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MARINE RESERVES AND OCEAN NEIGHBORHOODS: The Spatial Scale of Marine Populations and Their Management

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■ **Abstract** The movement of individuals defines a spatial neighborhood that can help determine marine management strategies. Here, I briefly review four fields of marine biology that each differentially illuminate the scale of marine neighborhoods: effects of marine reserves, tagging studies, microchemistry, and population genetics. These suggest adult neighborhood sizes for many demersal fish and invertebrates as small as kilometers and up to 10 to 100 km. Larval dispersal may be shorter than previously suspected: neighborhood sizes of 10 to 100 km for invertebrates and 50 to 200 km for fish are common in current compilations.

How can small reserves protect such species? One conceptual framework is to set reserve size based on adult neighborhood sizes of highly fished species and determine spacing of a reserve network based on larval neighborhoods. The multispecies nature of fisheries demands that network designs accommodate different life histories and take into account the way local human communities use marine resources.

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INTRODUCTION

Effective management of marine ecosystems—either for fisheries or for conservation—must match the population biology and dispersal ability of target species.

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Many commercially exploited fin fish, echinoderms, mollusks, and crustacea consist of populations of relatively sedentary adults spread across huge geographic ranges connected by larval dispersal. Other species, such as whales, tunas, and squid, have highly migratory adults that range over large distances. As a consequence of these life strategies, management approaches for commercial marine species typically emphasize control of fishing effort over large geographic scales.

Recently, a much smaller scale approach to marine environmental management has been suggested. Marine Protected Areas (MPAs), zones in which fisheries exploitation is spatially limited, have been used to protect critical habitats, such as spawning sites and nursery grounds. Fully protected MPAs, also called Marine Reserves, have been established to protect all the species of a marine ecosystem, and this has resulted in strong increases in biomass and density of species that are otherwise heavily exploited.

Most marine reserves are small—typically less than 1 km^2—yet many species with seemingly high dispersal respond to protection in reserves. Does this mean that most species have only small scale population movement? Or does an MPA protect only the subset of species that happens to have the right scale of dispersal for that particular MPA? Though there is no doubt that marine population movements can be wide over evolutionary time frames, the generation-to-generation range of dispersal for most marine species is poorly known. As a result, matching the spatial scale of management with the scale of dispersal is difficult, and our understanding the role of MPAs in ecosystem protection is incomplete.

Sewell Wright (1) suggested a framework for measuring and interpreting the scale of population spread by exploring the influence of neighborhood size on the geography of genetic differentiation. He defined a neighborhood, statistically, as the variance in dispersal distances from offspring to their parents. Although useful mathematically and heuristically, such formulations are unlikely to be strictly useful in marine systems. There are few situations in which offspring and parents can be tracked accurately (the best known exceptions may be benthic colonial ascidians and whales), and marine species differ widely in the distances that individuals move at various life stages.

Because of these complexities, neighborhoods for marine species must be defined differently. Here I use a general definition of neighborhoods as the area centered on a set of parents that is large enough to retain most of the offspring of those parents. If adults move widely, neighborhoods are large and diffuse. If adults are sessile and larvae are restricted in their dispersal, then a neighborhood might be small and distinct. Other species with sedentary adults and highly dispersed larvae may have large neighborhoods if long-distance dispersal is common or small neighborhoods if long-distance larval dispersal is rare.

The scale of ocean neighborhoods is fundamental to understanding how marine species make use of the seascape and is therefore fundamental to future management. Once known, the scale of ocean neighborhoods may be uniquely valuable. Species with vast ocean neighborhoods may require the type of large-scale management that is the hallmark of current fisheries. But for species in which ocean neighborhoods are small, then smaller-scale management in marine parks or reserves may be more appropriate. There are also species for which adult neighborhoods are probably small but larval neighborhoods are large. These species may require different types of spatial management, such as networks of marine reserves.

Although it is possible to immediately think of many practical difficulties in accurately measuring ocean neighborhood sizes, our current ignorance of the scale of marine dispersal from generation to generation of most species is so profound that we have little idea of even the order of magnitude of dispersal. Do most successful marine larvae drift 10 km,100 km, or 1000 km before settling to their adult phase? Recently collected data from a variety of studies suggest the range of movements of adults and offspring in the sea. Small-scale marine reserves can be viewed as experiments in the functional application of spatial management to species with different ocean neighborhood sizes. By observing the impact of protecting species over small spatial scales, we can simultaneously gauge the importance of reserves and show which species have neighborhoods of the right size for particular sizes of reserves.

Other data are accumulating that also address the fundamental question of neighborhood size for different species. Tagging studies seem to relate most directly to efforts to define movement patterns of adults. These studies can distinguish species with highly vagile adults from those with sessile adults, but the results are very difficult to apply to larvae. Larval patterns of movement instead derive from data on the genetics of marine populations, from tracking invasive species, and on new information about chemical tags of fish otoliths and invertebrate statoliths.

Both the use of marine reserves to bolster coastal management and the measurement of ocean neighborhoods are in their infancy. However, progress on both these fronts encourages development of approaches that try to estimate the scale of population spread in marine species and incorporate this information into place-based management schemes. In this review, I highlight advances in marine reserve implementation and interpretation and place them in a framework that shows how scales of population spread and scales of marine management might be melded.

RESULTS FROM MARINE RESERVE PROTECTION

Fully protected marine reserves have been shown to generally produce striking increases in biomass of species that are heavily fished outside reserve boundaries (2, 3). Significant increases in population density and species diversity are also commonly reported. Overall, fish biomass increased 100% to 800% across 56 peer-reviewed published surveys of the effectiveness of reserves (4) based on data in Halpern (5). (Figure 1*A*,*B*). Among these 56 studies, density increases averaged between 60% and 150% across a wide range of countries in North America, in the tropical Pacific, and Africa. Lower values (increases of 20% to 35%) have been reported for the Mediterranean and the temperate South Pacific (Figure 1*B*). When

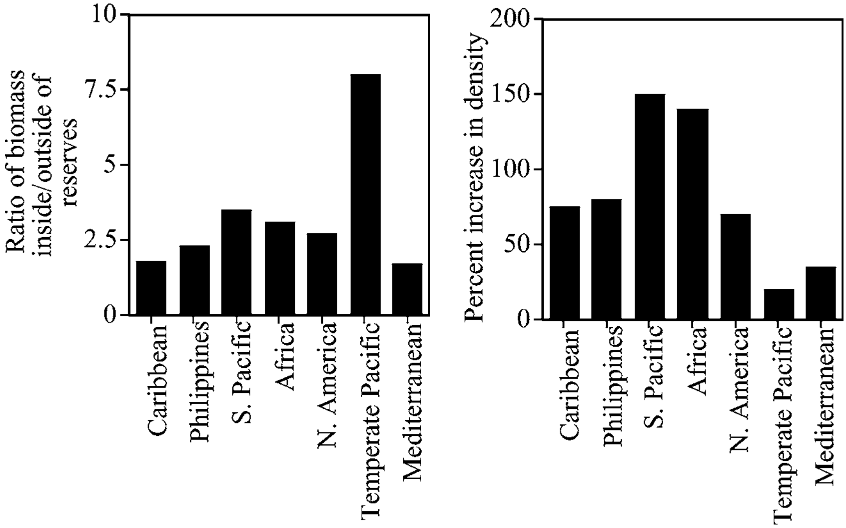

Figure 1 Increase in (*left*) biomass and (*right*) density of fish inside marine reserves from different parts of the world. Data are from studies summarized by Halpern (5) that were published in peer-reviewed journals.

multiple factors that might affect fish assemblages are examined, the presence of no-take reserves often outstrips other tested environmental effects, such as wave exposure, depth, or habitat complexity (6–8).

These broad compilations tend to average over multiple species and run the risk of obscuring declines in some species if other species increase markedly. However, some studies report results for individual species, and in these cases, patterns of response to protection are similar to those above. For example, on protected reefs in Belize, 16 of 30 species increased after protection compared to control reefs, whereas none decreased on these reefs (7). An earlier study in Belize showed 11 of 47 fish species had higher abundances inside areas with restricted fishing (3). In one of the first studies of reserve impacts, Bell (8) showed significant increases in 11 of 35 observed fish species and declines in a single species. Of eight fish families studied by McClanahan & Arthur (7) on protected reefs in eastern Africa, five showed significant increases in density, and seven showed significant increases in diversity. Few studies have examined a large number of invertebrate species inside reserves—typically such research emphasizes a few target species, such as limpets, lobsters, or abalone (9–11). However, in one study of 30 reef gastropods abundant enough for statistical analysis, McClanahan (12) showed increases of abundance in nine species and declines in three.

Despite overall increases in biomass, and despite increases in a larger number of species than decreases, some species in nearly every study do not benefit from a given reserve. In particular, species that are not exploited tend not to increase (13, 14). Such species actually serve as an additional control for the treatment effect of reserve protection. If, for example, reserves had larger biomass than control sites because they were all chosen in areas of high productivity, then we would expect nonexploited species to be higher inside than outside reserves. The generally poor response of nonexploited species suggests strongly that it is the protection from fishing that generates the strong differences between reserve and control sites—not some other invisible variable. This is important because studies of reserves do not generally have the same kind of rigorous before-and-after controls that carefully designed ecological experiments tend to include.

Species in different trophic groups also tend to respond differently to reserves. In a major metaanalysis of 20 studies of reserve effects, Micheli et al. (13) show that omnivores and detritivores respond poorly, if at all, to reserve protection. By contrast, species that consume algae, invertebrates, or plankton have moderate response. The strongest response comes from predatory fish, which nearly doubled in abundance across the 20 studies. These differences may be affected by fishing pressure. Predatory fishes, such as rockfish, groupers, and snappers, tend to be highly prized fishing targets and thus tend to respond to reserves because they are no longer heavily fished. Detritivores and herbivores may be less often fished and less likely to need protection. However, a second reason for the differences in response to reserves is that a higher abundance of predators may consume more prey, and if these prey are smaller species, then the middle trophic levels occupied by these smaller species may decline rather than increase. A strong example of this is the decline of sea urchins after creation of marine reserves in New Zealand (10). Experiments have shown that this decline results from an increased abundance of predatory lobsters inside reserves, which consume sea urchins and subsequently allow greater growth of kelp (15).

Micheli et al. (13) also show that there is a shift toward larger-sized individuals inside reserves. This trend is seen in most studies of reserve impact—the size of fish or invertebrates tends to increase markedly when protected from exploitation. Such protection is evident in areas heavily used by commercial as well as recreational fishermen. In the Hopkins Marine Life Refuge in central California, two species of rockfish caught almost exclusively by recreational fishing are larger inside the reserve than outside (16). Likewise, it is difficult to find a legal-sized rockfish or lingcod outside of the no-take reserves at the Edmunds Underwater Park in Puget Sound, Washington (17).

The larger size of individuals in reserves produces two of the most commonly cited benefits of reserve protection: increased biomass of fish and increased reproductive capacity (18). Reproductive capacity is particularly important because it tends to increase exponentially with adult size. Because biomass inside reserves is increased, and because this increase results from a larger proportion of larger fish, benefits of reserves for reproduction can be substantial. For example, a red snapper 62 cm long produces the same number of eggs as 212 individuals 41 cm long. Such huge differences can result in large increases in reproductive potential. Bohnsack (19) calculated that snappers inside tropical reef reserves produced

12 times more eggs than those outside. Likewise, ling cod in the Edmunds Underwater Park in the Puget Sound produce 20 times more eggs per hectare than do ling cod outside the reserve (17), implying that a reserve system encompassing 5% of the subtidal area would effectively double egg production. Manriquez & Castilla (11) showed a 1000-fold increase in egg production inside reserves for a heavily exploited Chilean limpet.

Unfortunately, there have been few demonstrations of the direct benefit of these increases in potential egg production to local reserves or to the number of larvae available to recruit into marine populations. Stoner & Ray (20) showed that the number of larvae of the heavily fished Queen conch was much higher inside a reserve in the Bahamas than elsewhere. Murawski et al. (21) reported increases in settlement of offshore scallops after adult populations increased inside trawler-exclusion zones near Cape Cod. An experiment by Tegner (22) in which local populations of abalone were experimentally increased by transplantation gave mixed results. There were some observations of increased local settlement, but in other areas, no such increase occurred before poaching reduced adult numbers. That there are few other examples may be because present-day reserves are so small that they contribute only a tiny fraction of the larvae available in a typical marine population. Alternatively, the extra larvae produced in some reserves may be lost to the overall population (e.g., by being swept offshore). Stock recruitment relationships in marine species are notoriously variable, and it may take long-term observations of recruitment in and near large reserves to confirm the general assumption that reserves will increase available settlers.

Increased fish populations have been noted within a few years of reserve implementation (23), and most reserves studied have generated substantial increases in fished species within five years of protection when the targeted species are short lived and fast growing (24). However, longer-term protection can lead to incremental increases in biomass and density (7, 25, 26). Especially for long-lived species, protection over the course of a full generation, which may require 20 to 50 years, may produce increasing benefits (7). Micheli et al. (13) show that this trend is strongest in predatory fish. Protection for 10 years or more resulted in a far greater increase in abundance compared to reserves that had been in existence for 10 years or less (13).

MARINE RESERVES AS EXPERIMENTS IN OCEAN NEIGHBORHOODS

The hallmark of marine reserve management is that resources are protected spatially. Individuals within the borders of the reserve are protected, and individuals outside are not. If all marine populations are highly vagile, then small marine reserves are not expected to have substantial impact (26). However, many marine invertebrates are sessile or sedentary, such as corals or sea urchins, respectively, and many adult fish appear to have small home ranges. As a result, small marine reserves have the potential to reduce fishing mortality in local populations—but only for those species whose neighborhood size is appropriate.

Simple mathematical models of marine reserves show that in order for the protection afforded within a reserve to create the optimal increase in population, the neighborhood size of a species should be less than about twice the size of the reserve (27, 28). Species with adult home ranges larger than a reserve's size will be protected for only part of the time. Furthermore, if the implementation of a reserve increases fishing pressure outside reserve boundaries, then a species that spends only part of its time in a reserve may have higher fishing mortality outside the reserve than before. In these cases, reserves may not afford much overall protection. If fishing effort is not displaced, then the impact of reserves on highly migratory species is similar to the effect of decreasing fishing effort by the same percentage as the percent area dedicated to reserves (29).

Highly migratory pelagic fish in general are thought not to respond well to reserves unless the size of the reserve is large. Of nine exploited pelagic species studied inside and outside reserves [reviewed by Micheli et al. (13)], only three showed substantial increases after reserve protection. By contrast, about 75% of non-pelagic species show increases inside reserves. Few reserves larger than 150 km^2 exist (5), and so far it has been impossible to document the size of reserve needed to protect highly migratory species. However, several such species have benefited from MPAs, such as in the large regions near Cape Cod, Massachusetts, that are closed to cod fishing. Over these areas, free-ranging fish seem to respond to protection and have nearly doubled in density in the 10 years since protection began.

If the poor response of pelagic fish to small reserves is the result of their high mobility, then what lessons are available from the large list of species that do respond well to protection in reserves? DeMartini (26) showed that the movement patterns of fish and invertebrates had a theoretical relationship to the ability of reserves to affect population size. The reduction in rate of fishing mortality that an individual experiences is related directly to the amount of time it spends in a reserve. For highly mobile fish, whose adult movements take them in and out of protected areas, this fraction is the same as the total fraction of a marine ecosystem that is protected by reserves. For most areas, this fraction is small—for example, the reserve system in the Florida Keys National Marine Sanctuary covers less than 1% of the sanctuary area. In such cases, highly mobile fish are unlikely to benefit from reserves. The small Caribbean island nation of St. Lucia has reserves in about 1/3 of the area along an 11-km stretch of reef, and in this case, it is possible that fish with neighborhood sizes of 11-km or less receive substantial protection. Fish with neighborhoods of several 100 km are much less likely to benefit. Roberts et al. (18) showed that fish densities outside reserves were higher after reserve protection than they were before, and they attributed this increase to the movement of fish from protected to unprotected areas. The species contributing most to the density increase outside tend to be in moderately mobile families (18).

For less mobile species, populations will increase inside reserves if the addition of new juveniles to the protected population is faster than the movement of adults from inside to outside the reserve boundaries. Thus, response to reserve protection is not merely scaled to adult movement; it is scaled to recruitment as well. As a result, species with low adult movement may show little reserve effect if their recruitment is low. A possible example may be the poor performance of fisheries in Jamaica, where reef overfishing has been so extreme that there are few adults left to provide recruits, and the buildup of fish populations is extremely slow (30). In such cases, only highly sedentary species may likely show a reserve response.

By contrast, even species with high adult movement may show a reserve increase if recruitment to reserve settings is high enough to balance loss. The variable reserve response of species with different recruitment strengths is poorly studied, but the possibility exists that recruitment levels and response to reserve protection are generally linked.

Additional traits that determine response to reserve protection may be difficult to discern for many fish species. Biological features beside the overall movement patterns may also be important determinants of impact. Micheli et al. (13) classified 544 species from 20 studies by level of mobility and response to reserve protection. Once pelagic species are removed, the proportion of species with low, medium, or high levels of movement are about the same among species that decrease in reserves compared to those that increase (Figure 2). In particular, the list of declining species is not dominated by those with high mobility, and the list of increasing species is not dominated by species with low mobility. The failure to see the predicted relationship between estimated mobility and reserve response suggests that our view of the important life history features of benthic fish is not yet complete enough to allow good prediction of which ones will respond to protection. Another possibility is that response to reserves is a combination of features of both the

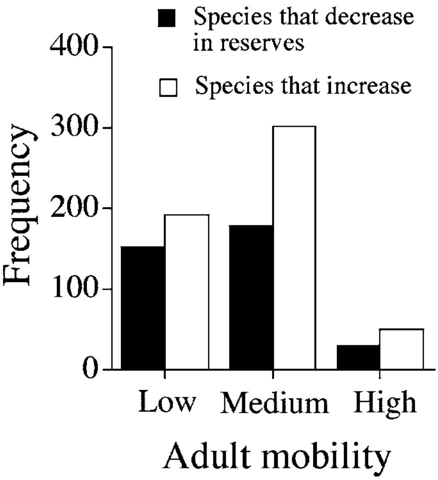

Figure 2 Number of species from different mobility classes for fish that increase inside marine reserves compared to those that decrease. From Micheli et al. (13).

targeted species and how humans use marine resources. For example, exploitation is generally higher for more mobile species (F. Micheli, personal communication), yet these are less likely to show a distinct reserve effect unless exploitation is very high and recruitment is consistent. Species with low movements, especially small reef fish such as butterflyfish and damselfish, may potentially show strong reserve effects. But because they are exploited only in severely overfished habitats, they will tend not to show a reserve effect except in extreme situations. Chapman & Kramer (31) estimated the effects of reserves on species of different potential mobilities. They concluded that low dispersal species did not show enhanced density or size in a reserve in Barbados.

THE SPILLOVER CLOUD

More poorly understood is the extent to which animals protected inside reserves move outside reserve boundaries and then enter local fisheries. This spillover effect is one of the key fisheries benefits of reserves, but this benefit has been well documented only a few times to date (18, 32, 33). From the standpoint of marine neighborhoods, measuring the spatial scale of spillover effects might tell us a great deal about how far populations tend to spread and the spatial scale of larval movement. Because the populations inside reserves are higher than outside, and because they potentially produce a large number of eggs and larvae, the existence of a successful reserve can be used as an experimental point source for tracking adult and larval movement, and thus it can provide a biological probe of neighborhood size. Unfortunately, current reserves are so small that larval clouds tend to be tiny, and most adult movement outside of reserves is monitored by the migration of fishing effort at reserve edges. As a result, we have little information about neighborhoods from these sources. However, a few preliminary data sets are available.

McClanahan & Mangi (32) monitored fish catch from the edge of a marine reserve in Kenya toward fished areas. Mass, size, and diversity of species dropped precipitously away from the reserve boundary. Higher fish abundance penetrates about 1 to 2 km into the fished areas on the south side of the reserve but only about 500 m on the north side. This difference may result from the prevalence of seine nets on the north side, suggesting the penetration of higher fish abundance depends on the intensity of fishing effort. If true, the extent of the spillover cloud can not be completely measured unless fishing is negligible, and if fishing is negligible, there will be no reserve effects and no spillover. In addition, the spillover effect appears variable across fish families even when mobility is similar. Rabbitfish, surgeonfish, and emperors decline significantly with distance from the African reserves, whereas goatfish, groupers, parrotfish, and snappers do not (32). Most of these families tend to be dominated by species with moderate to high rates of adult movement, and the differences in spillover pattern do not seem related simply to exploitation.

On Apo Island in the Philippines, Russ & Alcala have monitored the success of a small reserve since 1983 (34). Within a year or two of protection, large predatory fish showed a substantial increase in abundance within the reserve (35). Abundance of these species outside the reserve also increased, and 10–12 years after protection, mean adult density had increased severalfold (25, 34). Control sites that are 200–300 m from the reserve boundary showed nearly a 10-fold increase, whereas sites that are 400–500 m showed only about 50% increase. As in the case of Kenyan reefs, these data suggest that substantial spillover occurs over small distances.

Spillover from the set of marine reserves on the Caribbean island of St. Lucia has been suggested to have increased local fishing severalfold since the inception of the reserve system in 1995 (18). Along 11 km of coast, 4 to 5 reserves are interspersed with fished areas, and so the distance between fished areas and reserves is about 1 to 2 km. Spillover seems highest for moderately mobile fish families, such as parrotfish and grunts, groups that also showed movement across reserve boundaries during tagging studies (36).

Spillover from a reserve in Fiji derives from the movement of larvae. These reserves were established to allow regrowth of populations of clams (genus *Anadara*), which are heavily fished. Adult densities of clams are 14- to 18-fold higher in the locally managed Marine Area Network at the village of Uncunivanua, Fiji (37). Outside the area, within about a kilometer, densities of small postsettlement clams have increased about fivefold [see Tawake et al. in Gell & Roberts (38); Figure 3].

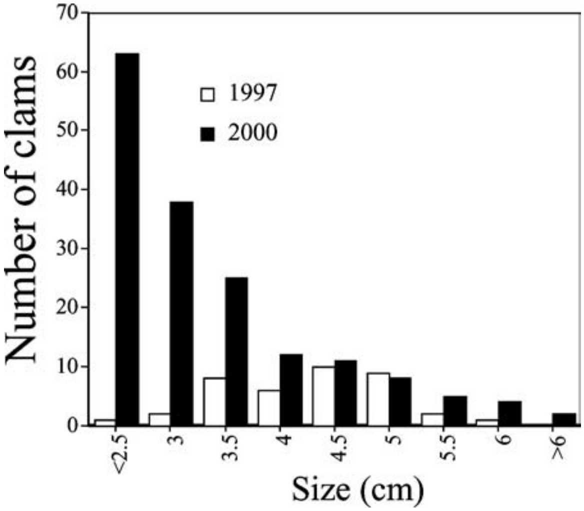

Figure 3 The number of clams (genus *Anadara*) outside marine reserves in Fiji in 1997 when the reserves were established and in 2000. Clams in fished areas outside of the reserves show an increase in postsettlement juveniles, probably as a result of spillover of larvae from large numbers of large adults inside adjacent reserve areas [redrawn from Tawake et al. (38)].

Because the adults are sedentary and the larvae are planktonic, this increase must be caused by export of larvae from the reserves. Other communities in Fiji have seen similar increases both inside and outside reserves. Although information about the magnitude of the larval spillover effect is available, the geographic scale of the effect is poorly known. Fished areas are interspersed with reserve zones, and measurements tend to compare fished and unfished populations over only small spatial scales. The shape and size of the larval cloud emanating from the reserves in Fiji is currently unknown, but this example suggests that it is now possible to use reserves as experimental sources of larvae to allow such measurements.

Similarly, Stoner & Ray (20) showed patterns of larval abundance for the commercially important Queen conch, *Strombus gigas*; these findings suggest spillover from a marine reserve in the Bahamas. Adults were 5–20 more numerous in the reserve compared to fished areas, and densities of early stage larvae were about 15 times greater. Offshore sampling about 1 to 2 km away from the reserve or fished areas showed approximately a 12-fold increase in abundance of larvae near the reserve, suggesting that larvae from the reserve were having an impact on larval abundance outside the reserve. However, the geographic extent of sampling was not high enough to show definitively that increased numbers of larvae are derived from reserve areas. As in the case of Fijian clams, no data showing the shape of the decline in larval abundance with distance from the reserve are available.

Larger-scale larval spillover has been reported for scallops in fishing closures on the Georges Bank in the Gulf of Maine. Since 1994, scallop (*Placopecten magellanicus*) densities have increased markedly in a series of zones closed to bottom trawling. Larger adults are available inside the trawl-free zone than outside. Though scallop fishing is now allowed in some of these previously closed areas, fishing has also intensified around the edges of zones that remain closed (21, 39). If this increased fishing effort is the result of spillover, then the geographic scale of spillover is at least 10 to 20 miles. Patterns of local current flow may dramatically affect the movement of larvae coming from protected populations, and it may be that oceanographic conditions on the Georges Bank favor larval retention near closed areas.

Though not derived from reserves, spillover clouds from marine restoration projects may provide some insight about neighborhoods. Peterson et al. (40) transplanted adult bay scallops (*Argopecten irradians*) into areas in North Carolina that had their previous populations destroyed by red tides. These restored populations sustained 10-fold increases in adult densities in a few transplant areas. Larval settlement and juvenile growth were also far higher near these restored populations than elsewhere in the region. Overall, larval settlement increased more than five-fold, but this increase was very local. One larval monitoring site within 2 to 5 km of several transplant areas (Emerald Island) showed large increases in settlement. A second site about 5 km from the closest transplant area showed no increase (40). Patterns of tidal inflow and outflow in the complex bay and estuary systems of North Carolina may constrain movement of larvae, and complicate patterns of larval dispersal. However, the clear increase in settlement after adult population restoration suggests that larval clouds can remain near adult populations and that local increases in adult densities can have a positive impact on recruitment to the next generation.

Few other clear examples of spillover clouds from reserves or restoration projects exist (41), possibly because reserves tend to be small and tend to have only a small effect on numbers of adults or larvae produced. In addition, data sets that suggest a spillover effect must be collected and analyzed carefully. For example, in St. Lucia, spillover was suggested by data that showed an increase in fish biomass outside reserves (18). However, there was no control for this experiment, and it is difficult to completely eliminate the possibility that fish biomass increased for reasons other than spillover. In such cases, monitoring biomass in a series of locations increasingly distant from reserve boundaries is an important component of an experimental design. Such studies of reserve spillover are becoming more common (23, 34). In the absence of such geographic sampling, the conclusion that spillover is occurring rests on the tacit assumption that no other changes have occurred that could significantly increase fish and invertebrate biomass. In the case of spillover of scallops from Cape Cod fishing closures, Murawski et al. (21) have pointed out that there were many changes in fishing regulations that could have increased scallop density outside reserves independently of a spillover effect. In the case of the St. Lucia reserves, no other fishing regulations were changed during the time of the study, and fishing elsewhere in the Caribbean was steadily declining (J. Hawkins personal communication) while fishing success in St. Lucia was increasing (18).

There are some cases in which spillover has been carefully investigated and is absent. Tewfik & Bene (42) showed that spillover of adult Queen conch from a protected area in the Turks and Caicos Islands is prevented by habitat barriers that surround the reserve. Similarly, a coral reef reserve in Barbados surrounded by sand patches 100s of meters wide shows little spillover (43). In other cases, some species showed spillover, but others did not. Spiny lobster in New Zealand (44) did not show a distinct spillover effect despite the fact that individuals are larger and more abundant in reserves (45). Long-distance movement of reproductively mature adults out of reserves may account for lack of spillover into adjacent habitats. In most cases, spillover from reserves is species specific: Although some species may move outside of reserves, others do not (46–48).

Because one quarter of the species inside a given reserve are not likely to show a reserve effect (13), and because only a fraction of the remaining three quarters of the species will have movement patterns appropriate to produce a spillover cloud (48, 49), it is perhaps not surprising that spillover is not universal. Spillover results that report summations of all species tend to show stronger positive effects than those that seek to understand patterns for just a few target species. Thus, it may be possible to document an overall spillover pattern across many target species without being able to pinpoint the way spillover is occurring for any single species. Such cases demand study of larger reserves but also suggest that statistical power of spillover investigations be carefully analyzed.

These problems have suggested the need for a different approach to understanding reserves, spillover, and the neighborhood size of fished species. As a result, the past few years has seen a marked increase in detailed studies of fish and invertebrate movement in natural and reserve settings. These studies complement investigations of biomass spillover and provide a very different view of the impact of reserves on fish and invertebrate populations.

TAGGING STUDIES OF ADULT MOVEMENT

Fish and invertebrates have been marked with a variety of methods that range from high-technology satellite transponders to low-technology colored thread (50). Physical tags are common for fish, crustacea, and mollusks (51), and range from coded archives that record environmental conditions after tagging to simple injected elastomer or tissue dyes that merely individualize an organism's appearance so that it can be recognized. More sophisticated devices record environmental variables while they are attached to an animal. Upon retrieval, these recorders can be read to estimate the geographic position of the tag while the host animal travels (52–56). Pop-up tags release themselves from the animal they were originally attached to and transmit geographic data via a satellite (57). Real-time data on geographic location have been gathered from triangulating audio receivers that pinpoint an individual's position or by detecting the sound of a unique sonic tag (58). Although this is not an exhaustive review of tagging approaches, I examined existing data from tagging studies to provide insight about movement patterns and adult neighborhood sizes.

There are few multispecies studies of movement based on tags. One long-term program has been the tagging of large pelagic billfish by recreational and commercial fishermen (59). Returns from 317,000 tagged animals over 50 years have established broad movement patterns and show that these large predators are truly ocean citizens. Moving over 1600 km in less than 6 months is a common result for black, blue, and white marlin, whereas sailfish and striped marlin tend to be found within 1000 km of their tagging site (59, 60).

Some fish are caught within 200 km of their release site even years after being tagged (59). However, proximity of release and capture sites may not necessarily translate to low rates of movement. For example, Takahashi et al. (61) fitted a swordfish with an archival tag off the eastern coast of Japan and recaptured the same animal 103 km away a year later. Archival tags collect data on environmental variables, such as temperature and day length. The combination of day length and date allows an estimate of latitude, and comparison of temperature data at that latitude with oceanic atlases allows an estimation of the longitude as well. Analysis of the archival data showed the fish tagged by Takahashi et al. (61) did not stay close to the tagging site but instead traveled 1000s of km to subtropical waters along the coast of New Zealand and then back to Japan. By contrast, bigeye tuna near Hawaii showed high levels of site fidelity, even using geolocation tags that record movements precisely (53).

Data on blue fin tuna show consistent seasonal returns to spawning grounds and a distribution among feeding grounds separated by 1000s of km (54, 56, 57, 62). Individuals in the Atlantic that are tagged off the coast of North America may spend several seasons in the western Atlantic, but then they move into the Mediterranean, possibly to spawn. Other individuals spawn in the Gulf of Mexico. A key insight of these data is that tuna move between eastern and western Atlantic stocks, suggesting that these management units are not a valid reflection of the basic biology of this species (11–14). Reconciling traditional delineations of stock structure with these new data is an important feature of future management.

It comes as no surprise that large pelagic fish in fact swim great distances and have ocean-scale neighborhoods (52). However, smaller pelagic fish may show more restricted movement. King George whiting (*Sillaginodes punctata*) showed movement patterns of up to 200 km, but even this level of movement seemed related to age. Younger fish did not travel far and tended to move long distances only when shifting habitats from shallow sea grass–dominated areas to deeper waters (63). Kingfish (*Seriola lalandi*) were recaptured typically within 50 km of point of tagging (64). Mackerel show a variety of movement patterns. School mackerel (*Scomberomorus queenslandicus*) moved small distances from their release point, on average 26 km (65). By contrast, the same study reported spotted mackerel (*Scomberomorus munroi*) moved 202 km on average.

Bottom-dwelling fish have less certain movement patterns, and even those that live in deep water can show remarkable site fidelity. Atlantic cod have been tracked by acoustic telemetry and show a complex pattern of seasonal migration. Acoustic tags emit an individually unique sound that can be monitored by a series of underwater receivers. By triangulating the directional signal collected by each receiver, the position of each tag can be estimated with great accuracy. Cod tagged off the Atlantic coast of Canada showed wide-ranging movements that took them to northern waters in two separate migrations (66). Fish overwintered in deep water but returned to coastal areas in spring. Some migrations were as short as 50 to 60 km, whereas others were over 200 km (66). Similarly, lingcod (*Ophiodon elongates*) in the northwest United States are resident in fairly small areas during part of the year but move seasonally to spawn (67). Red snappers in the Gulf of Mexico (*Lutjanus campechanus*) moved on average 29 km after an average 404 days at liberty before recapture (68), although hurricanes increase rates of movement considerably.

In the South African red steenbras (*Petrus rupetris*), tagging studies within the Tsitsikamma Marine Park have shown highly sedentary behavior of juveniles until about 70 cm length (Figure 4). Larger fish migrate 100s of km to the northeast, where they become resident and enter the fishery (69). Such ontogenetic shifts in mobility are a feature of many species (70–72). For example, deepwater Patagonian toothfish (*Dissostichus eleginoides*) have been tagged on fisheries' grounds and largely recaptured within about 25 km of their release point (73). One could interpret this to be a result of intense fishing that may make it more likely that a fish tagged on one fishing ground will be subsequently caught on the same ground. An alternative explanation suggests ontogenetic shift in mobility: These fish, similar to red steenbras, may be sedentary as juveniles on the banks that are heavily fished,

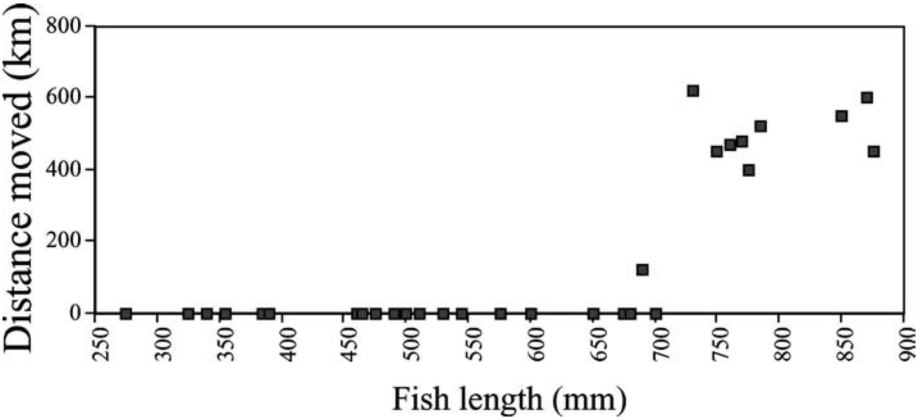

Figure 4 Ontogenetic changes in fish movement. Tag recoveries of red steenbras *Petrus rupestris* show low movement rates of juveniles. At the onset of sexual maturity, individuals migrate to adult habitats 500 km to the north. Redrawn from Brouwer (69).

but they may shift to a more mobile phase and thereafter become unavailable to the fishery.

Many benthic fish have been shown to be more sedentary as juveniles than adults (70–72). Yet, even adults can have remarkable small home ranges. Snappers in subtropical or temperate areas can have home ranges as small as a few 100 meters (74). The coral trout (*Plectropomus leopardus*) moved on average only about 2 km on Australian reefs. On temperate reefs amid kelp beds, three species of fish (*Chromis punctipinnis, Oxyjulis californica, Paralabrax clathratus*) showed no movement between adjacent but separated reefs (75). Perhaps the record for site fidelity goes to cardinalfishes, which over the course of more than a year consistently returned to within 1 m of their initially observed daytime resting positions (76).

Tagging studies of deepwater fish have been limited but Starr et al. (58) recorded movement patterns of two eastern Pacific rockfish using acoustic receivers deployed at about 100 m depth. Among greenspotted rockfish (*Sebastes chlorostictus*), 5 of 6 spent more than half their time within range of receivers dispersed over about 2 km. Among bocaccio (*Sebastes paucispinus*), 10 of 16 fish spent over 95% of their time within range of 5 receivers scattered along about 5 km of seafloor (Figure 5). However, in both species, some individuals moved outside of receiver detection, and in bocaccio, daily changes in depth caused animals to move short distances in areas of high vertical relief but move longer distances where the topography was more gentle (58).

Conclusions from these recapture surveys are limited. That some fish move more than others is no surprise. More detailed comparisons among species are hampered by vast differences in sampling effort between studies and by the largely descriptive nature of many tagging efforts. In addition, short-term movement patterns of an individual species tells us little about long-term residency. It is the combination of movement and timing that is likely to provide the most insight to neighborhood

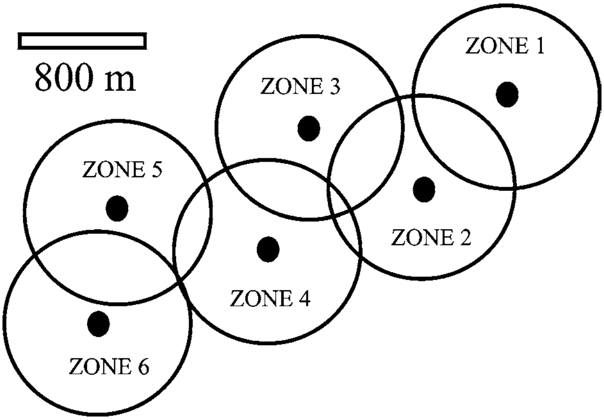

Figure 5 The geographic arrangement of acoustic sensors used by Starr et al. (58) to monitor movement of bocaccio (*Sebastes paucispinus*) on deep reefs off the coast of California. Most fish spent the majority of their time wholly within range of one of the sensors.

sizes. In this regard, data sets that show the relationship between time at liberty and overall movement are particularly useful (59, 68). From such plots, it might be possible to discern the area across which individuals tend to range over the course of a defined time period, such as a year. Nevertheless emerging patterns include the tendency of large pelagic fish to travel 100s to 1000s of km, and the tendency of smaller pelagics to have ranges more limited to 10s to 100s of km. Larger bottom-dwelling fish show movement patterns up to 100s of km, but some reef-associated species have home neighborhoods in the 10 km range. Finally, some benthic dwellers have such high site fidelity that they can be predictably found in an area for months to years (Table 1).

Across habitats, movement patterns seem to become larger from reefs to open bottom habitats to pelagics. Within habitats, movement tends to become more frequent with larger size, but such generalizations require larger comparative data sets than are usually available. For example, Kramer & Chapman (49) tagged a large number of species on reefs in Barbados and monitored resightings over time. On the basis of these data and a summary from the literature, they showed an exponential relationship between body size and movement pattern. In coral reef habitats, species with larger body size tend to have larger home ranges (Figure 6); species under 10 cm tended to have home ranges of 10 m or less.

In addition, Micheli et al. (13) documented a tendency of larger fish species to respond more positively to reserve protection—probably because they are more heavily exploited than smaller species and therefore show larger increases from even a low amount of protection inside reserves. The combination of these two trends is a pattern that seems counterintuitive: Species with greater tendency

TABLE 1 Some distances moved during tagging studies of benthic and pelagic fish

Species		Habitat	Scale	Evidence
Benthic or demersal				
Patagonian toothfish	*Dissostichus eleginoides*	Deep shelves	15 nm	Fishery recovery
Leafy sea dragons	*Phycodurus eques*	Kelp beds	5 ha	Acoustic
Snapper	*Pagrus auratus*	Kelp beds	500 m	Tag resighting
Red snapper	*Lutjanus campechanus*	Gulf of Mexico	29 km	Fishery recovery
Blue cod	*Parapercis colias*	New Zealand	100 m	Tag resighting
Atlantic cod	*Gadus morhua*	Northeast Atlantic	50–200 km	Acoustic
Coral trout	*Plectropomus leopardus*	Great Barrier Reef	2 km	Tag resighting
Cardinalfishes	Three species	Great Barrier Reef	<1 m	Tag resighting
King George whiting	*Sillaginodes punctata*		200 km	Fishery recovery
Small to medium pelagic				
Yellowtail kingfish	*Seriola lalandi*		50 km	Fishery recovery
School mackerel	*Scomberomorus queenslandicus*	Australia	26 km	Fishery recovery
Spotted mackerel	*Scomberomorus munroi*	Australia	202 km	Fishrey recovery
Large pelagic				
Black marlin	*Makaira indica*	Pacific	3–5000 km	Fishery recovery
Blue marlin	*Makaira nigricanus*	Global	2000 km	Fishery recovery
Sailfish	*Istiophorus platypterus*	Global	500–2000 km	Fishery recovery
Blue fin tuna	*Thunnus thynnus*	Atlantic	500–2000 km	Archival tags

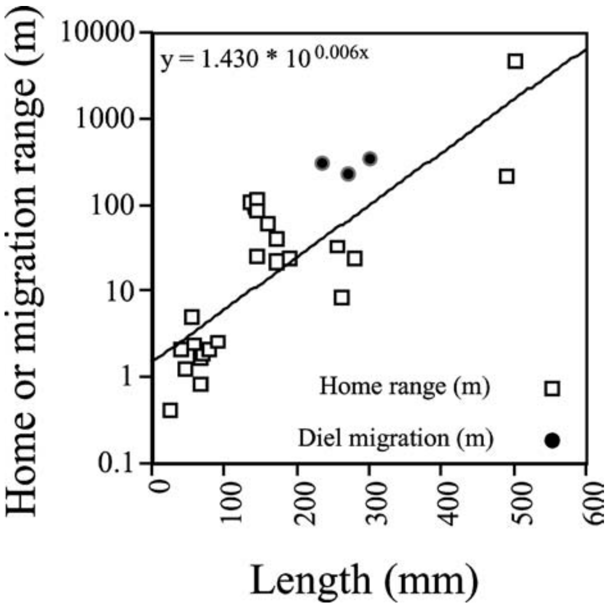

Figure 6 Relationship between home range size (or range of diel migration) and body size for coral reef fish. Data replotted from Appendix 1 of Kramer & Chapman (49).

to move outside reserves show a greater degree of reserve protection (Figure 7). Just the opposite prediction has usually been made: Sedentary species should be protected more completely (3, 26, 43). The emerging data, however, suggest that a combination of mobility, local fishing pressure, and reserve attributes are all critically important in determining response of a species to protection. Such complexities are very important to fold into expectations of the performance of marine reserves.

Other generalizations include the common observation that movement patterns shift over time in many species. Sometimes this seems associated with a shift from juvenile to adult phases (Figure 4). Other times, movement seems associated with seasonal migration of adults to spawning areas. In both cases, it becomes clear that a simple division of marine habitat use patterns into larval neighborhoods and adult neighborhoods is too simple.

CHEMICAL TAGS OF MOVEMENT IN OTOLITHS AND STATOLITHS

Tagging fish or invertebrates is generally limited to adults or larger juveniles, yet information about movements of smaller individuals is extremely valuable. Tags of larvae would be particularly useful in determining dispersal patterns (77).

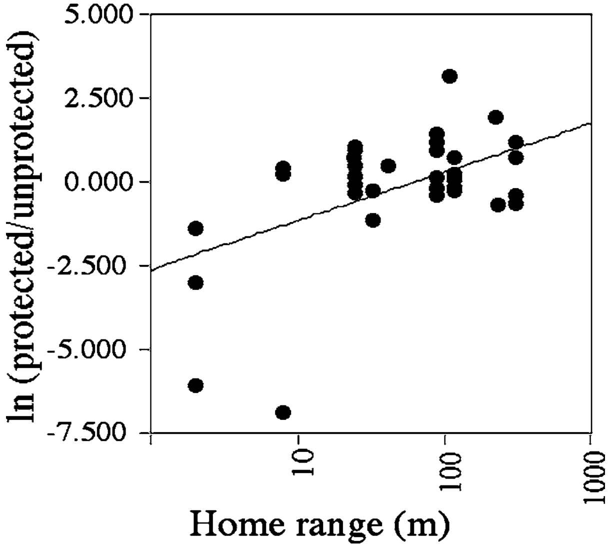

Figure 7 Response to reserve protection is higher in species with larger home range sizes. This counterintuitive pattern probably results from lower levels of exploitation in smaller fish that have low home range sizes (see Figure 6). Response is measured as the natural log of the ratio of abundance inside versus outside reserves [drawn from data in Micheli et al. (13)]. Home range sizes for these species were measured from movement patterns of tagged fish and are listed in Kramer & Chapman (49). All species are tropical reef fish, most of them from the Caribbean.

Movement of juveniles from nursery to adult habitats could be key to determining patterns of ecosystem use (78). To advance these capabilities, attention is increasingly focusing on the measurement of chemical signatures in calcified structures of fish and invertebrates. The tissues that form these structures incorporate elements such as barium, strontium, manganese, and magnesium into the calcium carbonate framework. Levels of incorporation vary with environmental availability of these various elements in sea water, and variation in the elemental signature can sometimes distinguish individuals that have lived in different water masses [see Campana (79) for review].

Most research focuses on the use of fish otolith microchemistry to identify distinct stocks of coastal fish (79–86). The simplest use of this technology is to completely dissolve the fish otolith (a small calcareous inclusion in fish ears) and measure the elemental signature in the resulting fluid. Such studies have shown that adult fish living in different estuaries or bays can have very different otolith signatures (82, 85, 87–92). For example, otolith chemistries (based on stable isotopes) inside hypersaline Shark Bay in western Australia are very distinctive compared to those from normal oceanic conditions. Individual pink snapper (*Pagrus auratus*) inside Shark Bay showed no sign of normal, oceanic otolith chemistries, and populations outside the bay never showed otolith chemistries characteristic of inside the bay. As a result, Edmonds et al. (90) concluded that adult pink snapper rarely moved and spent most of their lives either fully inside or outside Shark Bay (92). By contrast, the bluefish *Pomatomus saltatrix* showed individuals with both oceanic and bay signatures, and Edmonds et al. concluded they were more mobile. Similarly, Campana et al. (85) showed that otoliths of cod (*Gadus morhua*) differed between the southern and northern portions of the Gulf of St. Lawrence, and these otoliths could also be distinguished from those collected off the Nova Scotia shelf. They used different chemical tags to show how stocks mingled seasonally in the Gulf, a result similar to those reported for this species with acoustic tagging (66) [see also (79, 84)].

Otolith chemical signals often differ from place to place, but not all coastal areas differ in water chemistry. As a result, the spatial scale of discrimination for otolith studies can vary. Patterson et al. (91) showed that otoliths of Nassau grouper (*Epinephelus striatus*) were indistinguishable among localities in the Bahamas but were very different in Belize. Spatial discrimination among otolith studies seldom is less than 10 to 100 km, partly because differences among sites closer than this tend to shift over time. For example, chemical signatures in the Lessa and Lumpar rivers on the northwestern coast of Borneo were distinct in 1994 but not in 1995 (93). Similarly, discrimination of populations of shad (*Tenualosa ilisha*) was impossible over spatial scales of 100s of km in southeast India, largely because of strong differences in otolith chemistry from year to year (87). Discrimination in this species was successful in distant populations—Sumatra versus Kuwait versus India—which also showed genetic differences (87). By contrast, studies of spawning aggregations of cod in the northwest Atlantic showed otolith differences among most groups separated by as little as 50 km. These fine-scale results are associated with temporal stability of otolith chemical differences in cod. Over a period of two years, otolith signatures in cod remain largely consistent, although longer time periods showed substantial change (85).

In addition to studies on whole adult otoliths, increases in elemental discrimination allow the signatures of the central core of an otolith to be measured. This measurement allows the habitat of juveniles and adults to be compared and opens the possibility of measuring the retention of adults in natal spawning areas (94). Because it is not possible to predict the chemical signatures of otoliths from a knowledge of water chemistry (95), these signatures must be determined empirically for each fish species studied. Typically, whole otoliths from juveniles are compared among locations to generate a chemical atlas of signatures from different nursery areas. Then the cores of adult fish are assayed, and the juvenile atlas is used to estimate from which nursery area each adult is derived. These chemical assignment tests vary in power, but the tests can be assayed by asking how often they correctly assign juveniles to the nursery area from which they were collected (88, 96). Errors in assignments vary from 2% to 37% depending on the strength of spatial discrimination, but error rates of 5% to 10% appear typical (83, 88, 92, 96). Using these approaches, Thorrold et al. (96) showed significant differences in otolith chemical signatures among weakfish from estuaries separated by 100 to 200 km along the U.S. east coast. Error rates in assigning fish to their natal estuary were high in this study (29% to 37%) unless isotopic differences among estuaries were also included in the analysis. These authors also found significant differences among river systems within the Chesapeake Bay watershed, showing the potential for spatial discrimination over scales of about 50 km. When adult otolith signatures were compared to maps made from juveniles, Thorrold et al. (96) were able to show that adults tended to be found within the same estuary that they inhabited as juveniles (Figure 8). This homing of an estuarine fish back to nursery grounds shows spawning stock structure over scales of at least 100 km, with the possibility that finer-scale spatial structure may be found in the future.

Other juvenile-adult comparisons also show the degrees to which fish remain in the same region after recruitment or return to their natal nursery area to spawn. However, an unexpected complication is that the chemical atlas inferred from juvenile otoliths can shift significantly over time. For example, Gillanders & Kingsford (82) found marked spatial variation in otolith chemistries in a study of the trumpeter *Pelates sexlineatus*, but they also reported marked variation over time. Juvenile fish from the same estuaries showed significant differences in otoliths from year to year, and the ability to correctly predict the estuary from which a fish was collected actually decreased when data from two years were included in the analysis. Hamer

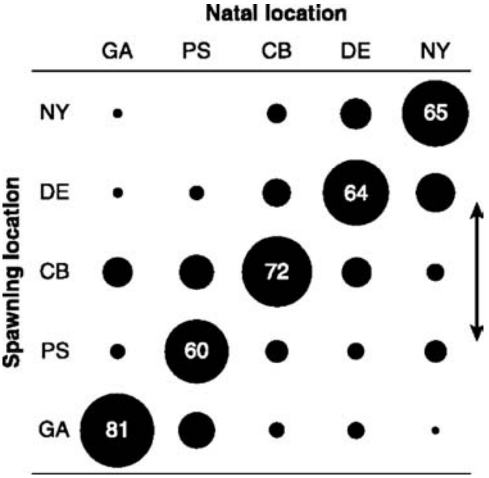

Figure 8 The degree of natal homing in weakfish as measured by chemical signatures in fish otoliths. Each circle represents the fraction of spawning fish that were juveniles in each of five estuaries along the U.S. east coast. Circle size is proportional to the fraction of juveniles from that locality. The abbreviations are GA, Georgia; PS, Pamlico Sound; CB, Chesapeake Bay; DE, Delaware; and NY, New York. Redrawn from Thorrold et al. (96a).

et al. (92, p. 261) provide parallel results for the snapper *Pagrus auratus* and conclude for this system: "Future classification of adults to nursery areas will require chemical tags characterised from juveniles of the same year classes as the adults being classified." Gillanders (78) used this approach and was able to show that a large fraction (89%) of the snappers caught on reefs near Sydney, Australia, settled as juveniles into adjacent estuaries.

Most of these studies to date have involved fish that use estuaries as either spawning or nursery habitats—fewer attempts have been made to apply these techniques to wholly oceanic species (97). In addition, these studies have tended to focus on habitat differences between juvenile and adult fish. Yet, the same techniques applied to distinguish the elemental signatures of the juvenile section of an otolith can be applied to the section of the otolith laid down in the larval fish as it develops in the plankton (84, 98). To date, attempts to use otolith chemistry to track larval movement have been limited by the technical difficulty of reading the signature of the tiny otolith core that was laid down during larval life, and the similarity in water chemistries in most open ocean settings where larval fish are found. However, both problems were solved by Swearer et al. (99) in a pioneering study of the movement of coral reef fish larvae. Taking advantage of the differences in water chemistry between the open ocean and coastal zones, Swearer et al. examined the otoliths of settling blue headed wrasses (*Thalassoma bifasciatum*) in St. Croix in the Caribbean. They asked the simple question—do settling larvae contain a signature of open ocean water? Or do they contain only a signature of coastal waters? If the latter were true, then the larvae could be assumed to have originated on St. Croix. Swearer et al. showed that 30% to 50% of the larvae settling in one area of St. Croix originated on the same island. This degree of larval retention was unexpected—conventional wisdom and current pattern diagrams suggested that larval wrasses would seldom complete development before being washed away from coastal zones. Further evidence suggested that periods of high settlement occurred when currents favored local retention.

A similar result derives from otolith studies on Lizard Island in the Great Barrier Reef, where the larvae of the damselfish *Pomacentrus amboinensis* were labeled with a fluorescent tag by Jones et al. (100). Collection of larvae returning to the same reef suggested that 30% to 60% of the settling larvae were retained around the island and, similar to the study of Caribbean wrasses, had much less demographic exchange among islands than previously thought.

So far, otolith studies do not identify the dispersal fate of larvae that are not retained on their natal island, and substantial long-distance dispersal may still occur. Recently a numerical model of ocean movements around Lizard Island suggested that this area acted as a major retention site within the Great Barrier Reef but also contributed substantially to regional larval pools (101). However, otolith investigations appear to have potential to map the movements of larvae, not just adults or juveniles. Furthermore, the basic approach of assaying elemental composition of larvae can be applied to larvae of mollusks and crustacea (98, 102, 103). Temporal shifts in chemical atlases, changes in the uptake of trace minerals from sea water depending on physiological condition or temperature, and the spatial resolution of significant differences in chemistry in nonestuarine settings (95) all complicate the interpretation of otolith data. Partly owing to these complexities, few measurements of larval dispersal patterns or distances are available yet from otolith studies. Further development of this technology may provide a new window into larval neighborhood sizes for a wide variety of species.

POPULATION GENETICS AND MEASURING DISPERSAL

Environmentally induced tags in larval fish and invertebrates have potential as markers of larval movement, but these environmental signatures can be difficult to find and use. Larvae and adults of all species also carry along with them a separate identity tag—their DNA—and this population or individual-level tag has been avidly investigated for several decades.

Most genetic studies of marine species emphasize patterns of genetic differentiation over evolutionary time frames, and many investigate genetics over spatial scales that range from 100s to 1000s to 10,000s of km (104–108). In general, patterns of marine genetic differentiation follow expectations based on larval life history. For species with relatively low potential for dispersal, genetic differentiation can occur over short spatial scales. Thus, animals or algae with crawl-away offspring tend to show genetic differences over scales of km (109–114), whereas species with larvae that are in the plankton for weeks or months generally show large genetic differences over only 100s or 1000s of km (106, 108, 115). Pelagic animals tend to have broadly dispersed population structure (116–118) except for species such as turtles (119–121) that have strong natal homing. Other animals with complex migration behaviors, such as whales, show strong genetic structure when offspring inherit their migration route preference or their spawning beach preference from their parents (122, 123).

Although the overall relationships between genetic structure and marine life histories seem to generally match, there are a growing number of exceptions that give us increased insight into marine populations. Working in the California Current, Bucklin et al. (124) showed that the euphaussid *Nematoscelis difficilis* differed genetically between inshore and offshore collections. Similar efforts in the Atlantic showed that the copepod *Calanus finmarchicus* had distinct genetic structure in different gyre systems (125). Morphospecies of planktonic foraminifera with global ranges have been shown to differ genetically between ocean basins and to sometimes consist of several sympatric cryptic species (126–129). Strong genetic differentiation in benthic species with extended larval durations have recently been reported, including stomatopods in Indonesia (130, 131) and gobies in the Caribbean (104). These data sets augment prior work showing genetic breaks at biogeographic boundaries in Atlantic (132), Indonesian (110, 133), and Mediterranean (134) marine species.

These cases in which an unexpected structure is observed provide powerful insights into the relationships between physical and biological oceanography (131, 132, 135). They imply that larvae are not moved like passive particles in ocean currents (130), that larvae may not survive the transit of deep water (104, 130, 136), or that the mixing of water in semidistinct ocean gyres does not significantly mix populations of plankton (126, 135). These genetic signatures of nominally high dispersal species are thus powerful allies in understanding the relationships between physical features of oceans and their biological populations.

Essentially, signals of strong genetic structure show regions across which gene flow is very low. A genetic signal is measured as the index F_{ST}, which is roughly the fraction of genetic variation that is distributed geographically. Values for F_{ST} in marine populations vary from very high (0.3–0.4) [e.g., Marko (112)] to vanishingly small (effectively zero), and a series of analytical methods and computer packages allow the calculation of F_{ST} from a wide variety of types of genetic data, including microsatellites, allozymes, restriction fragment length polymorphisms, and DNA sequences (137–139).

Interpreting the biological meaning of F_{ST} is more difficult than measuring it or testing it for statistical significance. Population genetic theory helps show how low gene flow must be before structure is observed, using a theoretical framework derived from work by Sewall Wright (1) and others on the Island Model of population structure (140, 141). A typical conclusion is that successful movement of even one migrant per generation is enough to prevent wholesale population divergence (142). Significant genetic differences can occur in cases of much higher rates of migration, but in these cases the populations are unlikely to evolve separately.

Some work has been done on different models of gene flow, including a stepping stone model in which populations exchange immigrants with populations only immediately adjacent to themselves (143, 144). Major advantages of these models are, for example, that they more realistically represent migration scenarios in the wild, especially of coastal marine species (4), and that they predict populations more geographically distant will show higher levels of genetic distinction at equilibrium (144). Furthermore, population arrays with lower gene flow show a greater accumulation of genetic distance over geographic distance (4, 143, 144), and therefore this signal of isolation by distance can be a powerful way to measure dispersal distances. In the past, these distances had been formally defined as genetic neighborhood size (1) and represented the variance of the geographic distribution of offspring relative to their parents. This is in effect the width of the dispersal cloud around reproducing adults, and it is a close approximation to the larval neighborhood size discussed in the Introduction.

For example, genetic differentiation of the coastal rockfish *Sebastes caurinus* builds up along the U.S. west coast so that F_{ST} increases by about 0.01 each 1500 km [(145), Figure 9]. Simulations of isolation by distance among 1000 populations each with 1000 reproductive individuals showed that this magnitude of geographic differentiation occurred when species had an average dispersal distance of about 50 to 100 km a generation (4), although this figure is sensitive to assumptions about the way larvae disperse, the overall population

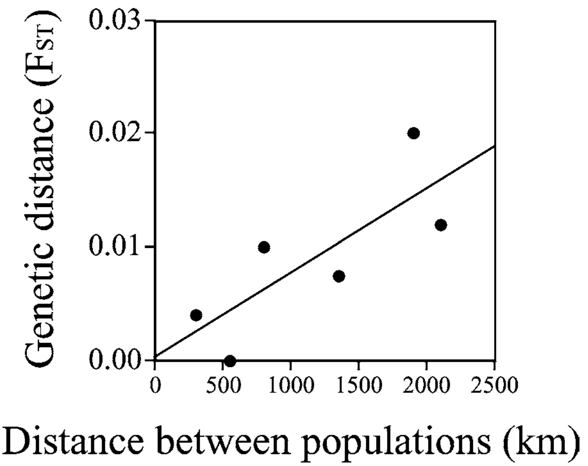

Figure 9 Genetic distance increases with geographic distance in populations of the copper rockfish (*Sebastes caurinus*) along the west coast of the United States. These signatures of genetic isolation by distance are consistent with limited gene flow between populations arrayed along a coastline and can be used to estimate average larval dispersal. Redrawn from Buonaccorsi et al. (145).

size, and the amount of time the population has had to reach drift-dispersal equilibrium.

Kinlan & Gaines (146) used this framework to estimate dispersal distances from a survey of genetic studies of marine plants and animals. They specifically excluded studies that showed no signal of isolation by distance and so excluded species that potentially have high enough dispersal to prevent genetic differentiation. However, the studies that did show isolation by distance reveal two interesting patterns of dispersal (Figure 10). First, taxa with generally low dispersal potential, such as algae, have low rates of dispersal—typically between 100 m and 1 km per generation. Second, taxa with generally high potential for dispersal, such as marine fish, have dispersal distances measured to be much higher—between 20 and 200 km. Marine invertebrates have a wide array of dispersal abilities (147) and show a correspondingly broad range of genetic dispersal distances (Figure 10).

Few of these dispersal estimates are above 200 km. The average for fish is about 100 km, and the average for invertebrates is about 10 km. These figures should be considered provisional for two reasons. First, they are calculated using a limited number of simulations, and the sensitivity of these estimates to changes in simulation conditions has not been fully explored. Second, taxa that did not show an isolation-by-distance signal are not included in this figure, so species with particularly high dispersal may have been eliminated from the analysis (S.D. Gaines, personal communication). Nevertheless, the relative ordering of results from these analyses are not sensitive to modeling conditions, and the relative ordering seems

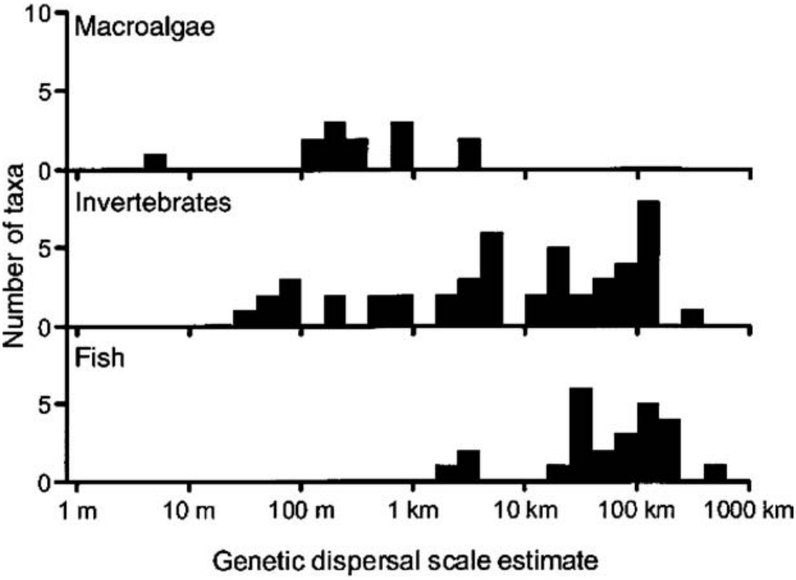

Figure 10 Dispersal estimates based on genetic isolation by distance for marine taxa summarized by Kinlan & Gaines (146), who used the methods of Palumbi (4). Taxa with dispersal high enough not to show an isolation-by-distance signal are not included in this analysis.

to make biological sense. In addition, the results are highly suggestive that genetic isolation patterns might be a powerful source of insight about larval dispersal profiles and that these profiles tend to cluster in the range of 10 to 100 km, not 100s to 1000s of km.

WHAT DO SUCH DIFFERENT TYPES OF DATA TELL US?

Movement patterns of marine species are highly variable, but emerging technologies allow a much more precise estimate of range occupation than ever before. Some approaches are designed to follow adult organisms over vast distances, some allow a continuous record of individual movement, and some can span life history stages to view the dispersal of planktonic eggs and larvae. Overall, emerging data show that the wide dispersion expected for mobile fish and larvae has many exceptions. Even some pelagic fish have more restricted movement patterns than thought previously, although as expected, this category of species appears to have the widest ranges. Across a variety of habitats, benthic fish appear often to have high site fidelities, pursue clear migration routes among habitats, or shift habitat use patterns in predictable ways with age. Individuals followed with acoustic monitoring may spend the majority of their time within a kilometer of a home site. Ranges of 10 to 20 km or above appear rare among nonmigratory benthic fish studied to date, although the number of careful studies is small, and species chosen for study may have low movement potential. Otolith chemistry and genetics have begun to delineate population boundaries in marine species, and these studies have been most successful at showing when and where adult populations do not mix. Between satellite responders, archival tags, acoustic surveys, chemical signatures of otoliths or other calcareous parts, and genetic analyses, methods now exist to follow virtually all individual marine organisms above about 10 cm. The potential to gain increased understanding of movement patterns in space and time is enormous, and it is possible to imagine high-resolution studies of marine species similar to those regularly conducted on terrestrial birds and mammals. Such detailed studies will contribute greatly to understanding the way species use habitats, the scales over which individual animals spend their lives, and the implications of protecting particular areas of the oceans from various types of human impact. Despite the ability to follow movement patterns of many species, there are very few comparative studies across taxa in the same environments. Such comparisons are essential if we are to build a picture of the way multiple marine species use habitats within the same ecosystem.

Larval movement patterns are vastly more difficult to discern than adult movement patterns, and the most promising approaches—otolith chemistry and genetics—require prodigious effort or a serious list of assumptions to turn raw data into discernable patterns. Yet, these methods have suggested an increasingly clear pattern of larval retention or evidence of restricted average dispersal. Summaries across many species for otolith microchemistry are not available, but a few studies have shown high levels of retention at the level of individual islands or along coastlines. Reviews of genetic differences based on stepping-stone models suggest larval movement of less than 100 km in the vast majority of cases in which genetic patterns are visible. These values are smaller than expected for highly dispersive marine larvae, and the values may reflect poor survival of larvae that move long distances, poor access to suitable settlement locations of larvae that are moved offshore, or the effect of large-scale environmental gradients on larval survival. The result of these overlayered processes of dispersal and mortality may be a small effective dispersal distance combined with occasional long-distance movement.

Data from marine reserves are far less valuable in determining patterns of movement—largely because fishing mortality changes the results dramatically. Spillover from reserves should measure fish movement rates, but the rate of fish removal outside reserves is the chief determinant of the extent of the spillover cloud. Even the expected pattern of decreased reserve protection for highly mobile fish is reversed in available data summaries (Figure 8). This is likely because highly mobile fish, which are protected less in small reserves, experience higher fishing pressure and thus show a greater benefit from even partial protection. Perhaps the clearest expected signal of dispersal from reserves will be the shape and size of the cloud of larvae released by adults within reserve borders. Monitoring the larval spillover cloud should provide one of the most direct views of the process of larval dispersal, but to date there are very few studies that have attempted these measurements.

NEIGHBORHOODS AND MANAGEMENT

Large migratory species have by far the largest neighborhood sizes. Baleen whales that migrate between polar feeding and subtropical breeding grounds, as well as marine turtles that move between feeding grounds and nesting beaches near different continents, can travel 10,000 km in a year. Ironically, these behaviorally complex species may often have a very fine scale population structure because individuals may return to the same areas year after year to breed. Thus, small scale spatial protection—particularly during breeding seasons—can be a powerful tool. However, the long-distance migration of these species requires at least low-level protection outside of breeding areas and times. Turtles and albatross, for example, are killed in great numbers by pelagic longliners when they forage far from breeding areas.

Similar patterns are seen in pelagic fish, many of which have migratory patterns that require movement over 1000s of km. For blue fin tuna, migrations between oceans are rare, but movement across ocean basins appears common (56, 57, 62). Whether tuna return to their natal spawning areas to breed is currently unknown, but this could be discovered through a combination of tagging and genetic surveys. Smaller pelagic fish can show much more restricted ranges—50 to 200 km for some mackerel or kingfish (9, 52)—and similar species may have different range sizes. Despite this potential for movement, moderately sized pelagic fish have been shown to respond well to protection in relatively small reserves (85), though this is likely a reflection of high fishing mortality.

Many benthic fish seem to fall into the same range of movement as small pelagic fish, moving 10s to 100s of km, although temperate and tropical reef fish may have home ranges of 1 km or less. These species may be as sedentary as many terrestrial mammals and nonmigratory birds, and they may be well protected by reserves that are just a few times larger than average home ranges. Even if individuals roam outside reserve boundaries (58), they may still receive significant protection from fishing mortality. Small benthic fish can have very small home ranges but are probably not often a target of strong fishing pressure unless overall fishing pressure is very high. In such cases, small reserves function well to protect populations. Likewise, many mobile benthic invertebrates probably have low range sizes, unless they engage in spawning migrations (148), although much less attention has been paid to understanding their movement patterns. In summary (Table 2), spatial management of marine populations over scales of 10 to 100 km may well cover the adult neighborhood sizes of a large fraction of species important in commercial harvest and ecosystem dynamics. Species not well covered by such management scales are species with spawning migrations or ontogenetic habitat shifts, or medium-to-large pelagic fish, turtles, and mammals.

Larval neighborhood sizes are likely far higher than these adult neighborhoods. For many marine species with planktonic larvae, gene flow across large distances

TABLE 2 Approximate adult and larval neighborhood sizes for a variety of marine life history groups[a]

Scale (km)	Adult	Larval
>1000s	Large migratory species	Intermittent gene flow, many species
100s–1000s	Large pelagic fish	Some fish
10s–100s	Most benthic fish Smaller pelagic fish	Most fish Most invertebrates
1–10s	Small benthic fish Many benthic invertebrates	Algal spores Planktonic direct developers
<1	Sessile species Species with highly specialized habitat needs	Benthic direct developers

[a]Values are based on emerging data from the variety of studies discussed here, contain significant exceptions, and require continued validation.

occurs commonly over evolutionary time frames (108, 149). These long-distance events may have only minor impact on population growth, except when they seed new habitats with species that typically did not occur there. Long-distance dispersal over ecological time frames has been difficult to document rigorously. One summary of patterns of genetic differentiation over distance suggests that larval dispersal clouds for fish are often in the range of 50 to 200 km. Invertebrates can have a wider distribution of dispersal distances due to their wider range of larval life histories and show buildup of genetic differentiation consistent with dispersal of 10 to 100 km in most cases studied. Both genetic and microchemical surveys of larval spread suggest cases in which local retention of larvae is surprisingly high, leading to the possibility that marine populations are not universally open over large geographic scales.

However, even these indications of lower-than-expected dispersal still tend to yield neighborhood sizes that are larger than most present-day marine reserves. In such cases, single, small reserves are unlikely to provide the best balance of conservation and fisheries' benefits (27), and networks of marine reserves are likely to be necessary. One approach to the design of reserve networks is to set the size of reserves on the basis of adult neighborhood scales and to set the spacing of reserves on the basis of larval neighborhood scales. Yet, the variety of these scales among species and the need for reserves to protect all species in a habitat make such simple rules quite complicated to implement. A second principle suggested by the data reviewed here is that species that are not overfished, and do not depend on fished species for shelter or food, have little response to reserves. Thus life history traits of unfished species may be less important in setting the scales of reserves than the species that differ strongly inside and outside reserves. A third principle is that even species with large adult neighborhoods benefit from reserves if the fishing pressure on them is severe. Reserve networks built using the variety of neighborhood sizes demanded by fished species and species otherwise affected by fishing may be the most practical way to proceed.

CONCLUSIONS

Information about marine neighborhood size can be gleaned from a large variety of sources. For example, marine reserves can be considered spatial experiments that may tell us a great deal about neighborhood size. Species that respond well to reserve protection may have neighborhood sizes that are the same as the scale of the reserve. A review of the reserve literature shows several nonintuitive patterns, especially that species with the largest adult neighborhoods show the strongest protection in small reserves. This results most likely from the overarching importance of fishing pressure on larger species that tend to move greater distances. Fishing pressure also dramatically affects the width of the spillover cloud of adults from reserves. One of the best uses of reserves as ecological experiments will be to measure the dispersal of larvae from these sources of highly fecund adults.

Numerous other methods, in addition to reserve experiments, have been developed to track movement patterns of marine species, and one or more will probably be appropriate for virtually all species over 10 cm in length. Data from physical tags, archival tags that send data via satellite, and acoustic tags supply information about movement on different scales of time and space, and in general tagging has shown the range of motion for pelagic and dermersal fish. Demersal fish can have surprisingly small home ranges, and even small pelagic fish have been shown to have limited neighborhood sizes. Not surprisingly, large pelagic fish can range over thousands of kilometers. Tagging data are limited by their tendency to be descriptive and by the difficulty in comparing results from one study to the next. The most informative data sets compare movement over time, but in some cases such detailed data are not available.

Larval dispersal patterns have been examined with microchemistry and genetics. Recent results hint at much smaller larval dispersal ranges than previously suspected but need corroboration among taxa. Chemical signals from otoliths have great potential to trace movement patterns of larvae and adults, but these studies are hampered by the need to document a detailed physical map of chemical availabilities before otolith data can be interpreted. Genetic results do not have this limitation but are impeded by small amounts of migration that may lead to very similar genetic signatures from place to place. This problem has been solved lately through use of models that use the geographic scale of genetic differentiation to measure average dispersal distances, but the link between genetic change and dispersal measured in kilometers requires a series of poorly tested assumptions.

Current data suggest the overall scale of neighborhood sizes for different species commonly studied in a variety of marine communities but provide incomplete guidance for reserve networks. This is largely because so few comparative surveys of larval dispersal patterns and adult movement patterns have been made for the wide variety of species currently used as fishing targets. For example, the National Marine Fisheries Service lists the following species as the most important to the commercial fishery of California (in order of declining revenues in 2000): squid, crab, sea urchin, swordfish, salmon, sardines, sablefish, and lobster. Recreational fishing is highest on ling cod, halibut, barracuda, rockfish, and tuna. Of these species qualitative data on adult neighborhoods are available for ling cod, rockfish, tuna, crab, sea urchin, swordfish, and salmon, with patterns being similar to those in Table 2. However, little information is available for larval neighborhoods except for indications of low dispersal potential for at least one species of rockfish (145) and high dispersal in squid and sea urchins (150, 151). Obtaining more detailed information about adult neighborhoods is now possible through a combination of the tagging methods described above. Obtaining more information about larval neighborhoods awaits refinement of microchemical approaches and application of more intense genetic sampling.

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