

The Contribution of Marine Protected Areas to Resilience and Persistence in Marine Fish Species

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Abstract

Networks of no-take marine protected areas (MPAs, areas in which there is no fishing at all) have been widely recommended for the conservation of marine biodiversity. But for marine populations to gain resiliency and persistency that protect them from external factors which may cause declination of the population, individual MPAs must be simultaneously self-sustaining and adequately connected to other MPAs via larval dispersal. For marine species with a dispersive larval stage, populations within MPAs require either the return of settlement-stage larvae to their natal reserve or connectivity among reserves at the spatial scales at which MPA networks are implemented. Until now, larvae have not been tracked when dispersing from one MPA to the other, and the relative magnitude of local retention and connectivity among MPAs remains unknown. In this review, studies on the panda clownfish, the orange clownfish, the vagabond butterflyfish and weakfish provide the first estimates of connectivity in a marine fish species. The results show that populations are sustained by a significant amount of self-recruitment, but it also largely depends on larval dispersal from and to other populations within or outside the MPA boundaries. More generally, the knowledge from these studies provides new insights in MPA development, and hopefully adds to the resilience and persistence of marine fish species.

Introduction

Networks of no-take marine protected areas (MPAs) have proved to be an efficient tool for both marine biodiversity protection and fishery management [1-3], and an increasing number of networks are being planned and implemented [4-6]. They contribute to the conservation of biodiversity by achieving three conservation objectives: 1) maintenance of essential ecological processes, 2) preservation of genetic diversity, and 3) ensuring sustainable utilisation of species and ecosystems [7]. They also contribute to broader marine management objectives through habitat conservation, replenishment of depleted fish stocks, enhancing productivity and insuring against fisheries management failure [8-11]. In order to achieve these objectives the ultimate goal of marine biodiversity conservation is to conserve the full range of marine biodiversity in MPAs, from gene pools to populations, species, habitats and ecosystems, and to ensure their long term persistence [3, 12-14]. To promote population persistence, MPAs must be simultaneously self-sustaining [15, 16] and linked to other protected areas to promote recovery from local extinctions [17-20].

Connectivity is the exchange of individuals among geographically separated groups, which is a critical property of marine populations, both in and outside MPAs [21]. Connectivity rates determine colonization patterns of new habitats, the resiliency of populations to harvest and the design of MPAs [22]. Larvae typically spend times ranging from

days to months in the pelagic environment before seeking suitable habitat to begin their adult life. Prevailing oceanographic currents may transport these larvae over large distances to form demographically 'open' populations that are linked by larval dispersal [2, 23]. Because of the highly variable duration in which larvae spend their time in the pelagic, direct measurements of connectivity are challenging and beside natal origins of adults are almost invariably unknown [24-28]. This lack of knowledge is primarily due to the difficulty of conducting mark-recapture studies in species that are characterized by the production of large numbers of small pelagic offspring that suffer high initial mortality rates [22].

Recent evidence from diverse fields like physical oceanography [21, 29], molecular genetics [30, 31], and otolith chemistry (natural tag of natal origin) [22, 27] suggest that at least some larvae return to the same subpopulation as their parents. However, the spatial scale over which marine populations are connected by larval dispersal continues to generate controversy due to a lack of solid empirical data on how far larvae can potentially travel [32, 33]. This information is vital for practical terms, because the degree of connectivity among geographic areas set the scale at which management strategies for exploited marine species needs to be applied [34].

More insight in larval dispersal and natal homing could help in the development and optimization of marine reserves with higher

resilience and persistence which could protect these marine fish species from outside interference in a more efficient way than before.

In this paper, I approach the idea of how marine protected areas help in conserving marine fish species by focusing primarily on larval dispersal and natal homing behaviour.

Results

To gain insight in natal homing behaviour and dispersal distances in marine fish species, Jones et al. (2005; 16) combined mass-marking of larvae in the field with the application of DNA paternity analyses to estimate self-recruitment in a population of panda clownfish (*Amphiprion polymnus*) associated with a discrete aggregation of anemones (*Stichodactyla haddoni* and *Heteractis crispa*) located in shallow sandy areas adjacent to Schumann Island, in Kimbe Bay, Papua New Guinea (Figure 1A). The population was spatially divided into five subareas where no individuals were found in adjacent sand or coral habitats or within 1 km beyond any of the subareas (Figure 1B). Each anemone was colonized by a maximum of one breeding pair and up to eight juveniles and subadults. A total of 40 anemones were found in the five subareas, with 33 anemones supporting breeding pairs (Figure 1C). Females laid demersal eggs on the upper surface of shells or dead coral next to the anemone. The embryos of *A. polymnus* hatch after 6-7 days of development, providing an opportunity for in situ marking of embryonic otoliths (ear bones) via tetracycline immersion [28]. Late-stage-larvae then settled into anemones after a pelagic larval phase lasting 9-12 days [35].

During two 3 month periods (April-June 2002, and August-October 2003) egg production was monitored and otoliths of all embryos produced by females in the study area were labeled. In 2002, marking was restricted to subareas a-c. Otoliths of ten from a total of 63 recruits (16 %) collected tested positive for the tetracycline mark (Table 1). In 2003 the whole study site was taken. More adult pairs were marked over the whole population. They found that 23 fish from a total of 73 newly settled recruits (32 %) were marked and had recruited to their natal population (Table 1).

Spatial and temporal patterns in arrival were the same for both marked and unmarked recruits. In 2003, most of the marked recruits arrived at subarea c, which also had the highest recruitment as a whole (Table 2). Egg production and larval settlement seem to follow predictable patterns, with broad cycles of egg production followed by more discrete recruitment pulses at or shortly after the new moon (Figure 2). Only during the peaks in recruitment did larvae return to their natal population. The overlapping spatial and temporal patterns in self-recruitment and recruitment suggest that the arrival

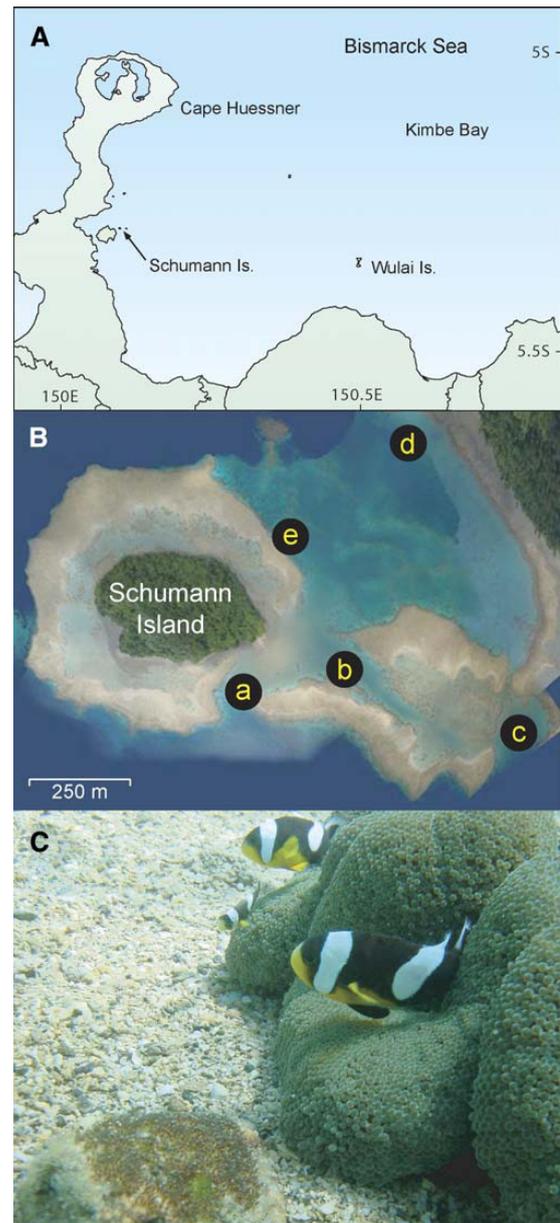


Figure 1. Study Location and species. (A) Map showing location of Schumann Island in Kimbe Bay, on the northern coast of New Britain, Papua New Guinea. (B) Aerial photo showing the five subareas (subareas a-e) of shallow sand flat supporting small populations of panda clownfish, *Amphiprion polymnus*. (C) Shows an adult pair of panda clownfish on the anemone *Stichodactyla haddoni* and a clutch of eggs on coral rubble.

of self-recruiters and immigrants are driven by the same processes.

A DNA paternity analysis was applied to all resident adult pairs arriving in 2003 using 11 microsatellites DNA markers to provide accurate identification of the paternity of newly settled recruits. Paternity analysis identified the location of the parents that produced offspring returning to the research area and created a measure of the distance between the settlement site and their natal anemone. On the basis of genetic markers, they found that 23 individuals from a total of 73 newly settled recruits

Table 1. Estimates of Self-Recruitment from Tetracycline Marking and Paternity Analysis

	2002	2003	
Total number of pairs marked	22	33	
Total area marking (km ²)	0.2	0.5	
Number of embryos marked	69,250	125,900	
Total number of recruits collected	63	73	
Number of recruits marked	10 tet	23 tet	23 pat
% Self recruitment	15.9%	31.5%	31.5%

Shown are the summary statistics for tetracycline marking of *Amphiprion polymnus* embryos at Schumann island in 2002 and 2003, and paternity analysis in 2003, including the number of pairs for which embryos were marked, the area over which marking took place, the total number of embryos marked, the total number of recruits collected, and the total number of marked recruits collected. tet denotes the number of tetracycline-marked juveniles collected, and pat denotes the number of juveniles collected that were classified to resident parents by paternity analysis.

were spawned by local adult pairs (**Table 1**) which is identical to the result provided by the mass-marking experiment.

No correlations were found between the number of self-recruiters and larval production or self-recruiters and adult numbers at the source subarea. The 23 newly settled recruits that returned to the study area came from either of the subareas a-c, but they did not contribute equally. Nine self-recruiters came from seven adult pairs in subarea a, where there were only nine adult pairs in total, compared to subarea c where only five self-recruiters were counted despite having the highest number (13) adult pairs and greatest overall egg production. The net direction of dispersal over the three months might indicate a local source-sink dynamic within whole Schumann Island population. Sixteen out of 23 newly settled recruits were collected in subareas a and d, and five returned to their natal subareas <50 m from their parents. None returned to the same anemone as their parents, indicating that direct kin relationships between adults and juveniles are likely to be rare.

Because the 9-12 days larval duration of *A. polymnus* is shorter than is typical for most other coral reef fishes [36], they might be expected to have relatively short dispersal distances. But although the local panda clownfish population is clearly sustained by significant self-recruitment, it

Table 2. Spatial Distribution of Self-Recruitment

Subarea	2002		2003		
	Total Recruits	Marked Recruits (tet)	Total Recruits	Marked Recruits (tet)	Marked Recruits (pat)
a	28	4	15	4	5
b	17	3	13	4	5
c	18	3	34	12	11
d	X	X	8	3	2
e	X	X	3	0	0

Recruitment and self-recruitment estimates to subareas a-e in 2002 and 2003.

does not explain where the remaining 68 % of larvae settling at Schumann Island come from or whether juveniles born at Schumann Island are successfully recruiting themselves to anemones within or outside Kimbe Bay. These results show that both extremely localized and longer-distance dispersal must be occurring in the panda clownfish.

Almany et al. (2007; 37) conducted a similar research as described above, but instead they focused on populations of two other species of coral reef fishes that differ in reproductive strategies, located around Kimbe Island in Kimbe Bay, Papua New Guinea. The orange clownfish (*Amphiprion percula*) spawns demersal eggs that hatch after several days of parental care, after which they spend ~ 11 days in the pelagic environment. In contrast, vagabond butterflyfish (*Chaetodon vagabundus*) release gametes directly in the water column (which means there is no parental care), and larvae spend ~ 38 days in the pelagic environment. The reproductive characteristics of the vagabond butterflyfish are also the most commonly found in marine fish species [37].

In December 2004, larvae of both species were tagged using stable barium (Ba) isotopes. These isotopes were injected into the mothers so they transmit these isotopes to their offspring before hatching and dispersal [38]. A total of 176 female clownfish and 123 butterflyfish from the reef surrounding Kimbe Island (**Figure 3**) were captured and injected with BaCl₂ solution. In February 2005 around Kimbe Island 15 clownfish and 77 butterflyfish were collected that had recently settled into reef habitats after completing their pelagic larval phase.

Assuming all clownfish larvae were tagged produced from Kimbe Island, 60 % of the juveniles displayed natal homing behaviour. A remarkable 60.1 % of juvenile butterflyfish returned to their natal reef, found in a variety of locations scattered around Kimbe Island, although the greatest number juveniles of both species occurred at the south-eastern corner of the island (**Figure 3**).

These results show that larvae are capable of returning to a very small target reef (only 0.3 km²), even after an extended larval duration. Although there is much indirect evidence for the limited dispersal of marine larvae [39], these results, in combination with two previous mark-recapture studies of larval dispersal [16, 28], suggest that self-recruitment in marine fish populations may be common and take place on a much smaller scale than previously realized. Even though high levels of self/recruitment were detected, ~ 40 % of the juveniles came from outside the MPA. Because the distance between Kimbe Island and the nearest reef is 10 km, and typically reefs in this region are separated by 5 to 20 km, ecologically important larval dispersal must occur between populations.

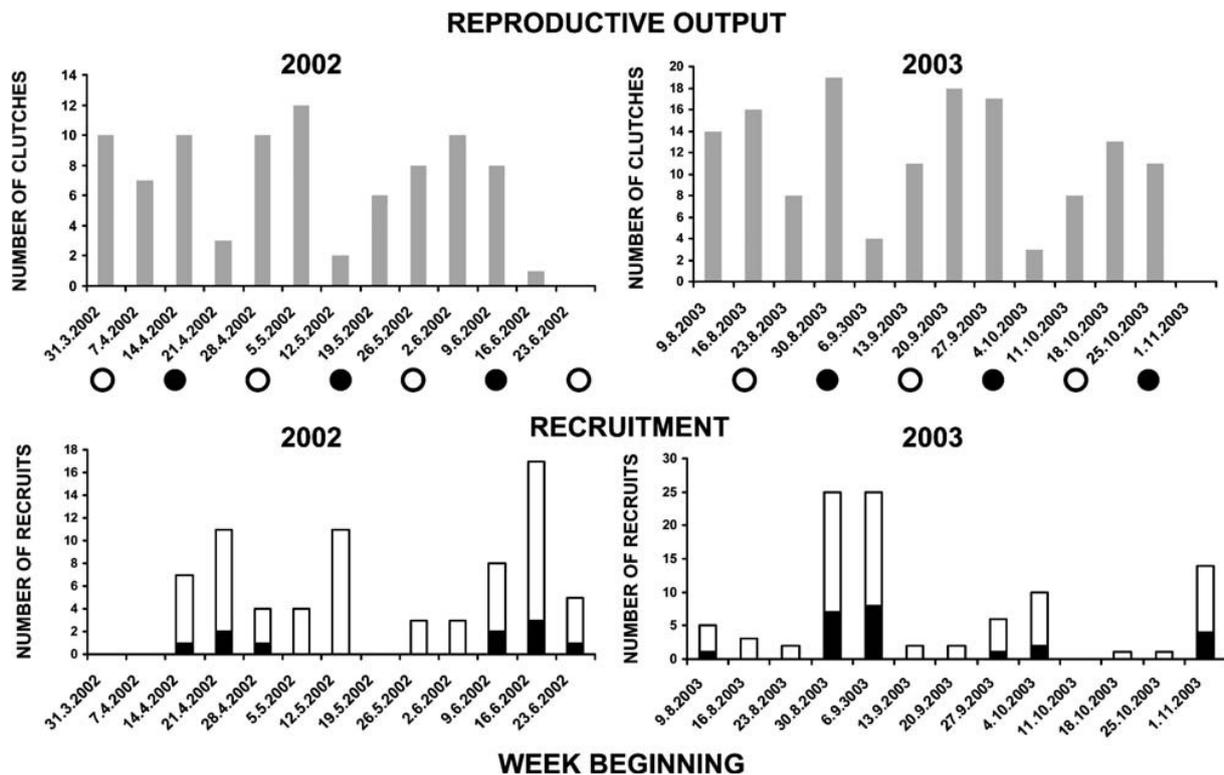


Figure 2. Timing of Egg Production and Recruitment
 The timing and magnitude of egg production (number of clutches laid), recruitment, and self-recruitment on a weekly basis over 3 month periods in 2002 and 2003. For recruitment, the bars represent all recruits, and filled portions represent numbers of self-recruiters on the basis of the presence of tetracycline marks. Open circles denote time of full moon, and filled circles denote time of new moon. The date given is the first day of each weekly interval.

Thus, the Kimbe Island MPA is likely to be both self-sustaining and providing recruitment subsidies to populations beyond its boundaries.

After Almany et al. (2007; 37) found evidence of high local replenishment to a population of ~ 200 adults living in anemones on shallow reefs near the island, Jones et al. (2009; 34) came back to Kimbe Island to do more extensive research on *A. percula*

larval connectivity, whereby they focused on generating direct estimates of larval connectivity by identifying the parents of *A. percula* larvae that returned to Kimbe Island and those that dispersed to adjacent subpopulations up to 35 km away. In order to generate these estimates, they used a large-scale application of DNA parentage analysis.

Sixteen polymorphic microsatellite DNA markers were screened from a total of 506 potential

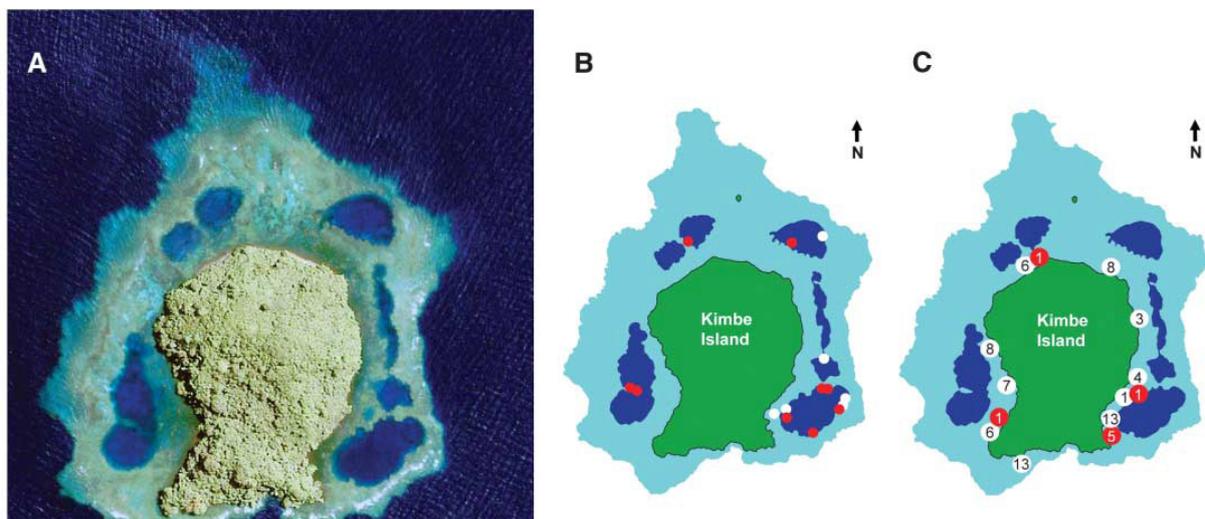


Fig. 3. (A) Satellite image of the Kimbe Island MPA (taken by the IKONOS-2 satellite at a resolution of 1 m). (B and C) Schematic diagrams of Kimbe Island showing the locations of tagged (red circles) and untagged (white circles) juveniles collected in February 2005. The locations of juvenile (B) *A. percula* (n = 15) and (C) *C. vagabundus* (n = 77) are shown. In (C), the number in each circle corresponds to the number of juveniles collected from that location.

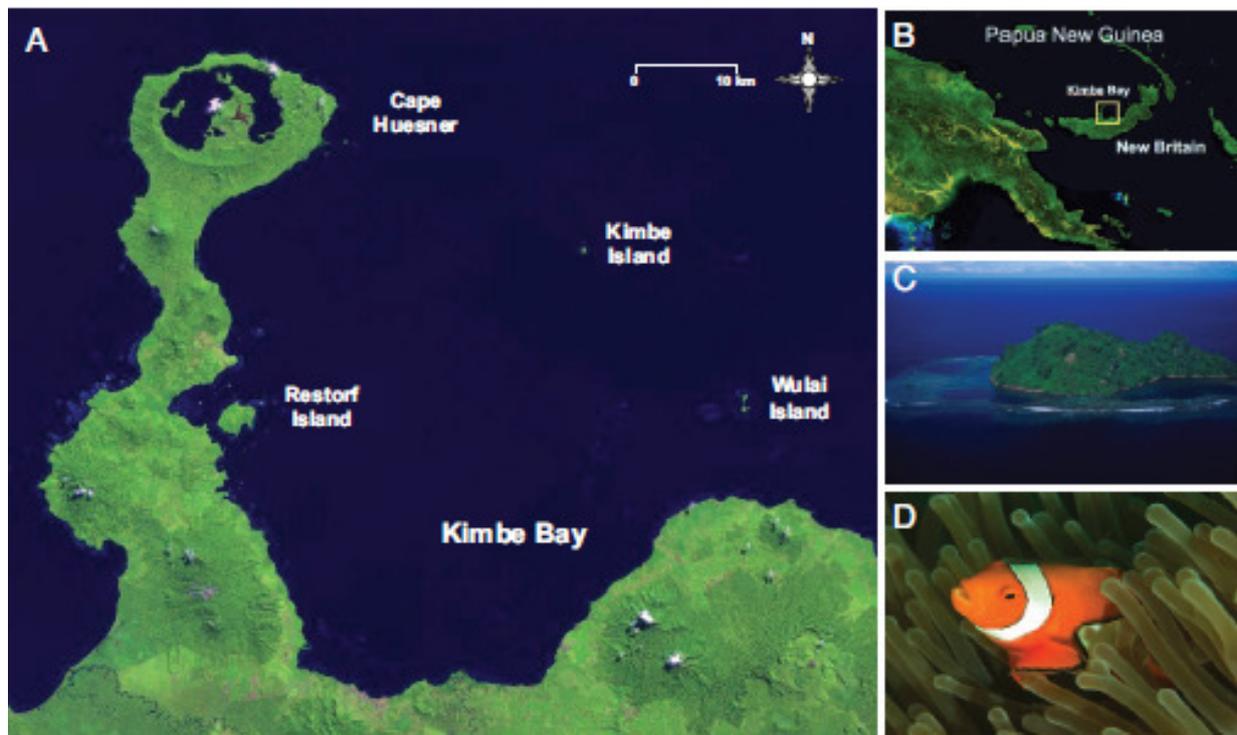


Figure 4. Location maps and focal species. (A) LANDSAT satellite image of western Kimbe Bay showing the study sites. (B) Location of Kimbe Bay on the north side of New Britain, Papua New Guinea. (C) Aerial photograph of Kimbe Island showing lagoonal habitats in which *A. percula* are concentrated in the study area. (Photo courtesy of Tami Pelusi.) (D) *A. percula* sheltering in an anemone, Kimbe Bay. (Photo courtesy of Simon Thorrold.)

A. percula parents at Kimbe Island sampled in December 2004. This was assumed to present the entire population. Then 400 newly settled juveniles were collected from Kimbe Island in December 2004 and April 2005 and also from anemones at Wulai Island, Cape Huesner, and Restorf Island in April 2005 (Figure 4A). Of the total of 400 juveniles collected in Kimbe Bay, 122 were identified as progeny of adults at Kimbe Island, based on parentage analysis by a maximum likelihood procedure. Of the 133 juveniles collected at Kimbe Island in December 2004, 56 (42 %) were identified as progeny of Kimbe Island adults, compared with 51 of 121 (42 %) collected in April 2005 (Figure 5).

DNA parentage analysis also allowed for documentation of levels of local replenishment at the individual lagoon scale (Table 3). In 2004, 23 of the 55 recruits (42 %) that were spawned by adults at Kimbe Island settled back in their natal lagoon, compared with 17 of 51 (33 %) in 2005. However, the Kimbe Island connectivity matrix revealed no relationship between the magnitude of connectivity and the distance between the lagoons (Table 3). Also 15 individuals were identified from Kimbe Island parents at surrounding reefs in Kimbe Bay (Figure 6). The parents of the only juvenile collected on South Bay Reef were located on Kimbe Island, and more surprisingly, they found juveniles that had been spawned on Kimbe Island reefs at the other 3 Kimbe Bay locations, indicating a larval

dispersal of 15-35 km. A total of 10 % (5 of 50) did Kimbe Island contribute to juveniles collected at Restorf Island, 6 % (6 of 105) of those collected at Cape Huesner, and 5 % (3 of 56) of those collected at Wulai Island.

The full geographic extent of this metapopulation remains to be determined, but given the fact that *A. percula* has a relatively short pelagic larval duration for a reef fish [37], significant demographic connectivity between the subpopulations in the MPA network appears to be likely for most other reef fishes as well. Lying ~ 30 km offshore of the north coast of New Britain in the Bismarck Sea, Kimbe Island is located within a hydrodynamic regime subject to eddies originating from instabilities in the South Equatorial Current and New Guinea Coastal Current [40]. Biophysical modelling for the tropical western Pacific region also suggests high levels of connectivity in regions where reefs are only 20-30 km apart, including species with a wide range of pelagic larval durations [41]. Levels of both local replenishment and connectivity for *A. percula* appear to be demographically significant and likely contribute to the persistence of discrete populations within the larger metapopulation.

These data provide evidence that larval subsidies from a single reserve may contribute to the resilience of subpopulations at other reserves within a network of MPAs.

Table 3. *A. percula* connectivity matrix among 5 lagoons surrounding Kimbe Island, calculated by identifying the natal origins of juveniles collected during 2 sampling trips in December 2004 and April 2005

		Settlement lagoon, December 2004 collection				
		A (n = 32)	B (n = 20)	C (n = 11)	D (n = 32)	E (n = 38)
Natal lagoon						
A		12	3	1	1	1
B		3	1	0	3	3
C		0	1	0	0	2
D		2	2	3	4	5
E		0	1	1	0	6
		Settlement lagoon, April 2005 collection				
		A (n = 29)	B (n = 23)	C (n = 18)	D (n = 18)	E (n = 37)
Natal lagoon						
A		5	1	1	1	5
B		4	2	2	0	2
C		2	2	2	1	0
D		3	1	0	1	1
E		5	1	1	1	7

Lagoon A, 69 anemones (n_{ane}), 125 adults screened (n_{scr}); lagoon B, $n_{ane} = 38$, $n_{scr} = 73$; lagoon C, $n_{ane} = 29$, $n_{scr} = 58$; lagoon D, $n_{ane} = 59$, $n_{scr} = 105$; lagoon E, $n_{ane} = 75$, $n_{scr} = 145$. All juveniles in the analysis were identified as being the progeny of Kimbe Island adults using DNA parentage analysis. Bold figures on the matrix diagonal indicate the number of juveniles that returned to their natal lagoon.

Another study conducted by Thorrold et al. (2001; 22) on weakfish (*Cynoscion regalis*) shows similar natal homing behaviour like that in *A. polymnus*, *A. percula* and *C. vagabundus*, only the difference between them is that *C. regalis* is an estuarine-spawning marine fish, living in eastern North America [22]. They used stable isotope and elemental signatures in otoliths of returning spawners to estimate philopatry and population structure in *C. regalis* to provide estimates of natal homing and population structure in the presence of significant connectivity among groups within the larger metapopulation.

Adult weakfish follow an annual migration pattern along the east coast of the United States that takes them from overwintering grounds south and

offshore of Cape Hatteras to spawning locations in estuaries and coastal embayments throughout the species range (Florida to Maine) in the spring and early summer [22]. Generally larvae are retained within natal estuaries through selective tidal stream transport [42], and reside in these estuaries until migrating to overwintering grounds in the autumn. Given the lack of dispersal, connectivity rates were primarily determined by the tendency for adult fish to return to their natal estuary to spawn.

Individual juveniles collected in 1996 were assigned to natal estuaries using linear discriminant function analysis (LDFA). They found that homing of spawning weakfish to natal locations was high, ranging from 60 % in Pamlico Sound to 81 % in Georgia. Straying was largely confined to

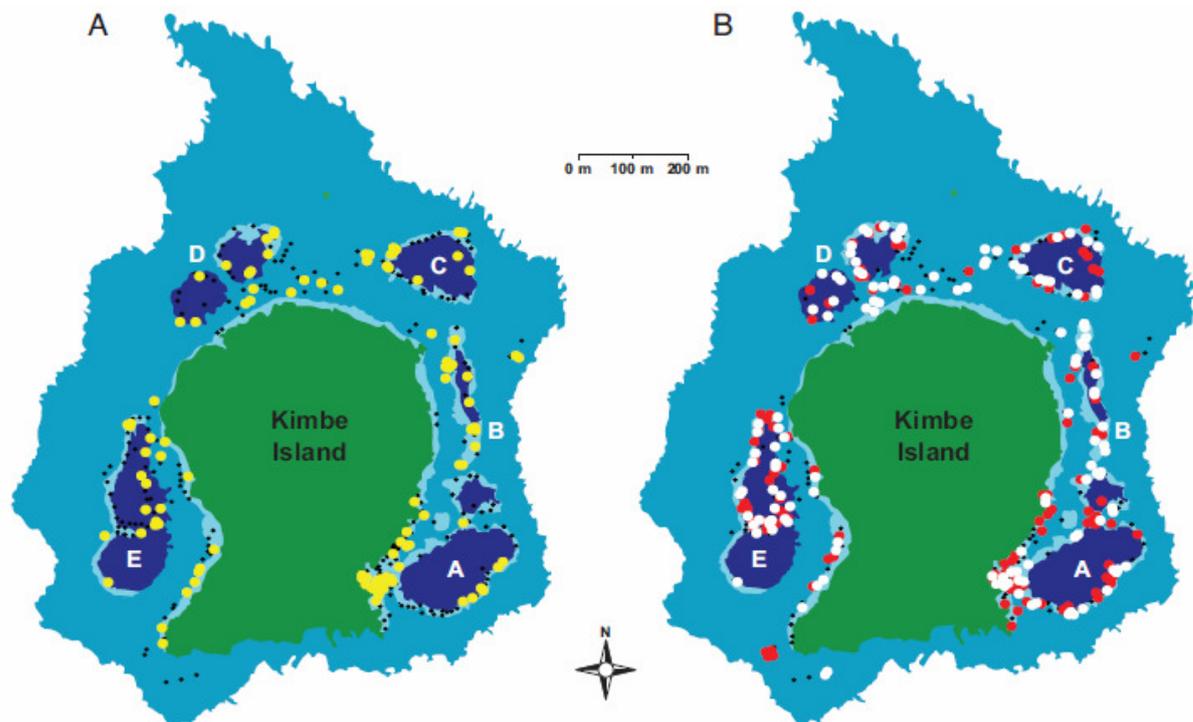


Figure 5. Map of locations of all anemones in each of the 5 lagoons (A-E) that harboured adult or juvenile *A. percula* around Kimbe Island. (A) Location of anemones with adult *A. percula* that either produced larvae that subsequently settled into anemones around Kimbe Island (yellow symbols) or did not produce larvae that returned to Kimbe Island (black symbols). (B) Location of anemones with recently settled juvenile *A. percula* that either were progeny of Kimbe Island adults (red symbols) or had dispersed from reefs at least 6 km away from Kimbe Island (white circles).

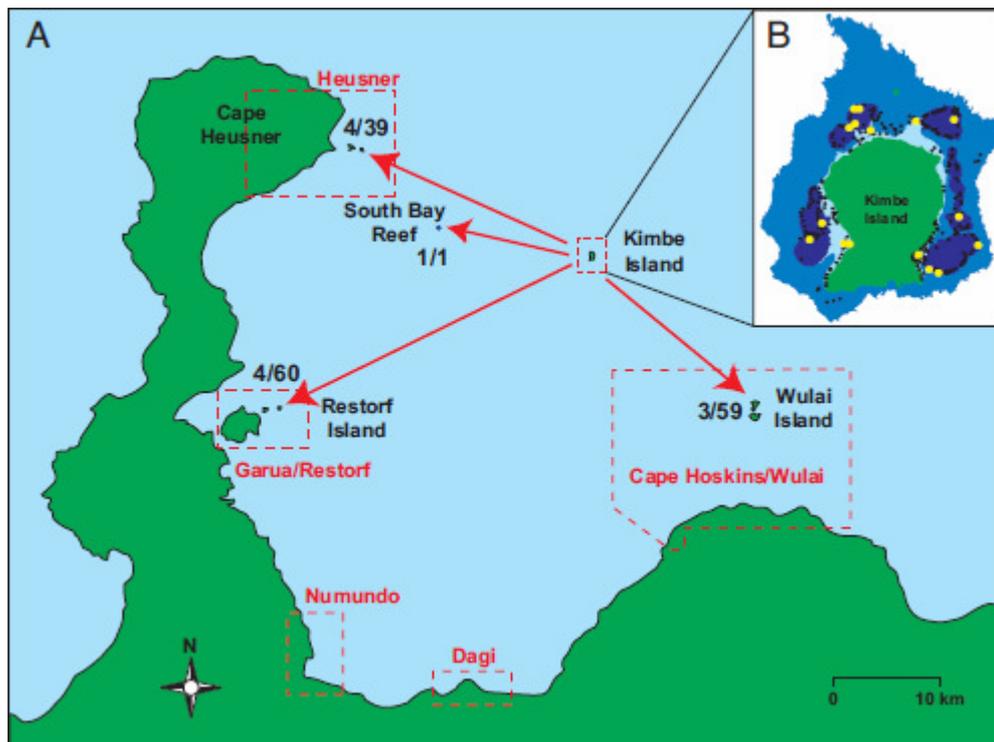


Figure 6. Larval dispersal of *A. percula* from Kimbe Island to other designated marine reserves in western Kimbe Bay. (A) Proportion of recently settled juvenile *A. percula* collected at each of 4 locations that were progeny of Kimbe Island *A. percula*. The red boxes outline proposed reserve boundaries [6]. (B) Location of adult *A. percula* that produced larvae that successfully dispersed and settled on anemones away from Kimbe Island (yellow symbols).

locations adjacent to natal estuaries, and was not due to a complete breakdown of homing behaviour. For instance, Delaware Bay strays were predominantly found in Chesapeake Bay, whereas strays from New York were only found in Delaware Bay.

Only speculations can be made on the mechanisms by which individual fish may be able to navigate back to natal spawning sites some 2 years after initial outmigration from juvenile nursery areas. The ability of adult salmon species to home to natal streams through the use of olfactory and other cues is well known [43]. Similar imprinting by juvenile weakfish while they reside in natal estuaries is possible, because juveniles may spend 3 to 5 months in these nursery areas before migrating out during the fall of their first year [22]. Alternatively, weakfish may learn of migration routes and spawning sites through social transmission or tradition, as has been suggested for the Atlantic herring [44].

Weakfish are currently managed as a single stock along the east coast of the United States on the basis of allozyme and mtDNA data that have suggested no genetic structuring throughout the region [22]. More recently, analyses of microsatellite and intron markers from the same juvenile weakfish used in the otolith assays detected no genetic differentiation among the five estuaries [45]. However, data from this study showed that there is much more spatial structure than is currently assumed by fisheries managers and that it might be helpful to consider weakfish population dynamics from a metapopulation perspective [22].

Connectivity estimates that were derived can be used to parameterize metapopulation models of weakfish dynamics that may, in turn, be used to evaluate novel approaches to fisheries management. For instance, the discovery of significant spawning site fidelity has considerable implications for the design of MPAs along the east coast of the United States. Weakfish population with high level of natal homing will be significantly more vulnerable to fishing activity than would be predicted on the basis of current stock models. Tracing population connectivity through larval dispersal and natal homing will be the most important element for the design and implementation of new MPAs [22].

Discussion / Conclusion

Tracing back juveniles to their parents after they finished their larval phase revealed significant larval homing behaviour in some marine reef fishes [16, 34, 37]. An extended larval duration does not seem to affect the ability of homing back to where they were born [37]. Although it has been shown that coral reef fish larvae may return to large natal populations [27, 28], *A. polymnus* shows that at least some marine fish species are able to accurately home back to their natal spawning ground at a scale of tens of meters rather than kilometers [16]. Because clownfish have a highly specialized association with a few anemone species [46], there may be a particular advantage to not dispersing away from a suitable habitat. Moreover, if the parental habitat is of sufficient quality for survival

and reproduction, you would expect some degree of self-recruitment [37].

The mechanisms by which larvae were able to maintain their position or find their way back to their natal population are as yet unknown [16, 37]. At Schumann Island, panda clownfish embryos often hatch in strong tidal currents, so posthatch larvae are likely to be transported away from the immediate area. Field evidence suggests that reef fish larvae migrate vertically in the water column to exploit currents at different depths and thereby avoid dispersal away from spawning locations [47]. Larvae are also capable of sustained directional swimming soon after hatching [48], and possess a range of well-developed sensory systems to locate and orient to reefs, including sight, smell and sound [48-51]. Thus interactions between physical oceanographic process and larval behaviour may lead to significant retention of larvae in near-shore waters adjacent to the natal population [52, 53]. That sensory systems and species behaviour may help to locate natal grounds has been backed up by studies conducted on salmonids [43], Atlantic herring [44] and probably for North American weakfish as well [22].

Self-recruitment has been observed in all of the fish species studied, but not all species rely equally on this phenomenon. Studies conducted on *C. vagabundus* and *A. percula* (2007; 37) show ~ 60 % of the settled larvae originate from inside the area, indicating that both self-recruitment and larval dispersal (other 40 %), both on a highly local scale as well as on a longer-distance scale, may play a huge role in the persistence of these marine fish species. However, two years later a similar research was conducted on *A. percula*, which shows that self-recruitment is actually lower than was observed in 2007. On the other hand, the *A. polymnus* study showed that the rate of dependency on larval dispersal among subspecies can vary greatly (68 % comes from outside the area) [16].

There is universal acceptance that understanding patterns of larval retention and population connectivity are critical for sizing and spacing closed areas in MPA networks [13, 24, 54-59]. The optimal design should be one in which individual MPAs are large enough so that populations within the MPA can sustain themselves, yet small enough and spaced so that a proportion of larvae produced inside the MPA is exported to unprotected areas [13, 16, 60]. Although it is widely speculated that MPAs may provide a recruitment subsidy to fished areas beyond their boundaries [54], these studies demonstrate that there are also significant recruitment benefits within the MPA and that the spatial scale at which coral reef MPAs can achieve these dual management objectives may be relatively small [16, 37]. Moreover, Planes et al. (2009; 34) conclude that the dispersal pattern found supports the contention that individual MPAs can be of a size that offers protection of resident population

and spaced within a network to allow for significant exchange of dispersers among MPAs [37, 61]. Theory suggests that low rates of migration often are sufficient to rescue individual populations from local extinction [38, 39]; thus, it is encouraging to find that for an MPA network designed with limited information on larval dispersal [6], one iconic reef fish species (the orange clownfish) appears to experience the conservation benefits of both local replenishment and larval connectivity among MPAs [34].

These four articles provide unique new insights about the role and importance of larval dispersal and natal homing on the resilience and persistence of marine fish species populations in MPAs and more generally in marine ecosystems. They also demonstrate that the methods in which MPAs are implemented currently are not perfect, and are still in need of improvement. Because of this, I find them very interesting and important for the scientific community. The downside of these articles is that they contain very few scientific results. A few results they back up with explanations, but in more cases explanations of their findings are lacking. Though I find these articles interesting and important, they were also very difficult to read. For example the structure in every of the four articles confuses me. Results, discussions and / or conclusions (if any) are scattered throughout the papers, making it very hard to understand the essence of their paper. The results they were presented contained a low statistical N, which gives me doubts about the degree of significance of the results. Figures are meant to clarify the content, but in some cases it did not clarify anything, it made things more confusing. Examples are figure 1 and 2 in 'Natal Homing in a Marine Fish Metapopulation' (Thorrold et al. 2001; 22) and figure 3 in 'Coral Reef Fish Larvae Settle Close to Home' (Jones et al. 2005; 16).

References

1. Agardy MT (1994) Advances in marine conservation: The role of marine protected areas. *Trends Ecol Evol* 9:267-270.
2. Roberts CM (1997) Connectivity and management of Caribbean coral reefs. *Science* 278:1444-1457.
3. Lubchenco J, Palumbi SR, Gaines SD, Andelman S (2003) Plugging a hole in the ocean: The emerging science of marine reserves. *Ecol Appl* 13:S3-S7.
4. Airame S, et al. (2003) Applying ecological criteria to marine reserve design: A case study from the California Channel Islands. *Ecol Appl* 13:S170-S184.
5. Fernandes L, et al. (2005) Establishing representative no-take areas in the Great Barrier Reef: Large-scale implementation of theory on marine protected areas. *Conserv Biol* 19:1733-1744.
6. Green A, et al. Designing a resilient network of marine protected areas for Kimbe Bay, Papua New Guinea. *Oryx*, in press.
7. Kelleher G (1999) Guidelines for marine protected areas. World commission on protected areas. Best practice protected area guidelines series no. 3. Gland, Switzerland: IUCN-The World Conservation Union; 107pp.

8. Kripke A, Fujita RM (1999) Marine reserve design considerations. Oakland, CA: Environmental Defense Fund; 10pp.
9. Tuck GN, Possingham HP (2000) Marine protected areas for spatially structured exploited species. *Marine Ecology Progress Series*; 192:89–101.
10. Gerber LR, Botsford LW, Hastings A, Possingham HP, Gaines SD, Palumbi SR (2003) Population models for marine reserve design: a retrospective and prospective synthesis. *Ecological Applications*; 13(1):S110–18.
11. Claudet J, Osenberg CW, Benedetti-Cecchi L, Domenici P, Garcia-Charton J, Perez-Ruzafa A, et al. (2008) Marine reserves: size and age do matter. *Ecology Letters*; 11:481–9.
12. World Resources Institute (1992) Global biodiversity strategy. Washington, DC: WRI.
13. Halpern BS, Warner RR (2003) Matching marine reserve design to reserve objectives. *Proceedings of the Royal Society of London B; Biol. Sci.* 270:1871–1878.
14. Secretariat of the Convention of Biological Diversity (2004) Technical advice on the establishment and management of a national system of marine and coastal protected areas, SCBD. CBD technical series no. 13; 40 pp.
15. Hastings A, Botsford LW (2006) Persistence of spatial populations depends on returning home. *Proc Natl Acad Sci U S A* 103:6067–6072.
16. Jones GP, Planes S, Thorrold SR (2005) Coral reef fish larvae settle close to home. *Curr Biol* 15:1314–1318.
17. Clinchy M (1997) Does immigration “rescue” populations from extinction? Implications regarding movement corridors and the conservation of mammals. *Oikos* 80:618–622.
18. Gonzales A, Lawton JH, Gilbert FS, Blackburn TM, Evans-Freke I (1998) Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science* 281:2045–2047.
19. Hill MF, Hastings A, Botsford LW (2002) The effects of small dispersal rates in extinction times in structured metapopulations models. *Am Nat* 160:389–402.
20. Allison GW, Gaines SD, Lubchenco J, Possingham HP (2003) Ensuring persistence of marine reserves: Catastrophes require adopting an insurance factor. *Ecol Appl* 13:S8–S24.
21. Cowen RK, et al. (2000) Connectivity of Marine Populations: Open or Closed? *Science* 287, 857.
22. Thorrold SR, Latkoczy C, Swart PK, Jones CM (2001) Natal Homing in a Marine Fish Metapopulation. *Science* 291, 297.
23. Roughgarden J, Gaine S, Possingham H (1998) Recruitment dynamics in complex life cycles. *Science* 242:1460-1466.
24. Sale PF, et al. (2005) Critical science gaps impede use of no-take fishery reserves. *Trends Ecol. Evol.* 20:74-80.
25. Warner RR, Cowen RK (2002) Local retention of production in marine populations: evidence, mechanisms and consequences. *Bull. Mar. Sci.* 70:245-249.
26. Thorrold SR, et al. (2002) Quantifying larval retention and connectivity in marine populations with artificial and natural markers. *Bull. Mar. Sci.* 70:291-308.
27. Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral reef fish. *Nature* 402:799-802.
28. Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. *Nature* 402:802-804.
29. Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. *Science* 311:522–527.
30. Barber PH, Moosa MK, Palumbi SR (2002) Rapid recovery of genetic diversity of stomatopod population on Krakatau: Temporal and spatial scales of marine larval dispersal. *Proc R Soc London Ser B* 269:1591–1597.
31. Gilg MR, Hilbish TJ (2003) The geography of marine larval dispersal: Coupling genetics with fine-scale physical oceanography. *Ecology* 84:2989–2998.
32. Mora C, Sale PF (2002) Are populations of coral reef fish open or closed ? *Trends Ecol Evol* 9:422–428.
33. Sale PF et al. (2005) Critical science gaps impede use of no-take fishery reserves. *Trends Ecol Evol* 20:74–80.
34. Planes S, Jones GP, Thorrold SR (2009) Larval dispersal connects fish populations in a network of marine protected areas. *PNAS* 106 no. 14:5693-5697.
35. Thresher RE, Colin PL, Bell LJ (1989) Planktonic duration, distribution and population structure of western and central Pacific damselfishes (Pomacentridae). *Copeia* 1989:420-434.
36. Lester SE, Ruttenberg BI (2005) The relationship between pelagic larval duration and range size in tropical reef fishes: A synthetic analysis. *Proc. R. Soc. Lond. B. Biol. Sci.* 272:585-591.
37. Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local replenishment of Coral Reef Fish Populations in a Marine Reserve. *Science* 316:742-744.
38. Thorrold SR, Jones GP, Planes S, Hare JA (2006) Transgenerational marking of embryonic otoliths in marine fishes using barium stable isotopes. *Can. J. Fish. Aquat. Sci.* 63:1193-1197.
39. Swearer SE, et al. (2002) Evidence of self-recruitment in demersal marine populations. *Bull. Mar. Sci.* 70:251-271.
40. Steinberg CR, Choukroun SM, Slivkoff MM, Mahoney MV, Brinkman RM (2006) Currents in the Bismarck Sea and Kimbe Bay, Papua New Guinea. Australian Institute of Marine Science and The Nature Conservancy. TNC Pacific Island Countries Report 6/06 (The Nature Conservancy, Brisbane).
41. Treml EA, Halpin PN, Urban DL, Pratson LF (2008) Modeling population connectivity by ocean currents: A graph-theoretical approach for marine conservation. *Land. Ecol.* 23:19-36.
42. Rowe PM, Epifanio CE (1994) Tidal stream transport of weakfish in Delaware Bay, USA. *Mar. Ecol. Prog. Ser.* 110:105-114.
43. Nevitt GA, Dittman AH (1998) A new model for olfactory imprinting in salmon. *Integrat. Biol.* 1:215-223.
44. McQuinn IH (1997) Metapopulations and Atlantic herring. *Rev. Fish Biol. Fish.* 7:297-329.
45. Cordes JF (2000) Application of genetic markers to provide species identification and define stock structure: analyses of selected marine fishes of the mid-Atlantic bight. Ph.D. diss., 142 p. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA.
46. Fautin DG, Allen GR (1992) A Field Guide to Anemone Fishes and Their Host Sea Anemones (Perth: Western Australian Museum)
47. Paris CB, Cowen RK (2004) Direct evidence of a biophysical retention for coral reef fish larvae. *Limnol. Oceanogr.* 49:1964-1979.
48. Leis JM (2006) Are larvae of demersal fishes plankton or nekton? *Adv. Mar. Biol.* 51:57-141.
49. G. Gerlach, J. Atema, M. J. Kingsford, K. P. Black, V. Miller-Sims, *Proc. Natl. Acad. Sci. U.S.A.* 104, 858(2007)
50. D. Lecchini, J. Shima, B. Banaigs, R. Galzin, *Oecologia* 143, 326 (2005).
51. S. D. Simpson, M. Meekan, J. Montgomery, R. McCauley, A. Jeffs, *Science* 308, 221 (2005).
52. James MK, Armsworth PR, Mason LB, Bode L (2002) The structure of reef fish metapopulations: Modelling

- larval dispersal. *Proc. R. Soc. Lond. B. Biol. Sci.* 269:2079-2086.
53. Kingsford MJ, Leis JM, Shanks A, Lindeman KC, Morgan SG, Pineda J (2002) Sensory environments, larval abilities and local self-recruitment. *Bull. Mar. Sci.* 70: 309-340.
 54. Gell FR, Roberts CM (2003) Benefits Beyond boundaries: The fishery effects of marine reserves. *Trends Ecol. Evol.* 18:448-455.
 55. Sala E, Aburto-Oropeza O, Paredes G, Parra I, Barrera JC, Dayton PK (2002) A general model for designing networks of marine reserves. *Science* 298:1991-1993.
 56. Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine reserves. *Ecol. Applic.* 13:S146-S158.
 57. Botsford LW, Hastings A, Gaines SD (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecol. Lett.* 4:144-150.
 58. Palumbi SR (2004) Marine reserves and ocean neighbourhoods: The spatial scale of marine populations and their management. *Annu. Rev. Environ. Res.* 29:31-68.
 59. Hastings A, Botsford LW (2003) Comparing designs of marine reserves for fisheries and for biodiversity. *Ecol Appl* 13:S65-S70.
 60. Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecol. Appl.* 13:S159-S169.
 61. Halpern BS, Warner RR (2003) Matching marine reserve function to stakeholder needs. *Proc R Soc London Ser B* 270:1871-1878.