



# Determining the extent and spatial scale of population connectivity: decapods and coral reef fishes compared

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## Abstract

Patchily distributed demersal marine organisms that possess a pelagic larval stage have the potential to form complex linkages among sedentary adult populations through larval dispersal. Unfortunately, determining the extent of this inter-population connectivity in specific cases is quite difficult: larval dispersal is a complex result of several biotic and non-biotic processes, and marine larvae are minute creatures that are difficult to track or manipulate. Nevertheless, effective management of such open populations requires that we know how they are organized and interact. Coral reef fishes and many decapod crustaceans share patchy demersal distributions and pelagic larvae. We review progress made in determining connectivity among crab, lobster and reef fish populations, considering the questions that need to be answered and the techniques that have been applied. We highlight common research strengths and gaps among researchers working on reef fishes and benthic decapods, as well as those areas given greater attention by one group, the lead of which the other group will need to follow. Finally, we suggest that greater progress towards understanding dispersal and connectivity in the future will best be achieved by integrating the approaches we review into large-scale, multidisciplinary, collaborative research programs developed and carried out in association with natural resource managers.

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## 1. Introduction

Patchily distributed, demersal marine species possessing pelagic larvae have the potential for considerable levels of connectivity among local populations. Mediated by larval dispersal, this connectivity is potentially of considerable importance for determining demography of local populations, because it determines the magnitude of immigration and emigration (Sale, 1991b; Caley et al., 1996). It also can be important in determining the dynamics of the overall population comprised of some number of inter-connected

local populations, particularly if connectivity falls within the range appropriate for the formation of a metapopulation (Sale, 1998; Mora and Sale, 2002). Although both local and global demographics may be interesting in their own right, knowledge of the extent of connectivity, and its demographic consequences, is particularly important for population management for fisheries or conservation.

Knowledge of patterns of connectivity will be important for any form of spatially explicit management of marine populations. This is particularly the case if management tools include use of marine protected areas (MPAs) (Sale, 2002b). Whether intended for conservation or for fisheries management, MPAs function by segregating some local population(s) within their borders, where they experience lessened direct human

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impacts, particularly fishing pressure. The immediate result is improved survivorship with resulting larger size distributions and concomitant greater fecundity of the protected individuals. The primary rationale for use of MPAs, particularly as a fisheries management tool, is that this improved survivorship and fecundity will have positive secondary demographic effects on populations lying outside the boundaries, either by “spillover” of individuals across the boundaries, or by “subsidy” of recruitment in these outside populations due to dispersal of larvae spawned within the MPA. While spillover will be limited to the immediate proximity of the MPA, the expectation is that subsidy will be important to enhancing production in a number of populations in the broad region surrounding the MPA. This expectation is not yet supported by empirical data for any MPA (Carr and Reed, 1993; Allison et al., 1998; Russ, 2002) despite some claims to the contrary (e.g. Roberts et al., 2001), and it is worth reflecting that, to enhance fishery yields sustainably, an MPA must enhance fishery yields outside its borders, by spillover and/or subsidy, by an amount that is greater than the yield lost by its establishment. Otherwise, the MPA is simply a way of surreptitiously reducing effort, while pretending to do something more. Although current levels of effort in many fisheries may need to be reduced, using tools that do this while claiming that they do something more is not an effective way to manage relationships between managers and the fishing community. We believe there is an urgent need to obtain reliable estimates of connectivity in order to validate this primary argument for use of MPAs as fishery management tools. There is also a real need to use estimates of connectivity when designing MPAs, so that they are sited and sized appropriately, in order to maximize their effectiveness in subsidizing neighbouring populations’ growth. At present, this is not being attempted.

Unfortunately, estimates of the extent of connectivity are difficult to make, because larval dispersal is a complex process mediated by a number of different factors, and pelagic larvae are minute creatures difficult to tag or to track (Stobutzki, 1998; Cowen et al., 2000; Montgomery et al., 2001; Mora and Sale, 2002). The fishes of coral reefs and crabs and lobsters of reefs and other spatially heterogeneous environments share a number of biological characteristics, particularly the possession of life histories featuring a relatively short

pelagic larval stage followed by a longer, relatively sedentary adult stage. Ecologists studying both groups have begun to explore the question of connectivity, so a comparison of the progress made and the approaches taken is timely. This paper, therefore, provides an overview of the types of empirical data that can be used to examine the process of larval dispersal and the resultant connectivity of spatially segregated sub-populations of adult coral reef fishes and benthic decapods. We do not aim to summarize the emergent biological patterns (this has been done effectively by McConaughy, 1992; Bradbury and Snelgrove, 2001, among others), but rather to assess the state of the research process. There is an extensive literature on larval ecology for a variety of other taxa, but we confine our review to studies on lobsters, crabs and coral reef fishes due to the similarities in their post-settlement ecology. Even having restricted our focus to these taxa, there is undoubtedly useful work that we have overlooked, especially within the grey literature. Nevertheless, we hope that we have succeeded in surveying what can be done and what has been done to investigate dispersal of these two broad groups of organisms, and therefore what will be fruitful directions for researchers working on each group in the future.

## 2. Types and application of data

There are two broad classes of data with which to investigate larval dispersal. The first is composed of information on the *processes* that determine dispersal. Process data consist of: (i) movement of water masses, (ii) timing and location of egg or larval release, (iii) pelagic larval duration, (iv) behaviour and sensory abilities of larvae, and (v) demographic rates of larvae. These causal agents collectively determine how many larvae move between any two locations at any given time. Predictions can be made about the nature of dispersal pathways by compiling and integrating these data. Then, data on biological *patterns*, the second broad class of data, can be used to test whether larvae have moved in the predicted manner. Patterns arising as a consequence of dispersal include spatial and temporal distributions of: (i) larvae, (ii) settlers, (iii) natural markers (genetic, chemical, parasitic, microbial), and (iv) animals tagged at particular source locations.

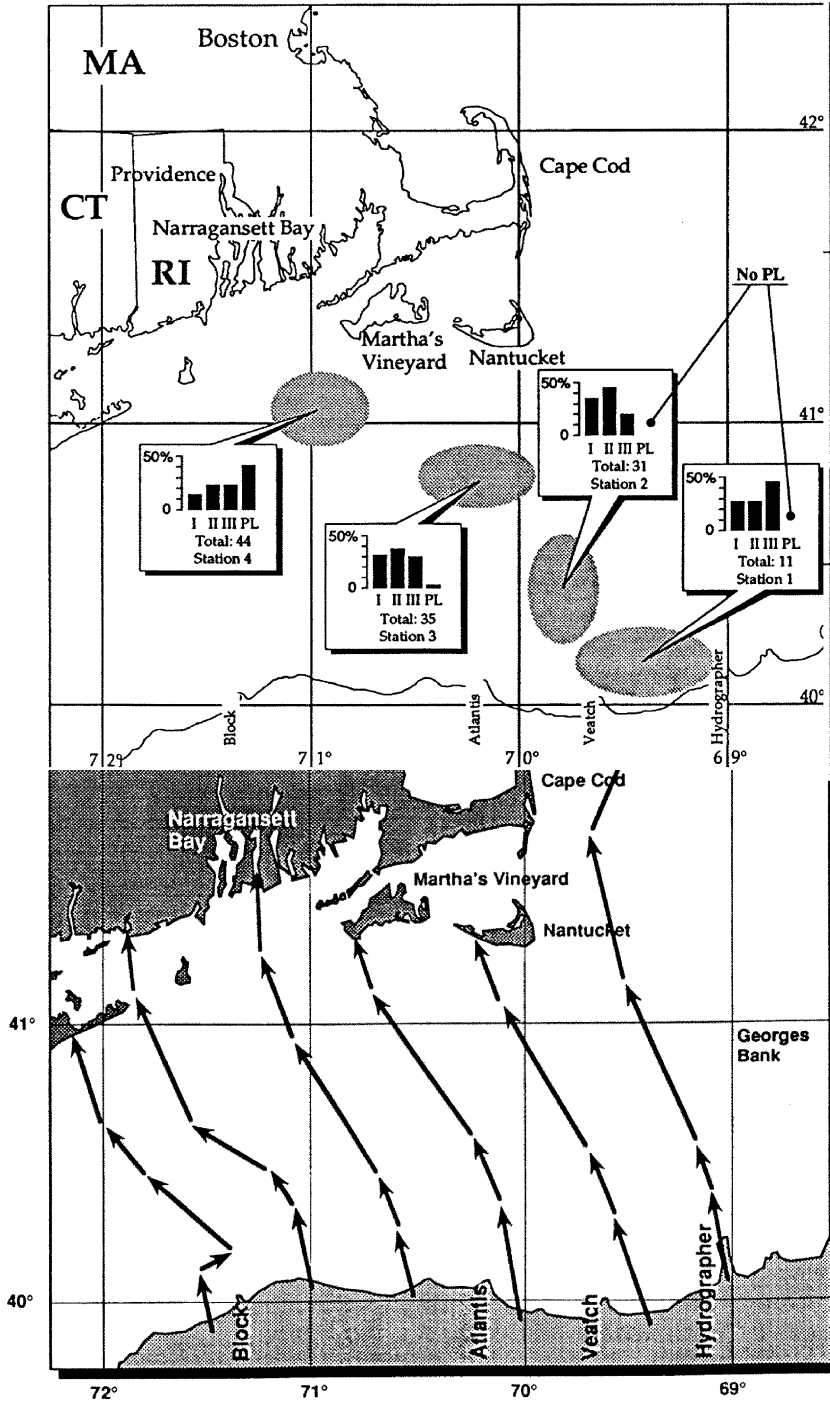


Fig. 1. Cross-shelf distribution patterns of stages I–III larvae and postlarvae of American lobster *H. americanus* (top) and offshore to inshore dispersal pathways generated by a simulation model incorporating currents, wind-driven transport and diel swimming behaviour of postlarvae that best predicted those distributions (bottom). Modified from Katz et al. (1994).

There are few examples of the integration of process data to predict larval dispersal followed by use of pattern data to test the predictions. Wolanski et al. (1997) examined dispersal by linking a hydrodynamic model with empirically derived assumptions about larval swimming and sensory abilities to predict the distribution of larvae around two Australian reefs. They then tested those predictions by sampling pre-settlement animals with light traps. Similarly, Katz et al. (1994) mapped stage-specific distributions of larval American lobster *Homarus americanus* off southeastern New England (Fig. 1). They then explained the larval distributions by progressively more complex dispersal models employing water movement, wind-induced transport and larval behaviour (Fig. 1). Schultz and Cowen (1994) developed a model of water movement between Cape Hatteras and Bermuda and subsequently used data on larval durations of several reef fishes to suggest that passive

transport times less than or equal to larval durations would occur too infrequently to produce observed patterns of species abundance and persistence (Fig. 2).

Studies such as these are the exception rather than the rule, due to the large data requirements and difficulty of obtaining many of the data. In fact, the two reef fish examples illustrate the limitations imposed by data requirements when attempting to examine dispersal by using a causal approach. Wolanski et al. (1997) employed a fair amount of detail but over a small spatial scale that excluded source reefs and tracked larval movements from an effectively arbitrary starting point midway through the larval stage. Schultz and Cowen (1994) adopted a larger spatial perspective, but excluded any information on larval behaviour that could alter their predictions based upon water movement.

Given the difficulties inherent in compiling all requisite process data, an alternative approach is to use pattern data to infer dispersal pathways. Larval

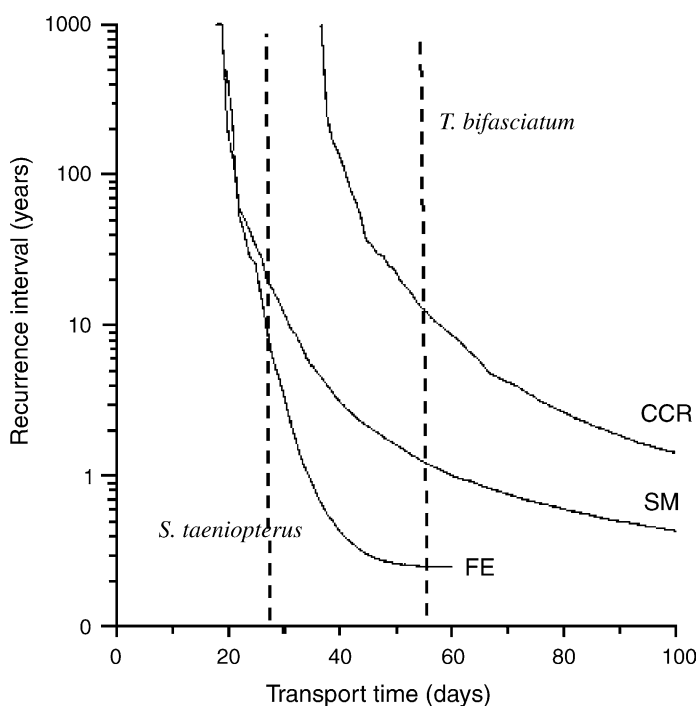


Fig. 2. Recurrence intervals of passive transport times between Cape Hatteras, North Carolina and Bermuda in three different hydrodynamic models (CCR: cold-core ring model; FE: fixed outbreak model; SM: outbreak southern movement model). Mean pelagic larval durations of two reef fishes are indicated. The larval duration of *Scarus taeniopterus* suggests that successful passive transport would only occur once per decade under the SM and FE models and never under the CCM model. Successful passive transport of *Thalassoma bifasciatum* would occur more frequently under all three models. Modified from Schultz and Cowen (1994).

distributions, genetic structure and other biological patterns are consequences rather than determinants of dispersal and can be used, in a sense, to look backwards at how the patterns arose (N.B. there is undoubtedly a genetic component determining dispersal (see Manuel et al., 1996), but analysis of population genetics typically involves overall genetic structure rather than the specific genes relevant to a process). Predictions about dispersal generated from different types of data can then be used to refute, corroborate or refine one another. The approach is essentially a meta-analysis looking for common themes in the dispersal predictions arising from multiple sets of pattern and possibly process data.

### 3. Work to date

#### 3.1. Process data

##### 3.1.1. Hydrodynamics

Hydrodynamics have relevance for biologists studying dispersal, but are not directly reliant upon the biology of focal organisms and therefore can be examined separately. However, physical oceanographers, like all scientists, need to make choices about the spatio-temporal scales and degree of resolution of their work, and the biological aspects of dispersal help define the relevant scales. Although dispersal has been considered in the context of very large-scale current patterns (hundreds to thousands of kilometres) averaged over long periods of time (e.g. Roberts, 1997), the modelling studies described above illustrate that potentially important hydrodynamic determinants of connectivity can operate on much smaller spatial scales (tens of kilometers or less; Wolanski et al., 1997) or only sporadically through time (e.g. episodic long distance transport, Fig. 2; Schultz and Cowen, 1994). Decapod researchers have also uncovered the importance of smaller scale and periodic hydrodynamic phenomena in determining dispersal (e.g. Wing et al., 1995a,b, 1998a; Roman and Boicourt, 1999). Mean dispersal and recruitment patterns can be disrupted by severe storm events, and such episodic anomalies can have important implications for connectivity. For example, survival of blue crab *Callinectes sapidus* larvae is higher (Pile et al., 1996) and their recruitment is more widely distributed

(Etherington and Eggleston, 2000) following tropical storms compared with periods of calm weather. In light of the important influences of weather and water movement, closer collaboration between biologists and physical oceanographers will be necessary to establish the appropriate spatio-temporal scales and resolution, and thus maximize the utility of hydrodynamic data for answering questions about dispersal.

##### 3.1.2. Timing and location of egg and larval release

Networks of moving water masses are spatially and temporally variable, and their effects on the movement of dispersive life history stages (eggs and larvae) will therefore depend upon when and from where those animals first enter the pelagic environment. Water movements can change on seasonal, lunar and diel cycles, and spawning often follows regular cycles on all of these scales. Many species of reef fish (e.g. *Plectropomus leopardus*; Samoily and Squire, 1994) and benthic decapods (e.g. *Panulirus ornatus*; Moore and MacFarlane, 1984) also undertake migrations to specific spawning sites. The temporary change in distribution arising from such migrations will expose eggs and larvae to current regimes that differ from those operating in the vicinity of their normal home ranges. These patterns will determine the appropriate starting points in space and time for the requisite hydrodynamic work addressed above. Due to the fact that the biology and behaviour of benthic adults are easier to study than those of the much smaller and more broadly distributed pelagic larvae, a fairly extensive body of literature on spatio-temporal spawning patterns exists for both decapods (reviewed by Forward, 1987b; Morgan and Christy, 1995) and reef fishes (reviewed by Robertson, 1991; Domeier and Colin, 1997).

##### 3.1.3. Pelagic duration

Knowledge of the length of time organisms spend as eggs or larvae permits at least coarse predictions about dispersal based upon processes (Fig. 2; e.g. Schultz and Cowen, 1994; Roberts, 1997). In the estimation of pelagic larval duration, we see the first example of a significant difference between research on dispersal of reef fish and decapods: the important insights attainable through the analysis of fish otoliths that unfortunately are without analog in decapods. Otolith-based estimation of reef fish larval durations is voluminous. For example, in individual papers Wellington and

Victor (1989) estimated larval durations of 100 pomacentrid species, Victor (1986) estimated larval durations of 100 labrid species, and Thresher and Brothers (1985) estimated larval durations of 31 pomacanthid species. Furthermore, analysis of otolith microstructure can reveal distributions of larval durations in addition to simple average and range estimates. These distributions allow links to be made between distinct spawning and recruitment events (Danilowicz, 1997) and permit greater insights into the range of potential dispersal distances and variability in developmental processes during larval life (Sponaugle and Cowen, 1994).

Estimation of larval duration for decapods is much less common than for reef fishes. Lacking access to an internal 'diary' akin to the fish otolith, researchers often estimate decapod larval durations using laboratory studies (e.g. Costlow and Bookhout, 1959; Gore and Scotto, 1982; Anger, 1991; Harvey, 1993; Strasser and Felder, 1999). Reef fish ecologists have learned that larval durations can differ drastically between field and laboratory settings. For example, Green and McCormick (1999) found that larvae of the anemonefish *Amphiprion melanopus* would settle at 8 days post-hatching in the laboratory, but Wellington and Victor (1989) estimated larval durations ranging from 15 to 22 days for wild *A. melanopus*. Research on decapod larval durations might encounter similar biases, although McConaugha (1992) notes that a lab-based estimate of the larval duration of *C. sapidus* (Costlow and Bookhout, 1959) is approximately equal to the time between the major spawning and recruitment events in the Chesapeake Bay (McConaugha et al., 1983). Given that larval duration is such a fundamental trait in understanding dispersal, obtaining estimates in the field or validating estimates derived in the lab will be an important challenge for decapod biologists.

Although mean larval durations vary widely among reef fishes and benthic decapods, decapod larval durations are often much longer than those of reef fishes. For example, the larval duration of the golden king crab *Lithodes aequispinus* has been estimated to be approximately 191 days (Shirley and Zhou, 1997), whereas the western Australian rock lobster *Panulirus cygnus* can spend up to 11 months (approximately 330 days) as a planktonic larva (Phillips, 1981). In contrast, most reef fish larval durations are in the range of 20–30 days, with relatively few species reaching extreme val-

ues of around 90 days (Victor, 1991). As with many ecological traits, higher mean values for larval durations are typically accompanied by greater variability about the mean (Victor, 1991). This greater variability about higher mean values will likely increase the range of potential dispersal distances achieved by individuals spawned at a common location and time. Decapod researchers might therefore be confronted with a more difficult task in investigating dispersal. The mean larval durations of decapods will be harder to pinpoint, and will often be longer and more variable, complicating resultant connectivity estimates among locations.

While the compilation of large samples of otoliths from newly settled reef fish has provided good estimates of the distribution of larval durations within species, the lab-based approach taken by decapod researchers has permitted important insights into the factors that determine the variability in larval durations, even if the absolute estimates themselves might be biased by laboratory conditions. The influence of ecological factors such as temperature (Sulkin and McKeen, 1989, 1996; Anger, 1991; Field and Butler, 1994; Sulkin et al., 1996), salinity (Anger, 1991; Field and Butler, 1994), food availability (Shirley and Zhou, 1997) and underlying substrate characteristics (Christy, 1989; Brumbaugh and McConaugha, 1995) on decapod larval durations has been investigated. With this information, dispersal patterns within a given year can be more accurately predicted by measuring relevant environmental parameters and considering how they modify mean larval duration. For instance, larval durations of mitten crab *Eriocheir sinensis* decrease with increasing temperature (Anger, 1991), so shorter dispersal distances might be predicted in warmer years. Although larval durations of their focal organisms are generally shorter, reef fish ecologists would benefit from comparable experimental work.

#### 3.1.4. Behaviour and sensory abilities

The movement of water and the amount of time fish remain in the plankton will undoubtedly have some effect on dispersal, but larval fish and decapods are not inanimate propagules subject only to passive transport. Rather, they are animals capable of sensory perception and movement and these abilities can have tremendous effects on dispersal. Understanding sensory abilities and the response of animals to different stimuli can help determine how larvae will behave

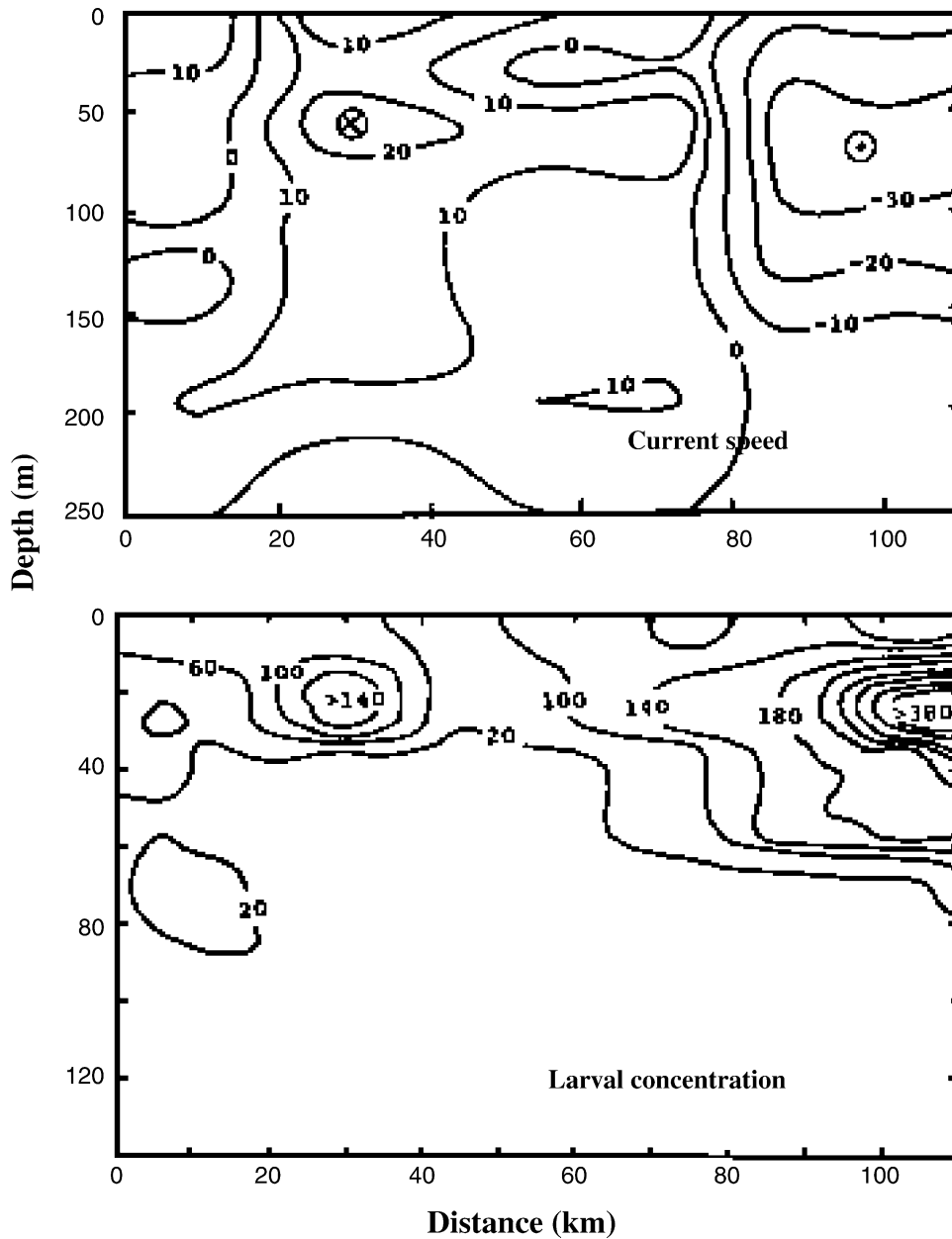


Fig. 3. Vertical distribution of current speeds along a transect near Barbados (top) and vertical patterns of reef fish larval concentrations along two proximal transects (bottom). These data collectively illustrate that neither water movements nor larval distributions are uniform throughout the water column. Modified from Cowen and Castro (1994).

in and move among different physical environments. Their responses will partly determine where larvae position themselves in the water column, and understanding this vertical migration behaviour will iden-

tify which water layers will affect larvae at different points within the pelagic stage (Fig. 3). Estimates of swim speeds can then reveal the extent to which larvae can increase or resist passive transport by swimming

with or against the currents encountered at different layers. Of course, distinguishing when exactly fish will swim with or against currents will have profound consequences for predictions about dispersal.

Behavioural and sensory research on decapod larvae has a longer history and, therefore, has produced a more diverse body of information than similar work on reef fish. Like the experimental work examining factors that modify decapod larval durations, the progress toward understanding behavioural and sensory abilities of decapods seems to be a consequence of the greater emphasis on lab-based research. Nearly 30 years ago, Mileikovsky (1973) produced estimates of swimming speeds for a variety of invertebrate larvae, including decapods. Since that time, additional swim speed research (Cobb et al., 1989; Rooney and Cobb, 1991) has been supplemented by work examining the mechanisms of swimming behaviour (Chu et al., 1996), effects of diet on swimming ability (Chu et al., 1996), and stage-specific vertical migration behaviour (Cobb et al., 1983; Sulkin, 1984; Chu et al., 1996). Also, tremendous insights into the responses of decapod larvae to stimuli such as light intensity, hydrostatic pressure, temperature and salinity have been gained by experimental biologists, particularly Forward (1985, 1987a, 1990) and Forward et al. (1984, 1989) (among other papers) as well as others (e.g. O'Connor and Epifanio, 1985).

Reef fish science lacks the broad research tradition on larval behaviour and sensory biology seen in decapod research. Nevertheless, in recent years important steps have been taken in this area in two Australian labs headed by Bellwood and Leis. Stobutzki (1998) and Stobutzki and Bellwood (1994, 1997) have estimated sustained swimming abilities of late stage larvae of several reef fish taxa through experiments in flow tanks. Notably, their estimates of sustained swim speeds of up to  $70 \text{ cm s}^{-1}$  (Stobutzki and Bellwood, 1994) are significantly greater than those for larval crustaceans (e.g.  $18 \text{ cm s}^{-1}$  for American lobster *H. americanus*; Rooney and Cobb, 1991), suggesting that coral reef fishes will have a greater capacity than crustaceans for modifying dispersal from that due to water movements. Fisher et al. (2000) recently extended the approach of Stobutzki and Bellwood to larval stages from hatching onwards, permitting a broader understanding of the fishes' abilities to control their position throughout larval life. Fisher

and Bellwood (2001) have also examined how food availability affects swimming ability, illustrating the type of experimental studies reef fish researchers will need to develop to understand how aspects of larval biology, such as behaviour and larval duration, can be modified by environmental conditions. Complementing these laboratory studies Leis and Stobutzki (1999), Leis and Carson-Ewart (1997–1999, 2001) and Leis et al. (1996) have estimated swim speed, direction and other aspects of behaviour through field observations. Sensory work on reef fish larvae is not as well developed, but Stobutzki and Bellwood (1998) have illustrated that larvae are capable of nocturnal orientation behaviour in the field, although the exact cues to which fish were responding could not be identified. More recently, Tolimieri et al. (2000) found that larval traps emitting sound caught more fish than did silent traps, suggesting, as Stobutzki and Bellwood (1998) hypothesized, that sound is an important cue.

### 3.1.5. Demographic rates

Connectivity is ultimately determined, not only by the potential dispersal pathways larvae might follow, but also by how many larvae successfully follow each pathway (Cowen et al., 2000). Therefore, a broad understanding of larval mortality will be critical in understanding population dynamics. This broad understanding should include age-, stage- or size-specific mortality estimates, since larvae are unlikely to experience a single rate throughout the pelagic stage due to the drastic changes in size, morphology and behaviour they experience (Fig. 4; McConaugha, 1992). Given that mortality, swimming ability and feeding success are often functions of body size, larval growth is also an important topic of demographic research (Leis and McCormick, 2002). Both mortality and growth rates will vary with surrounding environmental conditions and, as with other aspects of larval biology such as pelagic duration and swimming abilities, understanding these effects will greatly improve our predictive capacity.

Despite the importance of larval demographic rates, these are perhaps the least well studied of the processes determining connectivity. One reason for this paucity of information is undoubtedly that it is extremely difficult to study small-bodied organisms living in vast expanses of ocean (McConaugha, 1992; Leis and McCormick, 2002). In his synthesis of dispersal,



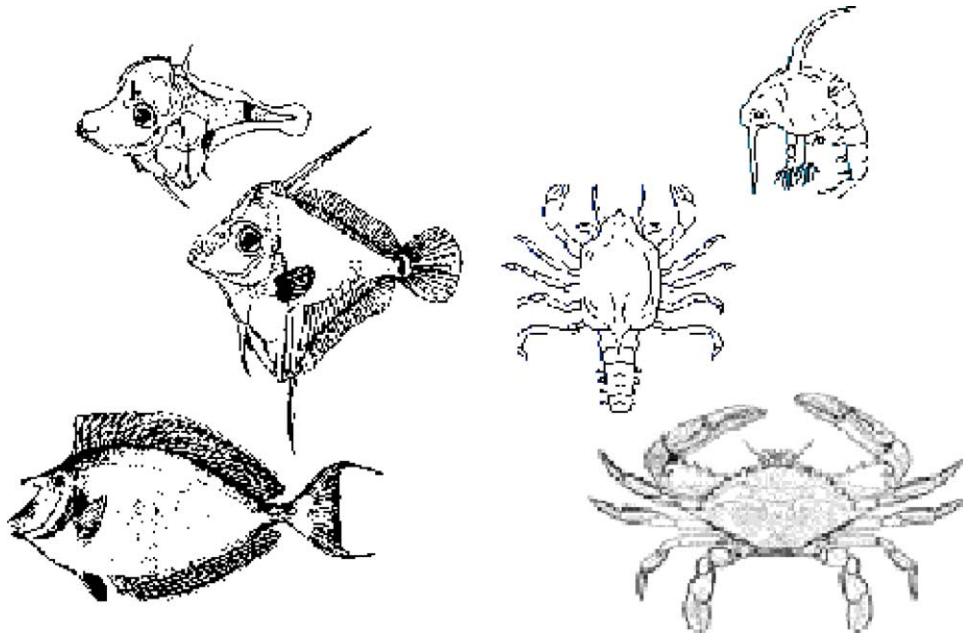


Fig. 4. Young larva (3.0 mm fork length, FL), old larva (8.3 mm FL) and adult (300 mm FL) of a coral reef unicornfish (*Naso* sp., Acanthuridae) (left) and zoea (0.25 mm carapace width, CW), megalopa (2.5 mm CW) and adult (120 mm CW) of a blue crab (*C. sapidus*) (bottom), illustrating the pronounced changes in size, anatomical development and morphology that exist both between larval stages and between larvae and adults. Fish images from Leis (1991a). Crab images courtesy of Vince Guillory, Louisiana Department of Wildlife and Fisheries (<http://www.blue-crab.net/>).

mortality and ecology of decapod larvae, McConaugha (1992) noted the general lack of data on larval mortality and was only able to cite his own work as an example of estimation of stage-specific larval mortality rates. The intervening years since McConaugha's paper do not seem to have filled the void. Reef fish ecologists are confronted by similar logistical difficulties, but also seem to be dissuaded from working on larval fish during the pelagic stage because they can retrospectively examine larval life using the condition of new settlers and the growth histories recorded in their otoliths (Leis and McCormick, 2002). Using new settlers to hindcast larval biology means that the pelagic stage is typically viewed as a single life history phase and only overall demographic rates for this period are estimated (e.g. Wellington and Robertson, 2001). Unlike decapod ecologists, who frequently work directly with distinct larval stages, the limitations of the retrospective approach seem to foster a perspective on the pelagic larval stage of fish that ignores the important transitions occurring within it (Fig. 4; Balon, 1991).

Ecologists working on both reef fish and decapods have important steps to take toward estimating age-, size- or stage-specific demographic rates. As with larval durations and behaviours, the factors determining larval growth, survival and condition will ultimately need to be identified to predict how dispersal patterns will vary with environmental conditions. Either laboratory experiments (e.g. Pletl and McConaugha, 1990; Field and Butler, 1994; McCormick and Molony, 1995) or correlations between field measurements (see Pepin, 1991 for a review based upon primarily temperate fish species) can identify how larval demography might change across space or time with changes in the surrounding environment.

### 3.2. Pattern data

#### 3.2.1. Larval distributions

The first pattern that will emerge as a consequence of the dispersal process is the distribution of larval organisms (and, in some cases, eggs) in the pelagic

environment. Distributional data can test predictions describing where animals should be located based upon process data including the timing of release, hydrodynamics, larval duration and sensory and behavioural capabilities, as well as the relative number of animals that should be present based upon demographic rates. However, owing to the general absence at present of requisite process data, and therefore the general inability to fully develop predictions using a causal approach, data on larval distributions might be more useful in predicting dispersal pathways.

Decapod larvae are incredibly abundant in the water column, at times comprising more than 50% of the planktonic biomass (McConaugha, 1992). They are consequently relatively easy to sample and studies conducted at a variety of locations on a variety of spatial scales have generated predictions about dispersal based on the observed spatial and temporal distribution of larvae. Clancy and Cobb (1991) speculated that physical factors might be important in retention of crab larvae near Block Island, USA, based on much higher densities there than in other areas of the North Atlantic. In perhaps the largest spatial scale study of the distribution of decapod or fish larvae, Booth and Ovenden (2000) sampled larval *Jasus* rock lobsters at stations spanning 16,000 km of ocean between Africa and New Zealand. Their finding that most larvae occur in the vicinity of adults can set an upper bound for the scale of connectivity for their focal species, with subsequent research on smaller scales refining the resolution of dispersal pathways. Often, decapod ecologists use supplementary environmental data in conjunction with larval distributions to infer transport mechanisms. The importance of winds (Johnson et al., 1986; Botsford and Shenker, 1988; Hobbs et al., 1992; Hudon and Fradette, 1993), tides (Queiroga et al., 1994) and relaxation of upwelling events (Wing et al., 1995a,b, 1998a) in moving larvae to eventual settlement sites has been proposed by correlative studies. Larval distribution data from the Chesapeake Bay estuary, its tributaries and the adjacent continental shelf have been coupled with data on multiple physical factors to suggest an array of mechanisms by which decapod larvae are moved within the region (Provenzano et al., 1983; Maris and McConaugha, 1988; McConaugha and Maris, 1988; McConaugha et al., 1995; Roman and Boicourt,

1999). Also, stage-specific vertical distribution patterns of decapod larvae have been used to make inferences about diel migratory behaviour (e.g. Hobbs and Botsford, 1992).

The relative scarcity of reef fish larvae makes them more difficult to sample (Leis, 1991a), and their superior swimming abilities could make them more successful at avoiding the towed nets that have been the primary sampling gear in larval decapod studies. Choat et al. (1993) found that passive aggregation devices collect more large larvae than towed nets, which might be due to the superior swimming abilities of older larvae. Nevertheless, reef fish ecologists have made progress in describing larval distributions. Initially, most of this work was done by Leis, first in Hawaii (Leis, 1982) but then more substantially near Lizard Island on the Great Barrier Reef. The majority of this Lizard Island work has been descriptive (Leis, 1981; Leis and Goldman, 1987), but other work has provided some of the first indications of the importance of behaviour in determining reef fish dispersal patterns. For instance, Leis has demonstrated diel differences in vertical positioning (Leis, 1986, 1991b) and low numbers of fish being passively advected away from reefs into the Coral Sea (Leis and Goldman, 1984). Beyond Leis' series of Lizard Island-based papers and his work at other locations (Leis, 1982; Young et al., 1986; Leis et al., 1998), other reef fish ecologists have slowly been taking up the challenge of documenting larval distributions (Kobayashi, 1989; Brogan, 1994; Hendriks et al., 2001; references in Leis and McCormick, 2002). Given that this work can both generate and test dispersal predictions, as well as provide specimens for behavioural and demographic studies, reef fish ecologists will need to continue work on their focal organisms during the pelagic stage. Also, reef fish ecologists need to follow the lead of decapod ecologists and collect more environmental data to help explain observed distribution patterns. Cowen and co-workers have made particularly notable progress in this area, suggesting the importance of tidal currents (Sponaugle and Cowen, 1996b), flow steered by seafloor topography (Cowen and Castro, 1994), and expansion and contraction of warm water (Hare and Cowen, 1991) in determining larval distributions. Sponaugle and Cowen (1996a,b) have also invoked larval behaviour in conjunction with environmental data to explain distribution patterns.

### 3.2.2. Rates of settlement

Like the release of eggs and larvae, rates of settlement to benthic habitat are easier to study than many aspects of the pelagic larval stage because the focus is on larger-bodied life history stages and more restricted expanses of habitat. Consequently, a wealth of information on settlement has been collected for both coral reef fishes and benthic decapods. The number of individuals joining benthic populations has long been an especial preoccupation among reef fish ecologists, particularly throughout the 1980s (reviewed by Doherty and Williams, 1988; Doherty, 1991) and this work continues to the present (recent references include Sponaugle and Cowen, 1994; Masterson et al., 1997; Lewis, 1997; Tolimieri et al., 1998; Schmitt and Holbrook, 1999; Holbrook et al., 2000). Decapod researchers have likewise compiled a broad array of data on patterns of settlement (recent references include Field and Butler, 1994; Gallardo et al., 1994; Herrnkind and Butler, 1994; Clancy and Cobb, 1996; Eggleston et al., 1998; Wing et al., 1995a,b, 1998b; Linnane et al., 1999; Palma et al., 1999; Robinson and Tully, 2000a,b). For both taxonomic groups, research to date has included a strong focus on habitat preferences of different species, which is important information not only in predicting dispersal but also in designing monitoring programs and spatial management strategies.

Settlement rates need not be examined solely by estimating the abundance of early juvenile stage animals in the benthic environment. In fact, use of data on the abundance of new settlers is somewhat limiting in that it can only be compiled one year at a time. In contrast, the age structure of the adult population can serve as a record of past variability in recruitment to the benthic habitat. The limitation of this approach is that density-dependent post-settlement mortality can reduce both spatial and temporal patterns of variation set by differential settlement. However, coral reef fishes often seem to settle at densities below those at which density-dependent effects operate (Doherty, 2002) and variability in settlement is therefore often retained in the age structure (Doherty and Fowler, 1994; Russ et al., 1996). Meekan et al. (2001) have recently suggested the importance of ENSO events in producing strong cohorts of reef fishes in the tropical eastern Pacific by examining population age structures. Methods of age determination for de-

capods based on bioaccumulation of lipofuscin are being developed (Sheehy et al., 1998, 1999) and might eventually enable decapod ecologists to also replicate settlement histories using adult age structures.

Unlike other types of pattern data, settlement rates alone hold little value in predicting dispersal. At the very least, settlement patterns must be linked with spawning patterns and estimates of pelagic larval duration to predict dispersal pathways. This approach assumes that settlement events lagging a distinct spawning event by a time period equivalent to the larval duration were likely produced by that spawning event (e.g. McConaughy, 1992; Danilowicz, 1997). However, if spawning is synchronized among multiple locations, then this approach will tell very little about dispersal. Even if reproductive output is highly variable among locations, one cannot assume that the largest settlement events are produced by the most productive locations because animals produced by a single spawning event can potentially follow multiple dispersal pathways. This means that an uncertain mixture of natal sources can be represented in newly settled cohorts. Additionally, very high and variable larval mortality means that patterns in settlement may be largely independent of patterns at the time of spawning (Danilowicz and Sale, 1999).

Despite their limited use in predicting dispersal, settlement rate data might be the most useful type of data for testing dispersal predictions generated using a full causal approach because settlement represents the culmination of all of the processes affecting dispersal. Even limited data sets on settlement can be useful in testing predictions about the general, if not specific, pattern of production and dispersal expected for a given species at a given location (Fig. 5; Danilowicz and Sale, 1999). To be most effective, however, ecologists studying reef fish and decapods will both need to collect settlement data on much larger spatial and temporal scales than is commonly done at present. Even if very comprehensive process data are obtained, sampling biases and limitations will often obscure relationships between predictions and empirical data (Walters and Ludwig, 1981) so larger data sets will be required to allow important patterns to rise above the variability (Hughes et al., 2000).

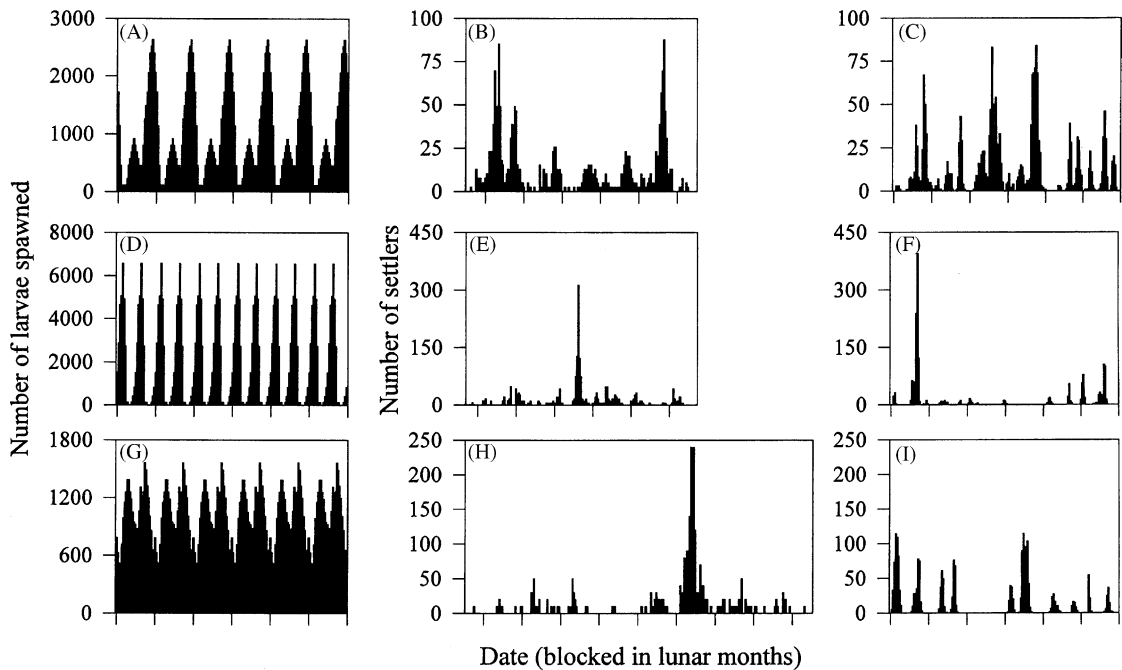


Fig. 5. Actual settlement data (B, E, H) compared with output of the best-fitting simulation models (C, F, I), assuming the spawning patterns indicated (A, D, G), for *Pomacentrus amboinensis* (top plots), *P. wardi* (middle) and *Amphiprion clarkii* (bottom). Simulation models incorporated different levels of individual and cohort-wide (e.g. environmental) influence on settlement variance, with the best-fitting model chosen based on the similarity between actual and model variance of settlement. The comparisons illustrate how mechanistic models can predict qualitative, if not specific, patterns of settlement. Modified from Danilowicz and Sale (1999).

### 3.2.3. Natural markers

The distribution of natural markers within individuals among populations can be used to speculate on the dispersal processes that generated those distributions. Regardless of focal taxon or system, the most common natural markers used by ecologists studying dispersal are undoubtedly alleles. Population genetics is an extensively developed, but still growing, field that has contributed much to the development of metapopulation perspectives on terrestrial organisms (Hastings and Harrison, 1994). However, some population genetic models suggest that genetic similarity among populations can arise through levels of connectivity that are substantially less than those that are significant in a demographic sense (i.e. 1–10 migrants per generation; Allendorf and Phelps, 1981). In other words, genetic homogeneity among populations can be compatible with substantial demographic independence. Existing models, however, rely upon assumptions that are rarely met in nature, so the

causes of genetic structure are likely more complex than existing theory suggests and better understanding of genetic markers and refinement of population genetic models is needed (Bossart and Prowell, 1998). Nevertheless, population genetics can assist in understanding dispersal pathways and developing metapopulation concepts relevant to reef fishes and benthic decapods (e.g. Planes et al., 1996). In fact, there is ample work on the population genetics of benthic decapods (reviewed by Thorpe et al., 2000) and a rapidly growing body of work on the population genetics of reef fish (reviewed by Shulman, 1998; Planes, 2002).

Chemicals taken up into tissues from the surrounding environment are a second type of natural marker. Analysing the microchemical structure of tissues is another area, in addition to larval duration and demographic research, where reef fish ecologists enjoy distinct advantages offered by otoliths. Since the otolith matrix is not shed or resorbed like some soft tissues, it provides a more accurate and permanent record of

previous physical environments. Swearer et al. (1999) recently used solution-based analysis of overall otolith microchemistry to argue that a high degree of local retention of *Thalassoma bifasciatum* occurs at St. Croix, US Virgin Islands. Otoliths confer another advantage in that they are formed incrementally and therefore provide a chronological record of physical environments in which the fish has lived. This enables far more detailed description of movements among water masses than is possible using overall tissue concentrations. For example, Dufour et al. (1998) were able to compare local water chemistry with the chemical make-up of otolith sections formed after fish moved to a French Polynesian lagoon, because they could identify the point at which otolith layers began to be formed within the lagoon and use solution-based analysis of only those layers. Furthermore, analyses with even finer temporal resolution are possible using laser ablation methods that target the otolith matrix associated with specific internal increments. To date, analyses of otolith microchemistry have focused largely on trace metal concentrations, but stable isotope ratios represent another potentially useful natural tag. For example, Kennedy et al. (1997, 2000) and Limburg (1998) have successfully used stable isotope ratios to estimate movements of Atlantic salmon and three herring species, respectively. Otolith microchemistry is an increasingly popular tool among reef fish ecologists and will likely play an important role in understanding dispersal (see Campana, 1999; Thresher, 1999; Campana and Thorrold, 2001 for reviews and critique of otolith microchemistry applications).

Despite the lack of permanent hard parts akin to otoliths, decapod researchers can apply similar techniques. For example, DiBacco and Levin (2000) and DiBacco and Chadwick (2001) illustrate that chemical signatures in tissues of whole crab larvae can distinguish natal sources in California (Fig. 6). Although it is unlikely that analysis of chemical signatures will ever be as powerful a tool for decapod ecologists as it will be for reef fish ecologists, it still seems to hold tremendous promise and should yield important insights into connectivity. In fact, the prevalence of aquatic pollution worldwide and the spatial disparities in water chemistry arising due to this pollution, in addition to that due to natural processes, should make dispersal patterns easier to map. For example, DiBacco and co-workers relied in part upon the dis-

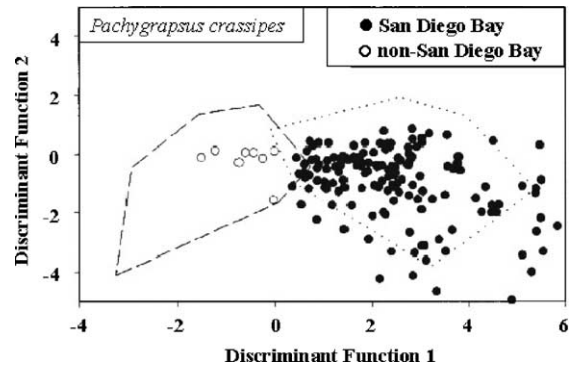


Fig. 6. Discrimination of larvae of the crab *Pachygrapsus crassipes* collected at the Coronado Bay Bridge, California into groups spawned at San Diego Bay and those spawned elsewhere using algorithms based on the known tissue chemistry fingerprint at San Diego Bay. Modified from DiBacco and Chadwick (2001).

tinct pollutant profile of San Diego Bay to identify larval sources.

Other natural markers that could be used to investigate dispersal include parasites or bacterial symbionts. Levin (1990) discussed the potential for these biological markers to help understand dispersal of marine invertebrate larvae over a decade ago, but the application of this approach in the intervening years has been rare. Likewise, reef fish ecologists have done little work of this type. However, Cribb et al. (2000) recently identified 13 different parasite species infesting 23% of settling reef fish in New Caledonia. If the spatial distribution of these parasites in the pelagic environment can be mapped, they might provide valuable information about waters through which larvae have moved and, therefore, connectivity.

#### 3.2.4. Induced markers

Traditional marking methods, wherein dyes, brands or externally affixed tags identify animals, are not useful for work with larvae because of their small body sizes. Alternatively, markers akin to the natural markers described above can be introduced into the tissues of larvae. Examples of such an approach are extremely rare. Genomic manipulation can result in unique and identifiable alleles but, unlike studies on natural allele frequencies, at present this does not seem likely to become a common approach. The most common application of distributions of artificial genetic modifications might eventually be done using the unique genetic

make-up of hatchery-reared animals. Salmon biologists have been particularly active in tracking movements and studying population inter-mixing using the distinct genetic fingerprint that arises through anthropogenic selection in hatcheries and aquaculture farms (e.g. Crozier, 2000). In addition to tracking salmon movements on the basis of identifiable alleles, salmon biologists have also induced distinct microstructural features into otoliths by temperature manipulations that can likewise be used to track movements (Volk et al., 1999). Neither technique is being used extensively outside of salmon biology.

Chemical marking of larvae, on the other hand, is receiving some early attention by ecologists studying reef fish and decapods and seems to present exciting and useful possibilities. Distinct chemical markers have been introduced into reef fish larvae by bathing them in water of a unique chemical make-up (Jones et al., 1999) and into decapod larvae by feeding them chemically labelled food (Anastasia, 1998). The use of natural chemical markers can lead to ambiguous results if the variation in environmental chemistry is not great. In contrast, artificial chemical tags can be extremely powerful in that they can unequivocally identify the source of larvae. Unfortunately, chemically marking animals is extremely difficult and many animals will be lost through the high mortality characteristic of the larval stage. This means that the proportion of marked animals among the overall cohort will be small and few marked animals will successfully settle. Thus, the significant limitation of these techniques is that a relatively small quantity of data is likely to be obtained. Chemical marking methods will be more effective if less labour-intensive means of marking, collecting and chemically analysing animals can be developed.

#### 4. Conclusions

Of the various topics relevant to understanding larval dispersal we have reviewed, there do not seem to be any that have been completely neglected by researchers working on either coral reef fish or benthic decapods. Rather, the relative emphasis placed upon different topics varies between the two groups and each can follow the lead of the other in filling those gaps. For example, coral reef fish ecologists have been

more active in estimating larval durations in the field, due largely to the ease of doing so through otolith analyses, but decapod biologists have taken greater strides toward understanding the processes that can extend or shorten larval stages, due to a broader tradition of laboratory experimentation. Unfortunately, decapod researchers will face a greater challenge in following the lead of their reef fish counterparts in estimating larval durations than will reef fish researchers in developing laboratory investigations into larval biology.

While one group has addressed some topics to a greater degree relative to the other, the treatment of some topics has been comparable between the two groups. Rates of settlement have been an especially common focus. Population genetics is a long established technique in decapod studies (Thorpe et al., 2000) and an increasingly common approach in reef fish studies (Shulman, 1998; Planes, 2002). Both groups seem to need more work on larval behaviour and demography, due to the tremendous importance larval biology has in determining dispersal and settlement success (Todd, 1998; Leis and McCormick, 2002). Finally, the analysis of either natural or induced non-genetic markers, especially chemical signatures, is a new and therefore infrequently used but promising technique that is receiving attention among researchers studying coral reef fish and decapods.

In broadly surveying the various aspects of dispersal research across two diverse groups of organisms, we have not explored the extent to which the research has yielded comprehensive answers for specific species. The fact that researchers working on either coral reef fish or decapods have spanned an array of approaches is significant in determining that the approaches can be and have been successfully applied to their focal taxa. However, a good understanding of dispersal requires applying a large proportion of this arsenal of techniques to a single species in a single region, because each approach has its limitations and the nature of patterns and processes can vary between species or regions. A variety of research on topics related to dispersal has been conducted for some decapod species that support major commercial fisheries, such as the blue crab, *C. sapidus*, American lobster, *H. americanus*, and western Australian rock lobster, *P. cygnus*. These represent a minor proportion of not only benthic decapods in general, but also of benthic decapods supporting fisheries. More comprehensive data sets

need to be compiled for a wider range of species. This need is perhaps more urgent for coral reef fishes. The most comprehensive data sets at present exist for the small site-attached damselfishes (Pomacentridae) that have been the focus of much of the ecological research on coral reef fishes (see chapters and references in Sale, 1991a, 2002a). It is possible that the ecological methods developed and theories generated by work on smaller coral reef fishes can usefully be applied to larger species supporting fisheries, but work on these larger species still needs to be done to confirm this broader applicability (Roberts, 1996; Levin and Grimes, 2002).

The study of larval dispersal is a diverse and exciting topic in marine science. Fully understanding dispersal requires a mixture of methodologies and disciplines, and therefore the involvement of field ecologists, experimental biologists, physical oceanographers and geneticists, among others. In addition, while this review has focused on empirical research, there are important insights to be gained from theoretical studies (e.g. Armsworth et al., 2001). In light of this requisite multi-faceted approach, as well as the large spatio-temporal scales over which research must occur, the most effective research programs will be broadly collaborative with data collected at regional scales (Sale, 2002b). Building and funding such programs will be an interesting challenge, but one well worth accepting. Our on-going project, ECONAR (Ecological CONNECTIONS Among Reefs), which commenced in April 2001, is an example of the type of project that needs to be developed. Its seven principal investigators include two reef ecologists, two fish geneticists, a trace element geochemist and two physical oceanographers, accompanied by a number of post-docs and graduate students. It is also designed explicitly to interface with components of a major international development project in coastal marine environmental sustainability with which it will share environmental data. Fieldwork for ECONAR is being done at several sites in the Turneffe Islands, Belize (in cooperation with the University of Belize), and 200 km north at several sites at Banco Chinchorro, Quintana Roo, Mexico (in cooperation with the management of Reserva Biosfera Banco Chinchorro). Local- and regional-scale physical models will define the water circulation through the region. Although it is too early to assess the success of ECONAR, in-

terdisciplinary projects of this scale are going to be essential if we are to gain definitive information on connectivity. Ideally, these collaborations will include resource managers in order to ensure that the science focuses on geographic areas of management concern and that all aspects and implications of the science are thoroughly understood by those best positioned to apply the knowledge (Sale, 2002b). Ultimately, understanding dispersal, and therefore connectivity, of patchily distributed benthic marine organisms will be crucial in establishing which geographic areas interact with each other and in strategically designing effective spatial management schemes.

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