The structure of reef fish metapopulations: modelling larval dispersal and retention patterns

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An improved understanding of the dispersal patterns of marine organisms is a prerequisite for successful marine resource management. For species with dispersing larvae, regional-scale hydrodynamic models provide a means of obtaining results over relevant spatial and temporal scales. In an effort to better understand the role of the physical environment in dispersal, we simulated the transport of reef fish larvae among 321 reefs in and around the Cairns Section of the Great Barrier Reef Marine Park over a period of 20 years. Based on regional-scale hydrodynamics, our models predict the spatial and temporal frequency of significant self-recruitment of the larvae of certain species. Furthermore, the results suggest the importance of a select few local populations in ensuring the persistence of reef fish metapopulations over regional scales.

Keywords: marine metapopulations; reef fishes; larval dispersal; self-recruitment; marine resource management

1. INTRODUCTION

Many marine organisms undergo a pelagic larval stage, during which they are exposed to ocean currents and can disperse substantial distances. By contrast, adults of many species have more restricted home ranges associated with particular substrate types. These organisms are distributed in metapopulations with dispersing larvae connecting local adult populations. Reef fishes typify such benthic–pelagic life histories. Almost all reef fishes have a pelagic larval stage lasting weeks to months. Adults are relatively territorial and are associated with particular reef habitats that are patchily distributed. Larval dispersal patterns are poorly understood, and the extent to which particular local populations within a larger metapopulation are closed (self-replenishing) or open (dependent on recruits from elsewhere) is unknown. Improved knowledge of dispersal patterns is a prerequisite for understanding the ecology and evolution of marine species (Holt & Gaines 1992; Caley *et al.* 1996; Warner 1997; Robertson 2001; Strathmann *et al.* 2002). This knowledge will prove important for the conservation of these species (Dayton *et al.* 1995; Allison *et al.* 1998) and the successful management of fisheries (Carr & Reed 1993; Tuck & Possingham 1994, 2000; Sanchirico & Wilen 1999; Russ 2002).

We use regional-scale hydrodynamic models to explore possible influences of the physical environment on reef fish larval dispersal in the Great Barrier Reef (GBR), Australia. The GBR comprises a geometrically complex and densely packed assemblage of reef structures on the shallow continental shelf off the east Australian coast (figure 1). Our study region lies in the northern half of the GBR,

and includes the management unit known as the Cairns Section.

Recent field experiments report significant levels of self-recruitment for some reef fishes (Jones *et al.* 1999; Swearer *et al.* 1999). In our study region, the mark–recapture experiment by Jones *et al.* examined the level of self-recruitment in *Pomacentrus amboinensis* (Pomacentridae) at Lizard Island in 1994. Those authors estimated that 15–60% of settling recruits of this demersally spawning damselfish were returning to their reef of origin. More extensive data on larval dispersal paths do not exist for our study region, although one might draw inferences about larval dispersal from available records on juvenile and adult abundance. For example, Williams *et al.* (1986) and Sweatman *et al.* (2001) recorded persistent cross-shelf species zonation patterns. However, it remains unclear whether such patterns are driven by larval dispersal or by differing ecological requirements of later life stages.

Obviously, any model results depend upon the physical and biological assumptions made. We investigate the sensitivity of our main conclusions with respect to some of our assumptions and find those conclusions to be relatively robust. However, there is much uncertainty regarding larval biology and behaviour. Given this uncertainty, it is our intention that the models only examine the role of the physical environment in determining dispersal potential. Our goal is to understand the challenge posed to spawning adults and dispersing larvae by the current regime around reefs, a challenge which their behaviour must overcome to allow a successful return to benthic habitats.

2. METHODS

(a) *Dispersal model*

We simulated dispersal of larvae from all reefs between latitudes 14 and 19° S in the northern GBR, with spawning taking

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place from October to December for the years 1977–1996. Approximately 240 million larval trajectories were simulated (12 million per season). Intensive replication was necessary to account for the extreme variability observed in simulated dispersal patterns.

Water currents in the GBR are forced by the tides, wind and oceanic influences of the seasonally varying East Australian Current (EAC). A numerical hydrodynamic model (Bode & Mason 1994) was used to compute the two-dimensional depth-integrated current field for the shelf-reef complex. Our modelling used all the available physical data for the region, including information on the structure and variability of currents in the Coral Sea. These data include current records from an array of off-shelf moorings maintained for more than a decade (Steinberg & Burrage 2000). Current meter data on the shelf are more limited. We used a three year record from Lark Reef (145°35' E; 15°17' S) to calibrate the low frequency currents. The historical wind record at Low Isles (145°34' E; 16°23' S) from 1977 to 1996 provides the wind field used to force the model in a spatially uniform manner. Currents were computed for the summer spawning season (October–February) each year. The model's grid resolution is one nautical mile, with a time-step of 30 min. A parameterization scheme (Bode *et al.* 1997) accounts for sub-grid-scale hydrodynamics associated with reef structures.

A total of 321 reefs are considered, 199 of which are within the Cairns Section. The remainder are located to the north or south of the Section, and allow for larvae that may be transported into this region from outside. The northern boundary of the model was placed near a large reef that straddles much of the shelf, and inhibits alongshore flow (see figure 1). Both prevailing wind-driven currents and the EAC flow northward here, and we anticipate minimal transport into the study region across this boundary. The southern model boundary was placed approximately one degree of latitude south of the southern limit of the Cairns Section.

We use a larval tracking model to predict where a larva with a particular set of behavioural characteristics would disperse if exposed to the simulated current field. Larval trajectories are computed using a second-order Runge–Kutta algorithm. In this algorithm, individuals are advected by the current velocity at their present position, obtained by bilinear interpolation of the velocities at the neighbouring grid points. No explicit horizontal eddy diffusion (e.g. via a random walk applied to individuals) is invoked. The model's spatial resolution is sufficiently fine for significant eddy formation and horizontal mixing to occur around reefs. Modelling studies by Parslow & Gabric (1989) also suggest that temporary trapping of particles near reefs contributes far more to the spread of initially compact patches than does any physically realistic level of imposed horizontal diffusion.

(b) *Biological assumptions*

Results are presented for a baseline case, and for variations to model parameters that illustrate the sensitivity of the principal conclusions to uncertainty in those factors. For all simulations, the spawning habitat was defined as a 100 m wide margin around the hard crest of each reef. In the baseline study, spawning took place at each high tide during daylight hours. Some evidence (Johannes 1978; Doherty 1983; Colin & Bell 1991; Robertson 1991) suggests that reef fishes may spawn or hatch from demersal eggs at times that take advantage of ebbing tides for transport off-reef. Setting the spawning or hatching times at

high tide means that simulated larvae are initially exposed to ebbing tides. Simulations were also performed with the following spawning schedules: (i) each day at dusk; (ii) at dusk on the three days before and after the new moon; (iii) at high tide on the three days before and after the new moon; (iv) at dusk on the three days before and after the full moon; and (v) at dusk on the three days before and after the new and full moons.

Before acquiring swimming abilities, virtual larvae were assumed to reside in the mid-water column (as appears to be the case for some species and ages, at least during daylight hours; Leis 1991a) and to move with the computed two-dimensional depth-integrated current. After this initial 'passive' period, larvae were assumed to enter an 'active' stage during which they are able to swim strongly enough to approach a reef (Stobutzki & Bellwood 1994, 1997; Leis & Carson-Ewart 1997; Wolanski *et al.* 1997). A baseline passive period of 14 days was used, as would apply for *P. amboinensis* (Fisher *et al.* 2000). Results were also obtained for a passive period of seven days. During the active period, larvae were assumed able to settle for a further three weeks (baseline case) or six weeks.

Field evidence indicates that late-stage larvae of some species can detect the presence of a reef at a range of at least 1 km (Leis *et al.* 1996). For the baseline case, we defined a 'sensory zone' of this width around each reef, and any active larva that entered such a zone was assumed to approach that reef and to attempt to settle there. Results were also obtained for a sensory zone of 4 km. No special preference was given to the original reef as a site for settlement.

Few data exist on pelagic mortality rates of larvae. Cowen *et al.* (2000) review what data are available and obtained estimates ranging from 3 to 46% mortality per day, with a mode of 18%. In our simulations, larvae were subjected to an 18% mortality rate per day.

(c) *Format of results*

A set of seasonal 321×321 connectivity matrices, $A(t) = [a_{ij}(t)]$, was obtained from the dispersal model; $a_{ij}(t)$ measures the proportion of larvae spawned on reef i that subsequently settle on reef j in season t . The 20 connectivity matrices were used to compare simulated self-recruitment with the experimental results of Jones *et al.* (1999). We also addressed these more general questions.

- (i) Can one generalize across space or time from available experimental results and, in particular, how commonly should we expect a high degree of self-recruitment in reef fish species in this region?
- (ii) What is the potential importance of self-recruitment to regional metapopulation dynamics?

To simulate the self-recruitment of *P. amboinensis* at Lizard Island, a fixed but spatially varying adult abundance distribution was assumed, and this determined the distribution of spawning productivity. Field surveys (H. Sweatman, unpublished data; D. Williams, unpublished data) indicate that *P. amboinensis* is significantly less abundant on inshore and outer-shelf reefs in this part of the GBR than on mid-shelf reefs. We approximated this pattern by distributing relative spawning effort with a maximum of 1.0 on mid-shelf reefs, falling to 0.25 on inshore and outer-shelf reefs. We investigated question (i) by computing simulated self-recruitment, as the proportion of settling larvae that are self-recruiting, for all reefs in the Cairns Section, and examining its temporal and spatial variability.

To address question (ii), the connectivity matrices were used to drive a simple age-structured metapopulation model. This time the spawner distribution was determined endogenously by the metapopulation dynamics, rather than being stipulated. The metapopulation model uses a time-step of one year, and larval dispersal patterns in each season were given by a connectivity matrix randomly selected from the set of 20 base-line matrices. The model covers five age classes, with 80% survival from one class to the next. Individuals mature at two years. Per capita survivorship from arrival at a reef to the census at the end of the first year is specified by a compensatory density-dependent relationship:

$$\frac{N_1}{K_1} = \frac{bS}{1 + bS},$$

where S is the density of settling larvae and N_1 is the density of resulting recruits a year later. K_1 determines the asymptotic limit and b is a parameter that determines how quickly N_1 increases with S , in the pre-saturation phase. A growing body of evidence suggests that early post-settlement mortality can be directly density dependent in some reef fishes (Hixon & Carr 1997; Schmitt & Holbrook 1998; Hixon & Webster 2002). Parameter b was chosen to ensure that local populations were strongly limited by larval supply.

3. RESULTS

(a) Dispersal dynamics

An animation that illustrates typical dispersal dynamics is available at <http://mmu.jcu.edu.au/larvae.html>. Figure 2 shows a snapshot from this animation, taken six days after spawning from Opal, St Crispin, Undine and Rudder Reefs (spawning date 11 November 1984). Clouds of larvae that move into relatively open waters are advected substantial distances and can be subjected to extensive stretching and folding. However, a significant number of larvae are retained locally. Those that disperse through the reef matrix are broken up into a widespread, patchy distribution, whereas those advected through open waters remain more cohesive.

(b) Connectivity matrices

Sample connectivity matrices are shown in figure 3 for baseline parameters. Source and sink reefs are indexed by latitude along the axes. Points on the diagonal line represent the probabilities that an individual spawned on a given reef subsequently settles on that same reef. Relatively strong connections occur over short distances (up to ca. 1° of latitude), but weak connections are present over large distances (at least 5° of latitude). There is potential for significant self-seeding on certain reefs in at least some seasons. Connectivity appears to be generally stronger in the northern part of the study region than in the south. There is considerable spatial and temporal variation among the seasonal matrices. In some seasons, simulated transport is predominantly to the south (e.g. 1985, points above diagonal line); in other seasons (e.g. 1996), there is significant transport to the north as well (points below diagonal line).

(c) Open versus closed populations

The connectivity matrices predict the relative importance of self-recruitment and inter-reef dispersal. We

simulated the experiment of Jones *et al.* (1999), which measured the proportion of settling *P. amboinensis* at Lizard Island in 1994 that were self-recruiting. We predicted levels of self-recruitment of *P. amboinensis* at Lizard Island that are substantially above the average across all reefs in our study region (figure 4). The Lizard Island results peak at ca. 55% in 1994, the year in which Jones *et al.* (1999) obtained their estimate for self-recruitment in the range 15–60%.

Simulated self-recruitment exhibits considerable temporal variation. For all reefs in the Cairns Section, the coefficient of variation (CV) ranges from 0.036 to ca. 4.5, with a peak in the distribution near 0.75. Spatial variability is also substantial. Time averages of self-recruitment over the 20 seasons were computed for all reefs (figure 1) using the same parameters as for figure 4. Returning larvae comprised less than 10% of the settling cohort on most reefs. However, for certain reefs, simulated self-recruitment was consistently high. Figure 1 identifies reefs in the Cairns Section for which, on average, returning larvae comprised more than 20% of the settling cohort. Larger reefs tend to fall into this category. Large reefs contribute more than smaller reefs to the local larval pool, from which they subsequently sample. In addition, large reefs can cause greater distortions to the surrounding current field, and retention might be enhanced in 'shadow' zones in the lee of such reefs.

(d) Metapopulation dynamics

We examined persistence conditions for the age-structured metapopulation. The existence of at least some source reefs with a strong link between local stock and recruitment is believed to be of particular importance in allowing metapopulation persistence (Armsworth 2002). Our simulations indicate that only relatively few reefs have a consistently strong direct link between local stock and recruitment in the study region. To assess the potential importance of such reefs in allowing metapopulation persistence, we conducted a numerical deletion experiment. The undisturbed metapopulation fluctuates around a spatially structured equilibrium distribution. We identified, under equilibrium conditions, the 20 strongest self-seeding reefs (mean self-recruitment greater than 0.2, CV < 0.3) in the model domain (including some to the north and south of the Cairns Section). Note, again, that the strength of self-seeding was computed as the proportion of settling larvae that are self-recruiting. With this measure, strong self-seeding does not necessarily imply a large value of a_{ii} . We then conducted 20 replicate simulations of metapopulation dynamics when subpopulations on these 20 reefs were permanently removed. We repeated this experiment for randomly selected sets of 20 reefs (125 replicates) and for the 20 largest reefs (20 replicates).

Removing local populations from our test set had a greater effect on metapopulation persistence than removing them from randomly selected sets of 20 reefs, or from the 20 largest reefs (figure 5). For the parameter set employed, removal of the 20 most reliable self-seeders led rapidly to metapopulation extinction. Removal of the set of largest reefs resulted in persistence at lower densities than the undisturbed equilibrium. Similarly, removal of a randomly selected set of 20 reefs also led to persistence.

Figure 1. Map of the study region in the Great Barrier Reef Marine Park. Coordinate labels show longitude (E) and latitude (S), in degrees. The inset shows the location of the study region on the east Australian coast. The model boundary defines the inner grid of a two-grid nested system. Reef outlines in the Cairns Section are coloured according to the time average of the simulated proportion of settling larvae that are self-recruits: blue, mean less than 0.1; green, mean between 0.1 and 0.2; red, mean of greater than 0.2.

(e) Sensitivity analysis

The principal predictions from the dispersal simulations regarding self-recruitment are

- (i) most local populations depend largely on externally supplied recruits;
- (ii) for a relatively small number of local populations, self-recruitment consistently makes up a significant proportion of total recruitment.

We investigated the sensitivity of these conclusions to various assumptions. We compared the distribution of mean self-recruitment over all reefs for the baseline model (with constant, uniform larval productivity) with that for changes to (i) the dimension of the sensory zone (from 1 to 4 km), (ii) the length of the passive and active periods (from 14 to 7 days, and three to six weeks, respectively),

Figure 2. Snapshot from an animation of simulated larval dispersal from Opal (tan), St Crispin (red), Undine (green) and Rudder (blue) Reefs. All simulations were initiated simultaneously on 11/11/84. The snapshot was recorded 6 days into the simulation. The continental shelf is colour-coded according to bathymetry. Scale bar, 10 km.

and (iii) the temporal spawning pattern (the five variations on the baseline case, as discussed in § 2).

In all cases, predictions (i) and (ii) continue to apply. The identities of the 20 reefs with the highest self-recruitment rates were stable (at least 18 reefs in common with the baseline case). Also, in all cases, the mean self-recruitment rate for Lizard Island was significantly higher than that averaged over all reefs. Shortening the passive stage has by far the greatest effect, increasing the mean self-recruitment, when averaged over all reefs in the Cairns Section, to more than double that for the baseline case. This reflects the fact that self-seeding occurs mainly through retention of larvae near the reef of origin. Larvae that develop more quickly have a greater chance of being retained until they are active and seek to settle. Changes to the temporal spawning pattern and to the duration of the maximum pelagic larval duration had negligible effects. Varying the mortality rate would also make little difference, since self-recruiting and externally supplied larvae would be exposed to roughly the same mortality before settlement.

(f) Comparison with adult distribution data

No direct tests of model predictions have yet been conducted, although such tests are planned (P. Doherty, personal communication) and a paper on their design is in preparation. Data on actual dispersal paths in our region are limited to the single study of Jones *et al.* (1999). How-

Figure 3. Images of the seasonal connectivity matrices for (a) 1985 (b) 1989 (c) 1996 and (d) the matrix averaged over all 20 seasons. Axes are labelled in degrees of latitude. Each element a_{ij} of the matrix is the proportion of all larval production in a season on reef i that settles on reef j . These elements are coded by colour (and size) as follows: red, greater than 0.02; blue, between 0.01 and 0.02; green, between 0.005 and 0.01; pink, less than 0.005.

ever, some limited corroboration of the model comes from a comparison with adult distribution data. Williams *et al.* (1986) conducted a census of fish communities on a transect of the shelf in the Central Section of the Marine Park (on the southern boundary of our study region). Those authors found that for 16 out of 18 species, there was a close relationship between the distributions of recruits and adults. Recruits tended to be found only in the same cross-shelf location as adults of the same species.

We analysed cross-shelf transport patterns under assumed spawner distributions representing different species. Figure 6 shows the results for our baseline parameters. Virtual larvae originating from reefs in one of three zones defined by Williams *et al.* (1986) tend to be transported to reefs within the same zone.

4. DISCUSSION

(a) Model predictions

When focusing on physical transport processes, the model predicts that most local populations in our study region depend largely on externally supplied larvae. Self-recruiting larvae comprise a smaller fraction of the settling cohort on most reefs (mean self-recruitment less than 9% of settling cohort on 80% of reefs in the area). Moreover, the model predicts that the total proportion of larvae settling back onto their reef of origin is lower than the total proportion settling on other reefs. These findings contrast with those from the modelling study of Cowen *et al.* (2000) of populations on more isolated oceanic reefs in the Caribbean.

Figure 4. Simulated time-series of the proportion of settling *P. amboinensis* larvae that are self-recruits. Dashed line, series for Lizard Island; solid line, series averaged over all reefs in the Cairns Section, Great Barrier Reef Marine Park.

A large degree of connectivity within reef fish metapopulations would have important ecological and evolutionary consequences. Extensive larval exchange between local populations will limit opportunities for local adaptation (Holt & Gaines 1992) and increase the evolutionary importance of phenotypically plastic traits (Warner 1997). If local populations in this region are largely open, then there are important implications that affect, for example: population regulation (Caley *et al.* 1996; Armsworth 2002); the resiliency of reef fish communities to local disturbance (Wellington & Victor 1985; Russ 1991; Hart *et al.* 1996; Roberts 1997); the spread of invading species (Randall & Kanayama 1972; Oda & Parrish 1982); and metapopulation growth rates, because of risk spreading and spatial averaging (Kuno 1981; Metz *et al.* 1983; Bascompte *et al.* 2002).

However, the model predicts that a few local populations can be expected to consistently replenish themselves with larvae. In the metapopulation simulations, these few local populations play a crucial part in sustaining the stock in the whole region, in agreement with theoretical predictions (Armsworth 2002).

The considerable spatial and temporal variation in connectivities poses a problem for experimental methods designed to determine dispersal patterns. Methods to determine the spawning location of settling larvae are only now being developed (Jones *et al.* 1999; Swearer *et al.* 1999). Such methods remain logistically challenging and do not permit extensive spatial and temporal replication. We advise caution when extrapolating from conclusions obtained from experiments in single sites in single seasons. The model predicted a degree of self-recruitment to Lizard Island in 1994 comparable with the findings of Jones *et al.* (1999). However, the model also predicted that such high levels of self-recruitment did not occur for the study species on many other reefs in the area (figure 1).

(b) Larval behaviour

More sophisticated assumptions can be incorporated as our understanding of larval biology and behaviour

Figure 5. Simulated adult number density averaged over all reefs (units relative to carrying capacity) versus time. The experiments examine the effects of removing populations (a) from all of the 20 strongest self-seeding reefs (20 replicate simulations), (b) from the 20 largest reefs (20 replicates), and (c) from randomly selected sets of 20 reefs (125 replicates). Full lines, average over all replicates; broken lines, mean ± 1 s.d.

improves. Reef fish larvae are highly specialized (Leis 1991b), and late-stage larvae of some species possess substantial sensory and locomotory capabilities (Stobutzki & Bellwood 1994, 1997; Leis *et al.* 1996; Sancho *et al.* 1997; Wolanski *et al.* 1997). If and how larvae use these capabilities to influence their dispersal is not known. We have assumed that these capabilities are employed only in the later part of the pelagic stage, and are used to approach reefs and to maintain position nearby until times favourable to settlement. Before the development of these capabilities, we have assumed that larvae remain mainly in the mid-water column, and are advected by the depth-integrated current. These assumptions impose important restrictions on how our results should be interpreted, but are consistent with our stated goal of understanding the role of the physical environment in determining dispersal potential. Elsewhere, we have begun to explore alternative behavioural hypotheses (Armsworth 2000, 2001; Armsworth *et al.* 2001).

Given its potential importance, we explicitly review here the possible implications of our assumption regarding vertical position of larvae during dispersal. Vertical profiles of current velocity were measured in summer near Endeavour Reef (145°35' E; 15°47' S); near Ribbon Reef Number 10 (145°43' E; 14°47' S); and near Lark Reef (145°35' E; 15°17' S) (C. Steinberg, personal communication). At Endeavour Reef, in *ca.* 20 m of water, these profiles showed that the current speed lies in a relatively narrow band (± 3 cm s⁻¹) about the depth-integrated value with only a slight bias outside the surface or bottom boundary layers. The current directions lie in a symmetrical band ($\pm 30^\circ$) about the depth-integrated value. A similar picture holds for data measured near Ribbon Reef Number 10, in *ca.* 30 m of water. Depths up to 35 m account for most of the shelf waters in our model domain. Therefore, assuming that these observations hold through-

Figure 6. Bar plots showing the extent of simulated cross-shelf transport and the degree of correlation between cross-shelf distributions of adult abundance and recruitment. Transport was simulated between cross-shelf zones: 1, inshore; 2, mid-shelf; 3, outer. Source reefs were located in the (a) inshore (b) mid-shelf and (c) outer zones.

out waters of such depths, use of the depth-integrated current field to model dispersal should be justifiable for larvae that reside in the mid-water column, although randomly varying vertical shear could cause rather more dispersion than predicted by the model. At a deeper site (*ca.* 50 m), near Lark Reef, there is more bias in the distribution of current speeds about the depth-integrated value, especially at the extremes of high and low speeds. The bias is lower in the mid-depth range than it is close to the surface or substrate.

Information on the vertical distribution of larvae and how it varies with ontogeny is limited. Sampling to a depth of 20 m, in waters less than 30 m deep, Leis (1991a) observed that the majority of taxa had highest concentrations of larvae in the 13–20 m depth range during daylight, depths over which our model would be expected to perform relatively well. However, the samples also indicated that at *any* depth, some species would maintain peak concentration. Further work is needed with more computationally intensive three-dimensional circulation models to investigate the possible effects of various known or proposed larval behaviours (see Cowen *et al.* 2000; Armsworth 2001).

(c) Conclusion

Our models represent a first but comprehensive attempt to understand the role of the physical environment in determining reef fish larval dispersal patterns over regional scales in the GBR. Much greater computing power has allowed enormous improvement over the pioneering work of Dight *et al.* (1990). The results provide a starting point based on strongly simplifying assumptions from which the potential importance of additional complexities can be investigated. The complexities include three-dimensional effects, the refinement of model grid scale and aspects of larval behaviour: these will be investigated in future work. Given the many uncertainties about larval biology and behaviour, it is best to interpret the present model as one that predicts patterns of dispersal when considering environmental forcing alone. Biological and behavioural characteristics of larvae will pass a filter over the predicted dispersal patterns and will determine the ultimate distribution of a settling cohort. Understanding the strength and nature of this biological filter, and which of the predicted dispersal patterns it will amplify and which it will suppress, is a major challenge in reef fish biology.

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