea's Biodiversity* (E. Norse, and L. Crowder, eds) Island Press, USA (in press)
 - 36 Lipcius, R.N. *et al.* (2001) A deepwater dispersal corridor for adult female blue crabs in Chesapeake Bay. In *Spatial Process and Management of Marine Populations*, pp. 643–666, AKK-SG-01-02, Alaska Sea Grant College Program
 - 37 Jackson, J.B.C. (2001) What was natural in the coastal oceans? *Proc. Natl. Acad. Sci. U. S. A.* 98, 5411–5418
 - 38 Christensen, V. *et al.* (2003) Hundred year decline of North Atlantic predatory fishes. *Fish and Fisheries* 4, 1–24
 - 39 Myers, R.A. and Worm, B. (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283
 - 40 Babcock, R.C. *et al.* (1999) Changes in community structure in temperate marine reserves. *Mar. Ecol. Prog. Ser.* 189, 125–134
 - 41 Shears, N.T. and Babcock, R.C. (2002) Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* 132, 131–142
 - 42 Lafferty, K.D. and Kushner, D. (2000) Population regulation of the purple sea urchin (*Strongylocentrus purpuratus*) at the California Channel Islands. In *Proceedings of the 5th California Islands Symposium* (Brown, D.R. *et al.*, eds), pp. 379–381, Publication 99-0038, Minerals Management Service
 - 43 Castilla, J.C. (1999) Coastal marine communities: trends and perspectives from human exclusion experiments. *Trends Ecol. Evol.* 14, 280–283
 - 44 Yamasaki, A. and Kuwahara, A. (1990) Preserved area to effect recovery of over-fished Zuwai crab stocks off Kyoto Prefecture. In *Proceedings of the International Symposium on King and Tanner Crabs, November 1989, Anchorage, Alaska* pp. 575–585 University of Alaska Fairbanks, Alaska Sea Grant Program Report 90-04
 - 45 Willis, T.J. *et al.* (2001) Evidence of long-term site fidelity of snapper (*Pagrus auratus*) within a marine reserve. *N.Z. J. Mar. Freshw. Res.* 35, 581–590
 - 46 McClanahan, T.R. and Mangi, S. (2000) Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecol. Appl.* 10, 1792–1805
 - 47 McClanahan, T.R. and Kaunda-Arara, B. (1996) Fishery recovery in a coral reef marine park and its effects on the adjacent fishery. *Conserv. Biol.* 10, 1187–1199
 - 48 Russ, G.R. (2002) Yet another review of marine reserves as reef fishery management tools. In *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (Sale, P.F., ed.), pp. 421–443, Academic Press
 - 49 Roa, R. and Bahamonde, R. (1993) Growth and expansion of an exploited population of the squat lobster (*Pleuroncodes monodon*) after 3 years without harvesting. *Fish. Res.* 18, 305–319
 - 50 Mora, C. and Sale, P.F. (2002) Are populations of coral reef fish open or closed? *Trends Ecol. Evol.* 17, 422–428
 - 51 Roberts, C.M. *et al.* (2001) Designing networks of marine reserves: why small, isolated protected areas are not enough. *Conservation Biology in Practice* 2, 10–17
 - 52 Maypa, A.P. *et al.* (2002) Long-term trends in yield and catch rates of the coral reef fishery at Apo Island, Central Philippines. *Mar. Freshw. Res.* 53, 207–213
 - 53 Kelly, S. *et al.* (2002) The value of a spillover fishery for spiny lobsters around a marine reserve in Northern New Zealand. *Coast. Manage.* 30, 153–166
 - 54 Rowe, S. and Feltham, G. (2000) Eastport Peninsula lobster conservation: integrating harvesters' local knowledge and fisheries science for resource co-management. In *Finding Our Sealegs: Linking Fishery People and Their Knowledge with Science and Management*

- (Neis, B. and Felt, L., eds) pp. 236–245, Institute of Social and Economic Research Press
- 55 Wallace, S.S. (1999) Evaluating the effects of three forms of marine reserve on northern abalone populations in British Columbia. *Canada. Conserv. Biol.* 13, 882–887
- 56 NEFSC (Northeast Fisheries Science Center) (2001) Assessment of 19 Northeast Groundfish Stocks through 2000. A Report to the New England Fishery Management Council's Multi-Species Monitoring Committee. *Northeast Fisheries Science Center Reference Document* 01-20 (<http://www.nefsc.noaa.gov/nefsc/publications/crd/crd0120/>)
- 57 O'Brian, L. and Munroe, N.J. (2001) Assessment of the Georges Bank Atlantic Cod Stock for 2001. *Northeast Fisheries Science Center Reference Document* 01-10 (<http://www.nefsc.noaa.gov/nefsc/publications/crd/crd0120/>)
- 58 National Research Council (2002), (2002) *Effects of Trawling and Dredging on Seafloor Habitat*, National Academy Press
- 59 Tawake, A. and Aalbersberg, B. Community-based refugia management in Fiji. In *Coastal Protection for and by the People of the Indo-Pacific: Learning from 13 Case Studies*, The World Resources Institute (in press)
- 60 Johnson, D.R. *et al.* (1999) Effectiveness of an existing estuarine no-take fish sanctuary within the Kennedy Space Center, Florida. *N. Am. J. Fish. Manage.* 19, 436–453
- 61 Stevens, P.W. and Sulak, K.J. (2001) Egress of adult sport fish from an estuarine reserve within Merritt Island National Wildlife Refuge, Florida. *Gulf Mex. Sci.* 2, 77–89