

- 42 Barbosa, A. and Møller, A.P. (1999) Aerodynamic costs of long tails in male barn swallows *Hirundo rustica* and the evolution of sexual size dimorphism. *Behav. Ecol.* 10, 128–135
- 43 Thomas, A.L.R. (1996) The flight of birds that have wings and a tail: variable geometry expands the envelope of flight performance. *J. Theor. Biol.* 183, 237–245
- 44 Rosén, M. and Hedenström, A. (2001) Gliding flight in a jackdaw: a wind tunnel study. *J. Exp. Biol.* 204, 1153–1166
- 45 Maybury, W.J. and Rayner, J.M.V. (2001) The avian tail reduces body parasite drag by controlling flow separation and vortex shedding. *Proc. R. Soc. Lond. Ser. B* 268, 1405–1410
- 46 Maybury, W.J. *et al.* (2001) Lift generation by the avian tail. *Proc. R. Soc. Lond. Ser. B* 268, 1443–1448
- 47 Ellington, C. *et al.* (1996) Leading-edge vortices in insect flight. *Nature* 384, 626–630
- 48 Hedenström, A. and Alerstam, T. (1996) Skylark optimal flight speeds for flying nowhere and somewhere. *Behav. Ecol.* 7, 121–126
- 49 Hedenström, A. and Alerstam, T. (1995) Optimal flight speed of birds. *Philos. Trans. Roy. Soc. Lond. Ser. B* 348, 471–487
- 50 Norberg, R.Å. (1981) Optimal flight speed in birds when feeding young. *J. Anim. Ecol.* 50, 473–477
- 51 Pennycuik, C.J. (1978) Fifteen testable predictions about bird flight. *Oikos* 30, 165–176
- 52 Liechti, F. *et al.* (1994) Effects of sidewinds on optimal flight speed of birds. *J. Theor. Biol.* 170, 219–225
- 53 Hedenström, A. (1993) Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. *Philos. Trans. R. Soc. Lond. Ser. B* 342, 353–361
- 54 Hedenström, A. and Alerstam, T. (1998) How fast can birds migrate? *J. Avian Biol.* 29, 424–432
- 55 Rayner, J.M.V. and Swaddle, J.P. (2000) Aerodynamics and behaviour of moult and take-off in birds. In *Biomechanics in Animal Behaviour* (Dominici, P. and Blake, R.W., eds), pp. 125–157. BIOS Scientific Publishers Ltd
- 56 Hedenström, A. Twenty-three testable predictions about bird flight. In *Avian Migration* (Berthold, P. *et al.*, eds), Springer-Verlag (in press)
- 57 Pennycuik, C.J. (1998) Towards an optimal strategy for bird flight research. *J. Avian Biol.* 29, 449–457
- 58 Pennycuik, C.J. *et al.* (1997) A new low-turbulence wind tunnel for bird flight experiments at Lund University, Sweden. *J. Exp. Biol.* 200, 1441–1449
- 59 Kvist, A. *et al.* (2001) Carrying large fuel loads during sustained bird flight is cheaper than expected. *Nature* 413, 730–732
- 60 Pennycuik, C.J. *et al.* (1996) Wingbeat frequency and the body drag anomaly: wind-tunnel observations on a thrush nightingale (*Luscinia luscinia*) and a teal (*Anas crecca*). *J. Exp. Biol.* 199, 2757–2765
- 61 Hedenström, A. and Liechti, F. (2001) Field estimates of body drag coefficient on the basis of dives in passerine birds. *J. Exp. Biol.* 204, 1167–1175
- 62 Raffel, M. *et al.* (1998) *Particle Image Velocimetry: A Practical Guide*, Springer
- 63 Spedding, G.R. (1987) The wake of a kestrel (*Falco tinnunculus*) in flapping flight. *J. Exp. Biol.* 127, 59–78

Are populations of coral reef fish open or closed?

Camilo Mora and Peter F. Sale

Dispersal plays a crucial role in several aspects of the biology, management and conservation of many species, including coral reef fish and other demersal marine organisms with pelagic larval stages. To know the origin of propagules that replenish benthic populations is a major challenge, yet, whereas earlier studies emphasized the broadly extensive dispersal of reef fish larvae, recent publications have emphasized the extent to which these larvae succeed in returning to their natal populations. Here, we critically analyse the evidence concerning the dispersal of coral reef fish, and conclude that: (1) at present, the extent to which reef fish populations are open or closed must be regarded as unknown; and (2) further improved research is likely to confirm that larval dispersal structures populations into more or less open populations depending on the particular attributes of species, physical oceanographical systems in which they occur and the scale at which the question is posed.

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DISPERSAL (see Glossary) is one of the most important life-history traits involved in species evolution and persistence [1–4]. It is also the primary determinant of CONNECTIVITY among local populations, which is a vital parameter for conservation strategies based on protected areas [5]. In addition to the intrinsic importance of dispersal for fundamental science, recent evidence of impacted fish stocks [6] and our growing awareness of coral reef degradation by human activity and climate warming [7] highlight the need for accurate understanding of dispersal. For demersal and benthic marine organisms with

pelagic larval stages, delineating patterns of dispersal remains a major challenge, both because the dispersing organisms are minute and difficult to track, and because dispersal is driven by multiple complex factors. Because of the potential for transport of propagules by currents, early work assumed that larval dispersal was largely passive, with an extent that was dependent on patterns of water movement and duration of larval life. Thus, local populations were expected to be replenished largely by larvae derived from elsewhere [5,8].

Fish of coral reefs typically have larval lives that are measured in weeks or months, but their larvae are capable behaviorally of participating actively in their own dispersal [9–14]. These attributes are compatible with various patterns of dispersal [11], but ecologists of reef fish have increasingly tended to emphasize that fish larvae remain in the vicinity of the natal reef [15–17]. Whereas the view in the late 1970s was that reef-fish populations were broadly open, the consensus has shifted to view them as substantially closed [15–22]. This change relies on a variety of evidence, including physical oceanography near reefs [16], larval behavior [9], tagging studies [18–19] and genetic patchiness among geographically separate populations [2,23]. It is also supported by some recent models of dispersal [22], and conforms to theoretical expectations that marine populations must achieve CLOSURE by

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developing life histories that retain offspring as 'members' of the reproductive unit [20–21]. Here, we critically analyse the evidence concerning dispersal in reef fish, identifying limitations in techniques and in data interpretation. At present, these limitations prevent an accurate assessment of the extent to which reef fish populations are replenished by local or exogenous recruits.

Scales of dispersal

The description of any system depends largely on the chosen dimensions of space and time. At biogeographical spatial scales, all populations are closed, whereas at meter scales, any population of organisms with pelagic larvae is likely to be open. Whereas most of the ecological investigations of fish on coral reefs were done at single local sites in the 1970s, it is now common to do research at sets of sites 10s of km apart [18–19]; some studies are undertaken on scales of 100s of km or more [24–25]. Therefore, the change in emphasis concerning the degree of openness of reef fish populations might be due partially to a shift in the scale at which they are routinely viewed. Nevertheless, although spatial and temporal scales at which studies are done can have important effects on how ecological patterns and processes are perceived, this is not the main limitation in studies of larval dispersal in reef fish.

Evidence for dispersal in reef fish

Tagging studies

By using tags to differentiate larvae from different populations, two studies have provided quantitative evidence for SELF-RECRUITMENT in coral reef fish. Over three months, Jones *et al.* [18] used tetracycline to tag ~10 million embryos of the damselfish *Pomacentrus amboinensis* around Lizard Island, Great Barrier Reef, Australia. Analysing the otoliths of 5000 recaptured late-stage larvae, they found 15 tagged larvae and calculated that between 15% and 60% of the recruits to that island were locally produced. Unfortunately, this imprecise estimate means that this population might be either almost entirely open (85% of recruits from elsewhere) or moderately closed (60% of recruits produced *in situ*). In addition, their estimate of self-recruitment might also be biased upwards. Most effort for collection of larvae was done on the windward side of the island, a location where a retentive CONVERGENCE ZONE occurs owing to complex patterns of water flow [26,27]. A broader distribution of sampling effort around Lizard Island might have led to a lower estimate of RETENTION.

The other study of larval tagging, by Swearer *et al.* [19], was based on the assumption that larvae developing in coastal waters have distinctive signatures (e.g. in growth and otolith microchemistry) compared with larvae developing in less productive open water. During three summer months in 1992, Swearer and colleagues found that ~70% of *Thalassoma bifasciatum* wrasse recruits to St Croix,

US Virgin Islands, presented signatures of coastal development. They suggested that these were evidence that larvae remained close to home and were recruited to the natal population. One limitation, noted by the authors, is that, if the time spent in open water was minimal, larvae might have coastal signatures, despite coming from outside St Croix, (conversely, animals produced and settled locally might have off-shore signatures after spending most of their larval life in off-shore waters). Based on the minimum number of days necessary for a larva to produce a coastal signature, Swearer and colleagues predicted that up to 50% of larvae with coastal signatures might have been produced on upstream reefs (i.e. elsewhere in the Lesser Antilles). This estimate implies that, during those three summer months, as few as 35% of the recruits of this wrasse to St Croix might be produced locally. During the autumn of 1992, most recruits to this island presented signatures of open ocean development [19]. Rates of RECRUITMENT in the sites sampled by Swearer *et al.* tend to be similar during summer and autumn (~1.1 and 0.95 fish m⁻² respectively [28]). Thus, the overall extent of retention might be less than that implied by Swearer *et al.* [19].

Overall, the study by Jones *et al.* [18] confirms, and that by Swearer *et al.* [19] strongly suggests, that these local populations of reef fish retain some larvae, but might also receive significant recruitment from other locations. The generalization of these results requires additional studies, which should involve a range of hydrographical regimes, including simpler coastlines with long-shore currents [29]. Although these two studies have motivated renewed interest in reef fish dispersal, their results provide only tentative support for retention as the motor driving the replenishment of reef fish populations.

Genetic comparisons

Variation in genetic markers, such as allozymes and mitochondrial DNA (mtDNA) among sub-populations (commonly quantified using fixation Index F_{st}) has been used to track patterns and levels of migration in reef fish [1,2]. However, several aspects of genetic studies become crucial when addressing questions of reef fish demography. Demographic studies require, for instance, that markers are able to drift distinctively among populations at temporal scales that are relevant to population replenishment (usually months). Allozymes and mtDNA are, however, not very sensitive to drift, particularly in large populations and over short periods [30]. Results based on allozymes and mtDNA are usually interpreted as a reflection of long-term processes, not on timescales that are relevant to population demography [1,30]. Microsatellites are promising markers that are not yet used for demographic studies of reef fish. They present high levels of polymorphism, and are probably neutral to selection. Their high rates of mutation also make them suitable for tracking genes on ecological timescales [1,30].

Box 1. Navigation by reef fish larvae: what do we really know?

Late-stage larvae can orient toward different reef stimuli [a] and are capable of independent movement [they can swim at field speeds of between 5 and 50 cm s⁻¹ (20 cm s⁻¹ on average [b]), and long enough to cover between 4 and 200 km before exhaustion depending on the species, [b-c]]. It seems probable, therefore, that reef fish larvae can navigate over large distances and towards reefs [a-d]. However, there are several problems with this conclusion.

- How reliably can fish orient towards reefs? Reef sound has been suggested to be the most probable stimulus for orientation [e-g]. Reef sounds are measurable at least 10 km from a reef [g], but physiological evidence suggests that larval hearing is not sufficiently acute to detect them [e], and field results show little behavioral response at distances of >1 km [f]. During the first pelagic day (when the eggs or larvae still lack swimming abilities), at a common current of 20 cm s⁻¹, a larva could be carried as far as 17 km away from a reef; thus, early in their life, larvae could be transported far from cues with which to locate reefs, especially the natal reef, and would therefore be unable to navigate. In addition, the ability to detect a cue does not automatically mean that the cue can be used reliably to determine a direction to find its source [g].
- What is the true extent of their swimming abilities? Laboratory studies have shown that late-stage larvae of many reef fish species are good swimmers, but how well do these skills transfer to natural conditions? First, published records of distances swum might be biased. They might overestimate abilities, because, in nature, it is unlikely that a larva will swim until exhaustion, as they do in the laboratory. They might also underestimate abilities, because the larvae are not fed during most experiments (one recent study shows that feeding does enhance swimming ability in one species [h]). There are also several reasons to believe that larvae do not swim continuously in the field. Swimming represents an energetic cost [i], which has negative effects on survival subsequent to settlement and recruitment [j]. Movements of larvae (e.g. when they are swimming) are also a cue for predators that detect the movements and turbulence of their prey [k]. Finally, significant displacement might increase the chance of encounters with predators.
- Are ecologists of reef fish overestimating the importance of swimming capabilities to dispersal? Fisher and Bellwood [l] have recently found that the sustainable swimming time decreases exponentially with increasing speed. They suggest that the abilities of larvae to avoid advection are limited to speeds below a threshold that can be maintained for a period of between 12 and 48 h. This is 7 cm s⁻¹ in the late-stage larvae of the damselfish *Amphiprion melanopus* or 50% of its U-crit (maximum swimming speed maintained for 2–5 min). U-crit in late-stage larvae of other species is 30 cm s⁻¹ on average (n = five species, [d,m]) and 4.7 cm s⁻¹ in newly hatched larvae (n = three species [d]). This suggests that currents of 7 cm s⁻¹ that last more than 12–48 h might not be overcome by late-stage larvae of *A. melanopus*; for other species, on average, late-stage larvae might be able to overcome currents slower than 15 cm s⁻¹, whereas early-stage larvae might cope with currents of only 2.4 cm s⁻¹. A substantial component of the spectrum of current

speeds that are likely to be encountered by larvae (5–60 cm s⁻¹ is usual) will be too strong to be actively resisted, even if the larvae could orient themselves to swim against it.

- There are also problems inherent to behavioral research, because behavior is a particularly labile characteristic of an animal's phenotype. Are larvae that were caught, held overnight and then placed into experimental apparatus or back in the ocean with divers in attendance likely to behave as they do naturally?
- Our final concern is about data interpretation. At present, all larval behaviors have been analysed with reference to dispersal. However, navigation to locate settlement places is just one although the final crucial objective of a larva during its pelagic stage. Larvae must also swim and orient towards food and away from predators.

References

- Leis, J.M. and McCormick, M.I. (2002) The biology, behavior, and ecology of the pelagic larval stage of coral reef fishes. In *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem* (Sale, P.F., ed.), pp. 171–199, Academic Press
- Leis, J.M. and Stobutzki, I.C. (1997) Swimming performance of late pelagic larvae of coral-reef fishes: *in situ* and laboratory-based measurements. *Proc. 5th Indo-Pac. Fish. Conf.* 1, 575–583
- Dudley, B. *et al.* (2000) swimming ability of the larvae of some reef fishes from New Zealand waters. *Mar. Freshw. Res.* 51, 783–787
- Fisher, R. *et al.* (2000) Development of swimming abilities in reef fish larvae. *Mar. Ecol. Progr. Ser.* 202, 163–173
- Myrberg, A.A., Jr and Fuiman, L.A. (2002) The sensory world of coral reef fishes. In *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem* (Sale, P.F., ed.), pp. 123–148, Academic Press
- Leis, J.M. *et al.* (2002) Sound detection *in situ* by the larvae of a coral-reef damselfish (Pomacentridae). *Mar. Ecol. Progr. Ser.* 232, 259–268
- Montgomery, J.C. *et al.* (2001) Active habitat selection by pre-settlement reef fishes. *Fish Fisheries* 2, 261–277
- Fisher, R. and Bellwood, D.R. (2001) Effects of feeding on the sustained swimming abilities of late-stage larval *Amphiprion melanopus*. *Coral Reefs* 20, 151–154
- Stobutzki, I.C. (1997) Energetic cost of sustained swimming in the late pelagic stages of reef fishes. *Mar. Ecol. Progr. Ser.* 152, 249–259
- McCormick, M. (1998) Condition and growth of reef fishes at settlement: is it important? *Aust. J. Ecol.* 23, 258–264
- Nielson, J.D. and Perry, R.I. (1990) Diel vertical migrations of marine fishes: an obligate or facultative process? *Adv. Mar. Biol.* 26, 115–168
- Fisher, R. and Bellwood, D.R. (2002) The influence of swimming speed on sustained swimming performance of late-stage reef fish larvae. *Mar. Biol.* 140, 801–807
- Stobutzki, I.C. and Bellwood, D.R. (1994) An analysis of the sustained swimming abilities of pre and postsettlement coral reef fishes. *J. Exp. Mar. Biol. Ecol.* 175, 275–286

In interpreting genetic data, it is also important to consider the forces that are influencing genetic structure. A common assumption is that genetic structure reflects a balance between gene flow and drift. Yet, selection can be a major force maintaining genetic differentiation even when gene flow is occurring [31]. In coral reef fish, rates of mortality are high, with up to 70% occurring during the first few days after SETTLEMENT [32]. This mortality is, in many cases, associated with variations in attributes, such as body condition [33], size [32], and possibly speed [34], and with habitat characteristics [35], suggesting that there might be substantial and differential selection among populations at and shortly after settlement. In fact, comparative studies between allozymes (selective markers) and mtDNA (neutral markers) show different results [1,2,30] suggesting that there

are effects of selection on allozymes and raising caution when interpreting data based on these markers (currently 73% of the available data for reef fish [2]). Thus, genetic differentiation might support the existence of CLOSED POPULATIONS (genetic differences arising through drift) or open ones (genetic differences arising because of differential selection in spite of gene flow). Genetic differences might also suggest the existence of barriers to dispersal, even though populations on each side of the barrier remain otherwise open [36,37].

At equilibrium (no selection included), as few as 1–10 effective migrants per generation will eliminate genetic differences between populations with 95% confidence [1–2]. Thus, genetic similarity among populations might suggest either that populations are broadly open (with substantial migration), or largely

Box 2. Vertical migration of larvae and consequences for larval dispersal

Reef fish larvae have been suggested to respond behaviorally to vertically stratified flows in ways that result in retention close to shore and to the source population (Box 3, [a]). This suggests that vertical migration is a response to different current directions at different depths. Certainly, many other physical or biological stimuli (e.g. light, temperature, food availability and predation) have been proposed to explain vertical migrations in fish larvae [b–c] and, in these cases, resulting horizontal displacement because of vertical migration would be random, depending on local currents.

There are two ways in which vertical migration could result in predictable horizontal transport. Either the species lives predominantly in regions where vertically stratified flows are a widespread and consistent feature that reliably transport water at specific depths towards shore, or the animal has the capacity to measure current directions and act accordingly. In the first case, evolution of a fixed pattern of vertical migration is probable, regardless of the cue used, and results in reliable transport (perhaps back to the natal shore). In the second case, more flexible migration behavior could be used, the larva positioning itself in the layer of water travelling in the preferred direction. Although, this second case is seductive, it requires much of the larva. There are no fixed references in the pelagic realm, so the larva would need the equivalent of a geographical positioning system plus knowledge of where to go. Such a navigation system might exist, but there is not yet evidence for it. Still, the recent discoveries of a magnetic receptor in a fish [d], and geomagnetic orientation in several vertebrates, suggest that there might be a common and sophisticated mechanism of orientation among these animals [e].

Even if vertical migration is an adaptive response used by larvae to return home, it does not appear to be a widespread adaptation among reef fish. Vertical distributions are diverse among species. Some species

can be homogeneously distributed throughout the water column [c,f], whereas others present aggregated distribution at particular depths, sometimes depending upon the THERMOCLINE [b,f]. Finally, premises about vertical migration require some caution, because they are based on quite limited field studies of larval distributions. Reliable data about larval distributions are few because reef fish larvae are usually sparse, they are difficult to sample, no sampling device can capture all developmental stages [f], and few studies have used multiple sampling devices. Most standard sampling designs also appear to underestimate the abundance of larvae in offshore locations [g].

References

- a Cowen, R.K. (2002) Larval dispersal and retention, and consequences for population connectivity. In *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem* (Sale, P.F., ed.), pp 149–170, Academic Press.
- b Nielson, J.D. and Perry, R.I. (1990) Diel vertical migrations of marine fishes: an obligate or facultative process? *Adv. Mar. Biol.* 26, 115–168
- c Hendriks, I.E. *et al.* (2001) Vertical distributions of late stage larval fishes in the nearshore waters of the San Blas Archipelago, Caribbean Panama. *Coral Reefs* 20, 77–84
- d Diebel, C.E. *et al.* (2000) Magnetite defines a vertebrate magnetoreceptor. *Nature* 406, 299–302
- e Brown, K. (2001) Animal magnetism guides migration. *Science* 294, 283–284
- f Leis, J.M. (1991) The pelagic stage of reef fishes: the larval biology of coral reef fishes. In *The Ecology of Fishes on Coral Reefs* (Sale, P.F., ed.), pp. 183–230, Academic Press
- g Clarke, T.A. (1995) Larvae of near-shore fishes in oceanic waters of the central equatorial Pacific. *Pac. Sci.* 49, 134–142

closed (genetic similarities arising because of the exchange of only a few individuals). Although the growing numbers of genetic studies on coral reef species suggest that dispersal is not usually as extensive as has been believed [2], answers using genetic data are not yet conclusive. More studies, particularly with rapidly evolving markers, are needed.

Larval behavior

Recent studies have highlighted the fascinating and diverse spectrum of behavior in reef fish larvae. Larvae of coral reef fish have good swimming abilities and sensory systems that enable them to control their dispersal (Box 1, [9–14]). However, it is not yet known whether they do this, and if they do, whether they use their abilities to enhance retention or dispersal.

Although there is a clear need to include larval behaviors when modelling larval dispersal [11–13,38], it is also clear that larval behavior (and other biological data) exhibits substantial interspecific variability. For instance, the pelagic period ranges among species from >100 to <10 days, and a handful of species lack it completely [10,39]. Swimming abilities also vary broadly among species (Box 1). Furthermore, swimming abilities, sensory systems and behaviors, such as vertical migration (Box 2), all develop during the larval period [10,39–41], so that even species with appropriate dispersal behavior achieve this capability at different ages, and have a period of passivity early in their life. Given the large set of physical oceanographical features with advective and retentive characteristics (Box 3), this behavioral variability ensures that the extent to

which larvae are retained will vary among locations (because of spatial differences in oceanographical conditions), and among species within a locality (because of interspecific variability in responses to the physical environment). Recognition of this cross-species and cross-locality variation must be part of the debate on the nature of dispersal in reef fish [42–44].

Dispersal models

In the absence of a direct way to track reef fish larvae through their entire pelagic phase, modelling approaches have been used to infer patterns of larval dispersal [5,22,45]. By considering the complex set of variables affecting the larval period (Fig. 1), models can be used to explore the importance of particular features, and to make predictions about larval dispersal. Nevertheless, a characteristic common to most models to date is the omission, or gross simplification in modelling of many factors affecting the larval period, with the result that model outputs cannot yet be assumed to predict dispersal accurately. Roberts' [5] model, for instance, has been strongly criticized, because it did not include larval behaviors, such as swimming ability [43] or vertical migration [44]. Schultz and Cowen [45] included larval duration as a variable in their model, but did not consider larval swimming abilities. Capable swimmers could either enhance or reduce ADVECTION effects owing to other model components [12]. Cowen *et al.* [22] included values for diffusion based on passive particles, but the larvae of many reef fish species have demonstrated some ability to aggregate actively in the pelagic

Box 3. Oceanographic features and potential consequences for larval dispersal

Although oceanographers cannot yet specify the patterns of water movement in close proximity to complex topography, such as reefs, there is a range of small to mesoscale oceanographic features that provide opportunities for predictable transport of larval fish.

- Eddies (rotary currents) can form downstream of reefs and can aggregate buoyant particles and prevent broad dispersal. Within such eddies, reef fish larvae have been found in large abundance at some locations (e.g. Florida Keys [a], Hawaii [b] and Johnston Atoll [c]) but not at others (e.g. Myrmidon Reef, Great Barrier Reef [d]). Such eddies also vary in their persistence (e.g. a few days at Johnston Atoll or several months in the Florida Keys), further suggesting that the influence of eddies on larval dispersal will vary.
- Upwelling systems are probably important if the larvae exhibit vertical migrations. An upwelling occurs usually where winds move superficial water in an offshore direction and as a result deep water flows in an opposite onshore direction. By descending in the water column, advected larvae can be returned to the reefs. However, because reef fish species vary in vertical migration behavior (Box 2), the effects of upwellings on patterns of larval dispersal are species-specific. Moreover, because similar physical processes can result in downwellings (when superficial waters move onshore), an inflexible larval response to depth can also result in advection.
- Surface slicks resulting from convergence zones created by complex interactions involving the thermocline, internal waves, opposing currents and winds might also affect larval dispersal [e]. Converging currents can accumulate organisms around slicks that flow in the direction of the wind. Such circumstances can act to accumulate diffused larvae offshore into aggregate lines that flow onshore [e],

or alternatively prevent diffusion of eggs and larvae and move them from onshore to offshore localities.

- Currents flowing along the coast can disperse larvae of a given population along the coast reinforcing advection or can generate peripheral eddies that entrain fish larvae and favor retention [f–h].

References

- Lee, T.N. *et al.* (1994) Evolution of the Tortugas gyre and its influence on recruitment in the Florida Keys. *Bull. Mar. Sci.* 54, 621–646
- Lobel, P.S. and Robinson, A.R. (1986) Transport and entrapment of fish larvae by ocean mesoscale eddies and currents in Hawaiian waters. *Deep-Sea Res.* 33, 483–500
- Boehlert, G.W. *et al.* (1992) Horizontal and vertical distribution of larval fishes around an isolated oceanic island in the tropical Pacific. *Deep-Sea Res.* 39, 439–466
- Williams, D.M. and English, S. (1992) Distribution of fish larvae around a coral reef: direct detection of meso-scale, multi-specific patch? *Cont. Shelf Res.* 12, 923–937
- Kingsford, M.J. and Choat, J.H. (1986) Influence of surface slicks on the distribution and onshore movements of small fish. *Mar. Biol.* 91, 161–171
- Hutchins, J.B. and Pearce, A.F. (1994) Influence of the Leeuwin current on the recruitment of tropical reef fishes at Rottneest Island, western Australia. *Bull. Mar. Sci.* 54, 245–255
- Limouzy-Paris, C.B. *et al.* (1997) Translocation of larval coral reef fishes via sub-mesoscale spin-off eddies from the Florida current. *Bull. Mar. Sci.* 60, 966–983
- Possingham, H.P. and Roughgarden, J. (1990) Spatial population dynamics of a marine organism with a complex life cycle. *Ecology* 71, 973–985

environment [10,17]. In this case, the pattern of diffusion could be very different to that modelled under passive dispersal [46]. Cowen *et al.* [22] also had to estimate larval mortality rates. Although larval mortality is generally assumed to be high, there are very few empirical data available. That larvae of reef fish can be collected several 100 km away from the nearest reef [47–49] proves that some fish larvae survive and do disperse far into the ocean, in numbers

that are sufficient to show up in small plankton nets [3]. The model developed by Cowen *et al.* does not show this, which suggests either that the model might be unrealistic or that the distribution of larvae in open waters is far patchier than has been supposed.

The difficulty of simulating the complex world in which larvae move (Fig. 1) explains many of the discrepancies between empirical data and model predictions. For instance, Roberts [5] predicted a general pattern of larval dispersal over long distances, based on very simple models of long-term average surface currents in the Caribbean. This pattern was directly contradicted by the known pattern of spread of the *Diadema* pathogen in this region [50] suggesting that, because the pathogen was presumably passively dispersed, even a model of passive dispersal requires more detailed hydrodynamics than that used by Roberts [44]. Cowen *et al.* [22] built a more complex physical model of circulation in the eastern Caribbean coupled to estimates of larval mortality and diffusion, and predicted that the concentration of larvae falls essentially to zero at a distance of only 140 km from the larval source. They argued that this indicates that substantial dispersal of larvae is unlikely, although other studies have shown that long-distance dispersal does sometimes occur [47–49]. The problem of modelling the physical environment adequately is also shown in a recent study that compared local concentrations of coral larvae observed around Bowden Reef (Great Barrier Reef) with concentrations predicted from a model of dispersal using the local hydrography [51]. Coral larvae are passively

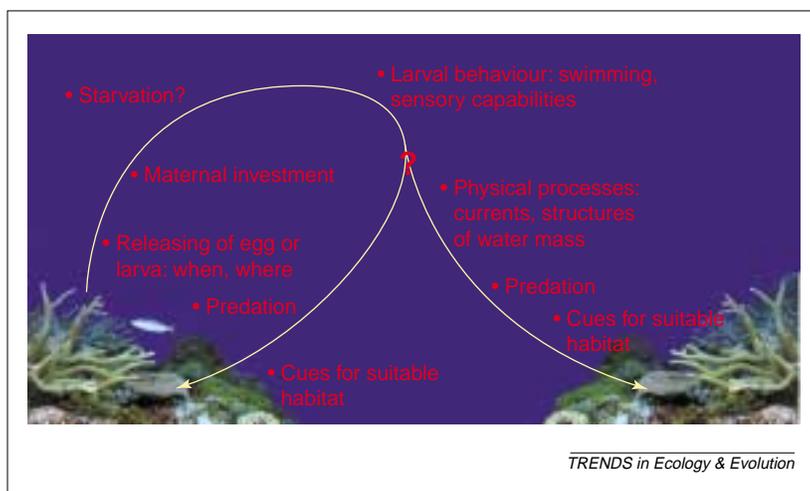


Fig. 1. Factors affecting larval dispersal. The path taken by a larva might lead to it returning to the natal reef or dispersing to a more or less distant site. The path taken is determined by a mix of factors, which act synergistically over the larval period to determine the dispersal of each member of a larval cohort. Where and when eggs or larvae enter the water column, their quality, and the food resources and predators that they encounter will affect survival, condition and growth rates. Condition and growth rates will determine the development of swimming and sensory abilities, and these will determine how larvae respond to the physical environment and to any cues from reefs. We can predict considerable variation among cohorts and locations in the paths travelled, as well as among species, but we cannot yet do much more. We lack information on most of the factors operating.

Glossary

Advection: the passive dispersal of larvae away from a natal site due to entrainment in a moving parcel of water caused by a physical process such as a current, or an upwelling.

Closed population: a population that receives its recruitment primarily as larvae produced from spawning activity by its own residents.

Closure: a population achieves closure when the life cycles of its members are such that offspring remain within it, or return to become members of the reproductive unit.

Connectivity: the demographic connection maintained between neighboring populations of a species due to the migration of individuals (particularly dispersing larvae) between them.

Convergence zone: a zone in a water body where two currents come together. It is usually marked by a surface of complex ripples and accumulated flotsam. A downwelling region may lie below this surface sign.

Dispersal: the movement of individual organisms away from a starting location, such as the site where they were spawned. Dispersal may be passive or active.

Open population: a population that receives its recruitment primarily as larvae produced by spawning in other, neighboring or distant, populations.

Recruitment: the addition of a new cohort to a population, or the new cohort that was added. Magnitude of recruitment depends on the time, and life history stage at which it is recorded.

Retention: avoidance of dispersal from a natal site either due to specific hydrographical features, or by active behavioral processes used by the larvae.

Self-recruitment: the new cohort added to a population (recruitment) consists largely, or entirely of larvae spawned by that population. Sometimes termed endogenous recruitment.

Settlement: the action of moving from the pelagic realm of open water to the demersal habitat. Settlement occurs at a distinct time in the life cycle of coral reef fish, and is usually closely associated with metamorphosis from larval to juvenile form.

Thermocline: the layer of a water body exhibiting a pronounced temperature gradient, and separating the upper epilimnion from the lower hypolimnion.

dispersed at the surface, yet this study found virtually no correlation between these two data sets. Modelling is an important technique that is capable of yielding novel insights, but we need to be aware of the limitations of models, and of our limited knowledge of the factors that they model.

Other approaches

The temporal link between local production of propagules (spawning) and subsequent recruitment has also been used to deduce the pattern of dispersal leading to recruitment at particular locations. The rationale for this approach is that, if larvae are exogenous, local patterns of spawning will not be correlated with local recruitment, whereas if larvae are self-recruited, patterns of spawning and recruitment should be coupled [52]. Although the relation between spawning and recruitment has been explored extensively [53], using this relationship to infer the pattern of dispersal is novel [52].

Examples showing coupling or lack of coupling between spawning and recruitment are broadly reported [53]; however, what these tell us about dispersal is unclear. Coupling of spawning and recruitment patterns might result when spawning is synchronized closely over a broad spatial scale, even if recruits are dispersed widely. Such large-scale synchrony in reproduction might occur for reef fish that spawn at similar times (i.e. specific moon phases [54]) at many locations. Neither does decoupling inevitably imply broad dispersal. Danilowicz and Sale [55] used a model to show how plausible patterns of mortality during larval life can decouple local production and subsequent recruitment even when recruitment is entirely endogenous. The presumed

link between spawning and recruitment will not easily advance our understanding of dispersal.

Observations of colonization of previously unoccupied areas (e.g. Eastern Pacific localities by Indo-Pacific species during El Niño events [56]), or of recruitment of fish after rafting in association with floating objects [57], demonstrate larval advection and prove the existence of OPEN POPULATIONS. Because of the long distances travelled in these cases, these events might have an important role in determining genetic connectivity and/or processes of speciation in reef fish. However, because they are relatively rare events, they probably do not contribute markedly to the replenishment of fish populations. Conversely, the existence of endemic species on remote archipelagos confirms that at least some fish populations achieve sufficient local recruitment to maintain their densities [58]. Of course, endemic species might still be structured as open systems within the local region in which they occur [52].

Passive drifters have been used extensively to suggest potential trajectories of larval transport. They reveal considerable complexity in the paths that are possible when several drifters are released simultaneously at a single site. However, because such devices ignore larval behaviors, and because these behaviors are considerable in many species (Box 1), drifter studies seem unlikely to be useful in defining paths travelled by larvae.

Conclusion and future directions

Among reef fish ecologists, the perception of reef fish populations as broadly open systems has shifted to a currently widespread emphasis on the retention of larvae at natal reefs. This dramatic shift has been made with important but as yet limited new evidence. Our review of evidence concerning reef fish dispersal shows that these limitations are serious and that, at present, the answer to whether reef fish populations are open or closed must be regarded as unknown. We can go further and state with confidence that there is not one answer. Different species in different places will be structured into more or less open populations depending on the capabilities of the species, the physical features of its environment, and the spatial and temporal scales at which the question is posed.

Our uncertainty about patterns of larval dispersal reveals a crucial gap in knowledge of coral reef fish. Apart from the intrinsic interest in the capabilities of these animals, if marine protected areas (MPAs) are to have any impact on conserving these species, or the management of fisheries based upon them, we need to know more about the spatial and temporal scales at which populations function, and the extent of connectivity among populations. Otherwise, there is no biological basis on which to decide the size, positioning, or number of MPAs that are required to protect these species.

In addition to new work using microchemical, genetic and other novel tagging approaches for

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defining the scales (both in space and time) and extent of larval dispersal among populations, major efforts are required to expand our knowledge of the behaviors that are actually used, and the cues to which reef fish respond during their larval period. The work completed is a good beginning, and the challenges in extending it are many, but scientists

and funding agencies must see this as a crucial area of research and support it accordingly. Finally, we need to encourage multi-investigator, multidisciplinary approaches combining physical oceanography, larval behavior, tagging studies and sophisticated modelling approaches, because this gap in knowledge cannot be filled by one approach alone.

References

- 1 Shulman, M.J. (1998) What can population genetics tell us about dispersal and biogeographic history of coral-reef fishes. *Aust. J. Ecol.* 23, 216–225
- 2 Planes, S. (2002) Biogeography and larval dispersal inferred from population genetic analysis. In *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem* (Sale, P.F., ed.), pp 201–220, Academic Press
- 3 Victor, B.C. and Wellington, G.M. (2000) Endemism and the pelagic larval duration of reef fishes in the eastern Pacific Ocean. *Mar. Ecol. Progr. Ser.* 205, 241–248
- 4 Caley, M.J. *et al.* (1996) Recruitment and the local dynamics of open marine populations. *Annu. Rev. Ecol. Syst.* 27, 477–500
- 5 Roberts, C.M. (1997) Connectivity and management of Caribbean coral reefs. *Science* 278, 1454–1457
- 6 Jackson, J.B.C. *et al.* (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–637
- 7 Roberts, C.M. *et al.* (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* 295, 1280–1284
- 8 Williams, D.M. *et al.* (1984) Transport mechanisms and potential movement of planktonic larvae in the central region of the Great Barrier Reef. *Coral Reefs* 3, 229–236
- 9 Kingsford, M.J. *et al.* Sensory environments, larval abilities and local self-recruitment. *Bull. Mar. Sci.* (in press)
- 10 Leis, J.M. and McCormick, M.I. (2002) The biology, behavior, and ecology of the pelagic, larval stage of coral reef fishes. In *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem* (Sale, P.F., ed.), pp. 171–199, Academic Press
- 11 Armsworth, P.R. *et al.* (2001) When to press on or turn back: dispersal strategies for reef fish larvae. *Am. Nat.* 157, 434–450
- 12 Armsworth, P.R. (2000) Modelling the swimming response of late stage larval reef fish to different stimuli. *Mar. Ecol. Progr. Ser.* 195, 231–247
- 13 Stobutzki, I.C. (2000) Marine reserves and the complexity of larval dispersal. *Rev. Fish Biol. Fish.* 10, 515–518
- 14 Leis, J.M. and Stobutzki, I.C. (1997) Swimming performance of late pelagic larvae of coral-reef fishes: *in situ* and laboratory-based measurements. *Proc. 5th Indo-Pac. Fish. Conf.* 1, 575–583
- 15 Warner, R.R. and Cowen, R. Local retention of production in marine populations: evidence, mechanisms, and consequences. *Bull. Mar. Sci.* (in press)
- 16 Cowen, R.K. (2002) Larval dispersal and retention and consequences for population connectivity. In *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem* (Sale, P.F., ed.), pp. 149–170, Academic Press
- 17 Warner, R.R. *et al.* (2000) Larval accumulation and retention: Implications for the design of marine reserves and essential fish habitat. *Bull. Mar. Sci.* 66, 821–830
- 18 Jones, G.P. *et al.* (1999) Self-recruitment in a coral reef fish population. *Nature* 402, 802–804
- 19 Swearer, S.E. *et al.* (1999) Larval retention and recruitment in an island population of a coral-reef fish. *Nature* 402, 799–802
- 20 Sinclair, M. (1988) *Marine Populations: An Essay on Population Regulation and Speciation*, Washington Sea Grant
- 21 Strathmann, R.R. *et al.* Evolution of local retention and its consequences for marine populations. *Bull. Mar. Sci.* (in press)
- 22 Cowen, R.K. *et al.* (2000) Connectivity of marine populations: open or closed. *Science* 287, 857–859
- 23 Planes, S. *et al.* (1998) Genetic evidence of closed life-cycles for some coral reef fishes within Taiaroa lagoon (Tuamotu Archipelago, French Polynesia). *Coral Reefs* 17, 9–14
- 24 Bernardi, G. *et al.* (2001) Gene flow at three spatial scales in a coral reef fish, the three-spot dacyllus, *Dacyllus trimaculatus*. *Mar. Biol.* 138, 457–465
- 25 Planes, S. *et al.* (1998) Genetic analysis of population structure in relation with larval duration in three species of coral reef fishes from New Caledonia. *Mar. Biol.* 130, 361–368
- 26 Milicich, M.J. (1994) Dynamic coupling of reef fish replenishment and oceanographic processes. *Mar. Ecol. Progr. Ser.* 110, 135–144
- 27 Leis, J.M. (1986) Vertical and horizontal distributions of fish larvae near coral reefs at Lizard Island, Great Barrier Reef. *Mar. Biol.* 90, 505–116
- 28 Caselle, J.E. and Warner, R.R. (1996) Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. *Ecology* 77, 2488–2504
- 29 Palumbi, S.R. (1999) The prodigal fish. *Nature* 402, 733–735
- 30 Avise, J.C. (1994) *Molecular Markers, Natural History and Evolution*, Chapman & Hall
- 31 Williams, G.C. *et al.* (1973) Genetic differentiation without isolation in the American eel, *Anguilla rostrata*. *Evolution* 27, 192–204
- 32 Mora, C. and Zapata, F. Effects of a predatory fish on early post-settlement abundance and body size of reef fishes from Gorgona Island, Colombia. *Proc. 9th Int. Coral Reef Symp. Bali, Indonesia* (in press)
- 33 McCormick, M. (1998) Condition and growth of reef fishes at settlement: is it important? *Aust. J. Ecol.* 23, 258–264
- 34 Leis, J.M. and Carson-Ewart, B.M. (2001) Behaviour of pelagic larvae of four coral-reef fish species in the ocean and an atoll lagoon. *Coral Reefs* 19, 247–257
- 35 Beukers, J.S. and Jones, G.P. (1997) Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114, 50–59
- 36 Davis, B.J. *et al.* (1981) Gene flow among populations of a teleost (Painted Greenling, *Oxylebius pictus*) from Puget Sound to southern California. *Mar. Biol.* 65, 17–23
- 37 Terry, A. *et al.* (2000) Restricted gene flow and incipient speciation in disjunct Pacific Ocean and Sea of Cortez populations of a reef fish species, *Girella nigricans*. *Evolution* 54, 652–659
- 38 Wolanski, E. *et al.* (1997) Directional swimming of fish larvae determines connectivity of fish populations on the Great Barrier Reef. *Naturwissenschaften* 84, 262–268
- 39 Leis, J.M. (1991) The pelagic stage of reef fishes: the larval biology of coral reef fishes. In *The Ecology of Fishes on Coral Reefs* (Sale, P.F., ed.), pp. 183–230, Academic Press
- 40 Fisher, R. *et al.* (2000) Development of swimming abilities in reef fish larvae. *Mar. Ecol. Progr. Ser.* 202, 163–173
- 41 Job, S. and Bellwood, D.R. (2000) Light sensitivity of larval fishes: implications for vertical zonation in the pelagic zone. *Limnol. Oceanogr.* 45, 362–371
- 42 Roberts, C.M. (1998) Fishery and reef management. *Science* 279, 2022–2023
- 43 Bellwood, D.R. *et al.* (1998) Fishery and reef management. *Science* 279, 2021
- 44 Sale, P.F. and Cowen, R.K. (1998) Fishery and reef management. *Science* 279, 2022
- 45 Schultz, E.T. and Cowen, R.K. (1994) Recruitment of coral-reef fishes to Bermuda: local retention or long distance dispersal. *Mar. Ecol. Progr. Ser.* 109, 15–28
- 46 Okubo, A. (1980) *Diffusion and Ecological Problems: Mathematical Models*, Springer-Verlag
- 47 Leis, J.M. (1984) Larval fish dispersal and the east Pacific Barrier. *Oceanogr. Trop.* 19, 181–192
- 48 Victor, B.C. (1987) Growth, dispersal, and identification of planktonic labrid and pomacentrid reef-fish larvae in the eastern Pacific Ocean. *Mar. Biol.* 95, 145–152
- 49 Clarke, T.A. (1995) Larvae of near-shore fishes in oceanic waters of the central equatorial Pacific. *Pac. Sci.* 49, 134–142
- 50 Lessios, H.A. *et al.* (1984) Spread of *Diadema* mass mortality through the Caribbean. *Science* 226, 335–337
- 51 Oliver, J.K. *et al.* (1992) Dispersal of coral larvae from a lagoonal reef: II comparisons between model predictions and observed concentrations. *Cont. Shelf Res.* 12, 873–889
- 52 Danilowicz, B.S. (1997) A potential mechanism for episodic recruitment of a coral reef fish. *Ecology* 78, 1415–1423
- 53 Meekan, M.G. *et al.* (1993) Larval production drives temporal patterns of larval supply and recruitment of a coral reef damselfish. *Mar. Ecol. Progr. Ser.* 93, 217–225
- 54 Robertson, D.R. *et al.* (1988) Temporal coupling of production and recruitment of larvae of a Caribbean reef fish. *Ecology* 69, 370–381
- 55 Danilowicz, B.S. and Sale, P.F. (1999) Modelling settlement in open populations of reef fishes. *Ecol. Model.* 121, 261–276
- 56 Robertson, D.R. and Allen, G.R. (1996) Zoogeography of the shore fishes fauna from Clipperton Atoll. *Coral Reefs* 15, 121–131
- 57 Mora, C. *et al.* (2001) Dispersal of juvenile and adult reef fishes with floating objects and their recruitment into Gorgona Island reefs. *Bull. Mar. Sci.* 68, 557–561
- 58 Robertson, D.R. (2001) Population maintenance among tropical reef fishes: inferences from small-island endemics. *Proc. Natl. Acad. Sci. U. S. A.* 98, 5667–5670