



CHAPTER 8

The Biology, Behavior, and Ecology of the Pelagic, Larval Stage of Coral Reef Fishes

Jeffrey M. Leis

*Fish Section, Division of Vertebrate
Zoology
Centre for Biodiversity and Conservation
Research
Australian Museum
Sydney, New South Wales 2010, Australia*

Mark I. McCormick

*Department of Marine Biology
James Cook University
Townsville, Queensland 4811,
Australia*

-
- I. Introduction
 - II. Near Ubiquity of a Pelagic Stage
 - III. Recently Developed Research Tools
 - IV. Off the Reef and into the Blue
 - V. Back to the Reef: The End of the Pelagic Stage
 - VI. Future Research Directions
 - VII. Conclusions

I. Introduction

Reef fish biologists are keenly aware that nearly all bony fishes on coral reefs have a pelagic larval phase that is potentially dispersive, and that this has major implications for reef fish populations not only at evolutionary (or biogeographic) scales, but also at ecological (or demographic, including management) scales. The literature is full of statements of how important this type of life history is for reef fishes, and for study and management of them. However, this realization has not been accompanied by a major shift in research effort to studying this pelagic phase, what one might refer to as “prerecruitment” studies. Neither has it led to a widespread view of the pelagic phase as much more than a “black box” that results in open populations and large fluctuations in recruitment. Even attempts to assess the population connectivity that presumably results from larval dispersal typically make simplifying assumptions, either explicitly or implicitly, that portray the larvae as little more than passive tracers of water movement that “go with the flow,” doing nothing much until they bump into a reef by chance and settle at once.

Are larvae really as simple and as uninteresting as the assumptions made by this “black box” view of

larval biology? We think not. The work reviewed here reveals larvae of coral reef fishes to have remarkably good swimming abilities, good sensory systems that develop early in ontogeny, and sophisticated behavior that is very flexible. Little of this would have been predicted from the much better known larval biology of temperate, nonreef species such as herring, cod, and plaice. We explore some of the reasons for this. The interaction of larval distributions with oceanography is the subject of Chapter 7 in the present volume, and we do not address that subject area. This chapter is not a revision of former work by Leis (1991a), nor does it cover ground already dealt with in reviews of coral reef fish larval biology by Boehlert (1996) and Cowen and Sponaugle (1997). Instead, here the focus is on recent research that examines reef fish larvae as animals interacting with their environment. The emphasis is on a perspective from the pelagic environment toward the demersal reef environment. The larvae have a similar perspective. Other studies take the opposite view, and indirectly examine the pelagic stage from the reef. These utilize information gleaned from otoliths of recruits or from abundance patterns either of settlement-stage larvae captured by reef-edge light traps and reef-based nets, or of recruits on the reef (e.g., Dufour and Galzin, 1993; Milicich, 1994; Sponaugle and Cowen, 1994; Thorrold *et al.*, 1994b,c; Robertson *et al.*, 1999). Studies of this sort provide valuable insight, but they are largely beyond the scope of the present review. We review here new information on the pelagic stage, from spawning to settlement, including metamorphosis, but not postsettlement issues.

There are large differences in biology between the larvae of coral reef fishes and those of the temperate fishes that dominate the literature. Predictions based on

these temperate species have often badly misled biologists working on reef fishes. Below, we examine some of the reasons why such large differences exist. We conclude that such predictions should be made very cautiously indeed, and have tried to avoid overreliance on the temperate literature. We can learn much from the excellent and extensive research done on larvae of temperate fishes, but recent experience shows that everything must be ground-truthed with larvae of reef fishes. Coral reef fishes are overwhelmingly of the order Perciformes, or perchlike fishes (here considered to include the Scorpaeniformes—see Chapter 1, this volume). In contrast, most research on temperate marine fish larvae has been on other orders, in particular the Clupeiformes (herrings, sardines, and anchovies), Gadiformes (cods), and Pleuronectiformes (flatfishes). These four orders have been distinct for at least 50–60 million years, and the Clupeiformes for much longer (Carroll, 1988). Further, the nonperciform fishes include few species that live on either temperate or tropical reefs as adults. Few would expect the biologies of the adults of these distantly related orders from different habitats to be similar, but similarities are somehow expected among the larvae.

There is a flip side to this coin, however. Tropical researchers are guilty of emphasizing the dispersal capabilities of reef fishes and not paying enough attention to what influences larval survival—a theme that has been the major thrust of temperate fisheries research for the last 100 years (Cowen and Sponaugle, 1997; Kingsford, 1998). Despite the taxonomic differences in study species, coral reef fish research can gain much from temperate research regarding the processes influencing larval mortality schedules, although the specifics, as emphasized above, will undoubtedly differ. Many of the recent advances in larval research have been through the application of techniques and philosophies gleaned from temperate fisheries research, such as the use of otolith analyses to examine larval mortality schedules and dispersal.

Some definitions and abbreviations are required. Nomenclatures applied to the early life history stages of marine fishes may be based on morphological criteria, ecological criteria, or some combination. Some terms were developed for use with pelagic fishes, such as clupeids, others for benthic fishes with pelagic larvae, such as reef fishes, and they reflect the different priorities and perspectives of the researchers, or often, tradition. Standardization is unlikely, if for no other reason than that the diversity of fish ontogenies makes no one system entirely satisfactory. To avoid these confusing nomenclatural issues, we use a broad definition of “larva” that includes everything from hatching to acquisition of full fin rays and scales, and loss of “special-

izations for pelagic life” (such things as transparency, elongate or ornamented fin spines, or head spination) not found in the adult. In some species, the ecological transition of settlement coincides with the morphological transition of metamorphosis. In others, it does not. The morphological transition may be gradual or abrupt, whereas the ecological transition is usually abrupt.

Lengths referred to here are “standard length” (SL; snout to base of the caudal fin rays, or to the tip of the notochord before the caudal fin forms), but total length (TL) is used in some of the cited literature. Swimming speeds are often standardized as “body lengths per second” (BL sec⁻¹). “Effective swimming” is swimming faster than ambient currents (Leis and Stobutzki, 1999). Pelagic larval duration (PLD) is the length of time the propagule is pelagic, i.e., the time between the leaving the reef and settlement. Lizard Island is referred to frequently—it is a midshelf reef complex on the northern Great Barrier Reef.

II. Near Ubiquity of a Pelagic Stage

A pelagic early life history stage is found in nearly all bony reef fish species (Leis, 1991a; Leis and Carson-Ewart, 2000). This is true regardless of whether eggs are pelagic, demersal, or brooded, or if the adults are viviparous. The pelagic stage may last as little as a week in some damselfishes (Pomacentridae) (Thresher *et al.*, 1989), or more than 64 weeks in some porcupine fishes (Diodontidae) (Ogden and Quinn, 1984).

Leis (1991a) was able to list only a few species of bony reef fishes that lack a pelagic stage, but in the past few years, three more have been discovered in the Indo-Pacific. The Banggai cardinal fish, *Pterapogon kauderni* (Apogonidae), orally broods both eggs and hatched young until the latter reach about 10 mm (Allen and Steene, 1995). The young remain on the reef and bypass the pelagic phase. In two species of the recently described chromine pomacentrid genus *Altrichthys*, larvae hatch from demersal eggs, and are tended by both parents for “an extended period” (Allen, 1999), thereby avoiding the pelagic phase.

Thus, we should perhaps expect the discovery of a few more reef fish species lacking a pelagic stage. These will most likely be apogonids and chromine pomacentrids, and will prove useful models to compare to species that retain a pelagic stage, such as *Acanthochromis polyacanthus*, previously the only pomacentrid known to lack a pelagic stage (Kavanagh, 2000). However, compared to other groups of marine animals (Strathmann, 1986; Strathmann and Eernisse, 1994), very few coral reef fishes, found in only 6 of

approximately 106 families, have lost or greatly abbreviated the pelagic stage.

Why Are Temperate Fish Larvae So Different from Reef Fish Larvae?

Most of the literature on fish larvae from temperate waters concerns species that are pelagic or live on soft (sand or mud) bottoms as adults rather than species from (rocky) reefs. This alone may confound temperate/coral reef comparisons. Adult pelagic fishes usually have habitat requirements that differ from those of their larvae, but they never make the abrupt changes entailed by settlement out of the pelagic environment and into the benthos. Except on oceanic islands, soft-bottom habitats are usually far more extensive and less discrete than reef habitats, so larvae of reef fishes have a much smaller target to find at the end of the pelagic phase than do fishes of soft bottoms. Further, it is thought that most reef fishes are relatively sedentary as adults, whereas adults of many pelagic and soft-bottom species undertake extensive migrations: thus, in contrast to

most pelagic and soft-bottom species, dispersal in reef fishes is thought to be limited largely to the pelagic larval phase.

A major difference between coral reef fishes and temperate marine fishes is the incubation period of their eggs. Pelagic eggs of most coral reef fish species hatch within 1 day (Watson and Leis, 1974; Tucker, 1998), far more rapidly than pelagic eggs of temperate fishes, which commonly have incubation periods of 3–20 days (Russell, 1976).

A second major difference between coral reef fish and most temperate fish larvae is that at any given size, the reef fish larvae are more developed. This is particularly apparent if one compares the state of development of well-studied temperate larvae such as herring and cod at the sizes at which reef fish larvae commonly settle (1–2 cm) (Fig. 1). At all sizes, the reef fish larvae have more complete fins. They develop scales at a smaller size, seemingly have better developed sensory apparatus at any size, and are morphologically equipped for effective feeding within a few days of hatching, and at a smaller size than the herring and cod (Table 1).

A

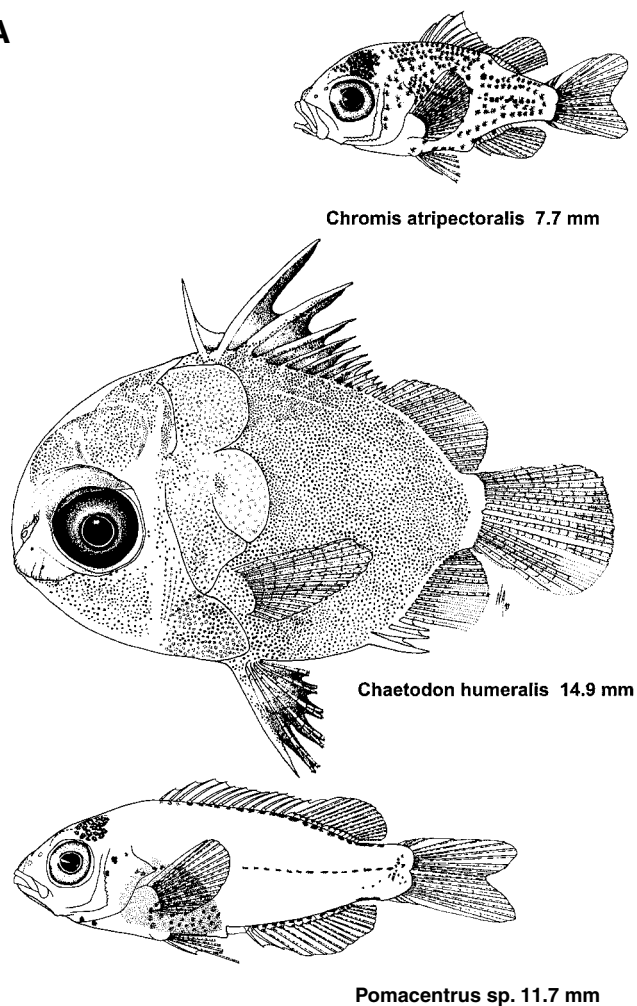


FIGURE 1 Comparison of developmental state in larvae of three species of reef fishes at settlement, with that of herring and cod at similar sizes. (A) Settlement stage larvae of *Chromis atripectoralis*, ~8 mm; *Chaetodon humeralis*, ~15 mm; and *Pomacentrus* sp., ~12 mm. *Chromis* and *Pomacentrus* from Leis and Carson-Ewart (2000); *Chaetodon* from Moser (1996). (B) Developmental series of larvae: Atlantic cod, *Gadus morhua*, 9, 11, and 16 mm (TL) (from Fahay, 1983) and Pacific herring, *Clupea pallasii*, ~8, 10, and 19 mm (from Moser, 1996).

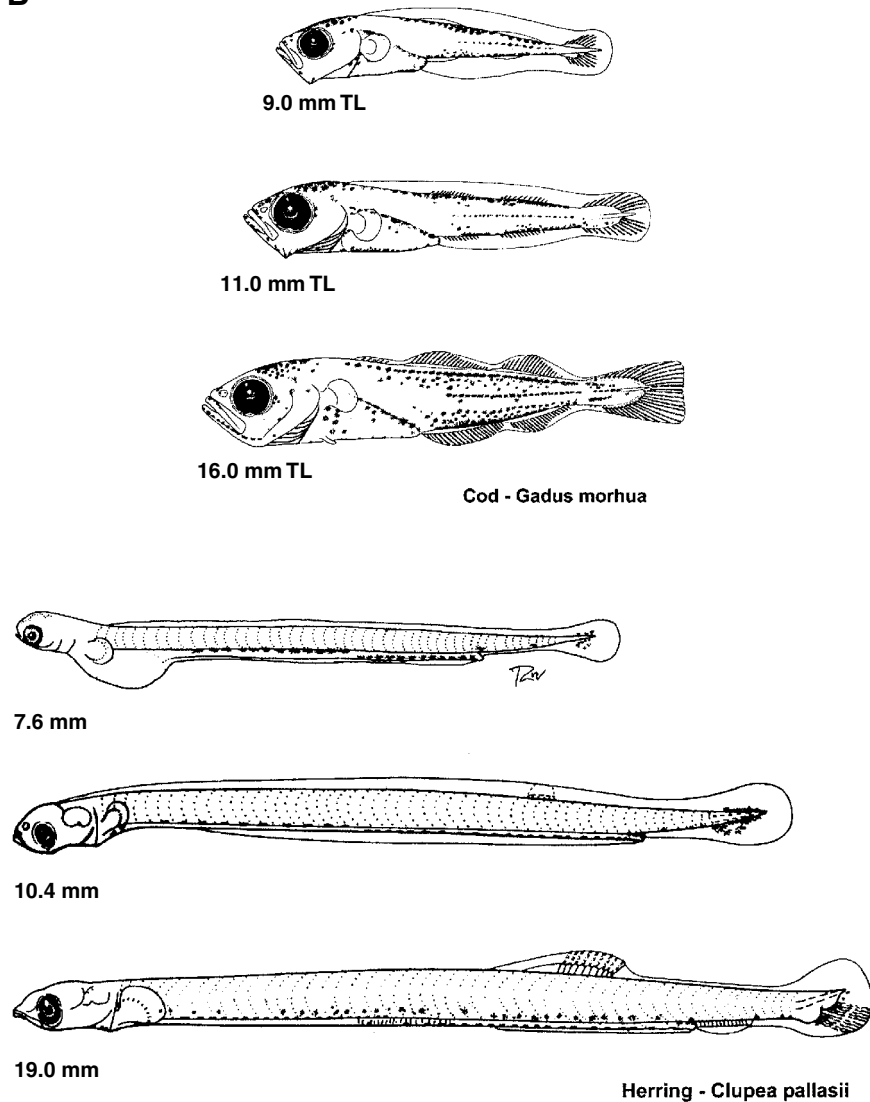
B

FIGURE 1 (continued)

Temperate perciform fishes (including many reef fishes), in contrast, reach developmental milestones at sizes similar to those of coral reef fishes (Moser, 1996; Fuiman *et al.*, 1999).

Reef fish larvae are much better swimmers at these sizes (1–2 cm) than are larvae of cod or herring (see Section IV,B,2). The few data on larvae of temperate perciform fishes indicate that although they are better swimmers as compared to temperate gadiform or clupeiform larvae, they are apparently much slower than coral reef fishes of similar size.

So, why are reef fish larvae better swimmers? As implied above, there is undoubtedly a taxonomic component, with perciform larvae apparently superior performers as compared to gadiform or clupeiform larvae.

Second, swimming may be more efficient in tropical waters (25–29°C) than in temperate waters (10–20°C) for both physiological and hydrodynamic reasons (Fuiman and Batty, 1997; Wieser and Kaufmann, 1998). Third, most of the temperate species were lab-reared larvae, usually evaluated in the laboratory, whereas the reef species were wild larvae evaluated in the field. Lab conditions may not be conducive to peak swimming performance, and lab-reared larvae and juveniles often swim much more slowly than do wild larvae or juveniles (citations in Leis and Carson-Ewart 1997; Leis and Stobutzki, 1999).

Other factors may favor better swimming by tropical reef fish larvae. As one approaches the equator, the magnitude of the Coriolis force decreases (Bakun,

TABLE 1 Comparison of Size at Various Developmental Milestones for Temperate and Tropical Fish Larvae^a

Taxon	Approximate size at first feeding (mm)	Size at caudal fin formation (mm)	Size at complete fin formation (mm)	Size at settlement (mm)
Herring (<i>Clupea</i>)	5–11	16–20	25–27	Not applicable
Cod (<i>Gadus</i>)	4–6	9–11	26–30	25–50
Benthic, temperate perciform fishes	2–3	3–5	4–8	8–20
Coral reef perciform fishes	2–3	3–5	4–10	7–75

^aInformation on cod, herring, and other temperate species from Moser (1996) and Fahay (1983) and on coral reef species from Leis and Carson-Ewart (2000).

1986). Some of the mechanisms that have been proposed to help structure “retention areas” in temperate systems involve Coriolis-force-mediated phenomena such as coastal upwelling (Bakun, 1986). To the extent that these phenomena might be less active in the tropics, there may be reduced scope for passive larval retention in the tropics, and therefore more selective pressure to attain active means of larval retention, including swimming. Finally, the selective regime in which reef fishes live—requiring, as it does, the location of small, scattered bits of habitat at the end of a pelagic stage—is far different from that faced by a cod or herring, and superior swimming performance by the larvae may be adaptive.

III. Recently Developed Research Tools

A. The Light Trap

The semiautomated light trap (Doherty, 1987b) is now widely used for sampling late-stage larvae for distributional studies. Little is known of how light traps actually catch larvae, why they usually capture almost exclusively late-stage (settlement stage) larvae, or what their catches actually represent in terms of larvae in the water column (Choat *et al.*, 1993). No one overtly claims that light-trap catches are quantitative, but, light traps are widely used for relative comparisons among locations or times. How catches might be affected by variations in ambient current speed, ambient light (either the moon, or cloud cover), or water turbidity is unknown. The radius from which a light trap draws its catch was estimated based on water clarity arguments to be up to 90 m (Milicich *et al.*, 1992), but this is untested, and seems excessive. Guessing a much smaller radius of 7–50 m, and depending on current speed, Choat *et al.* (1993)

estimated that a light trap could sample 40,000 m³ hr⁻¹, and argued that the ability to sample such huge volumes was a major advantage. Meekan *et al.* (2000) showed, primarily for pomacentrids, that capture efficiency of two light-trap designs was less than 10%, but that escape rates were relatively low and dependent on taxon: 5% of reef fish larvae, but 27% of clupeid larvae, escaped in 1 hour. They argued that low efficiency, provided it is relatively constant, is not an obstacle to use of light traps to study spatial and temporal patterns. Whether the range of efficiency values reported ($\pm 50\%$ of the mean) amounts to “relatively constant” depends on the research question. Larger fishes (clupeoids, scombrids, terapontids, etc), decapods, and cephalopods commonly enter traps, sometimes in large numbers, and may eat the captured larvae (personal observations), but nothing is known about the level of this “in-trap” predation and its effects on larval catches.

Light traps are highly selective on a taxonomic basis, working best with clupeids, lethrinids, pomacentrids, and some blennioids, serranids, and chaetodontids (Milicich and Doherty, 1994; Choat *et al.*, 1993; Brogan, 1994a; Hernandez and Lindquist, 1999; J. M. Leis and M. I. McCormick, unpublished results), but even within these families some species are virtually absent from catches. Light traps located directly over reefs or seagrass beds in shallow water sometimes capture large numbers of small, often just hatched, larvae from demersal eggs, primarily gobioids and blennioids (Brogan, 1994a,b; Riley and Holt, 1993; A. Cabanban, personal communication). Traps in slightly deeper water capture almost exclusively late-stage larvae ready to settle (Choat *et al.*, 1993; Milicich and Doherty, 1994; Hernandez and Lindquist, 1999), although at times light traps capture large numbers of pomacentrid larvae midway through larval development (Brogan, 1994a,b; J. M. Leis, unpublished data). Light-trap selectivity has led to a focus on the study of distributions

of larvae near the end of their pelagic phase (Kingsford, 1998).

Light traps also provide a convenient means to capture larvae without the damage often inflicted by towed nets. Light-trap-captured late-stage larvae can be used for a variety of both field and laboratory investigations (Stobutzki and Bellwood, 1997) on swimming abilities, settlement behavior, sensory abilities, orientation, physiology, and metamorphosis (see later). Light-trap larvae that have been allowed to metamorphose can be used in other field and laboratory studies of postsettlement issues that are beyond the scope of this chapter. All these studies have led to major advances in our understanding of larvae as animals, rather than as biologically inert drift cards. It is arguable that light traps have made their most significant contribution to reef fish biology in this way.

A critical unknown is the possible alteration to behavior or physiology that may result from attraction to, and retention within, a light trap. Usually, light traps are fished all night, so larvae may have been in the trap for several hours on recovery. Larvae of some species appear to be irreversibly "benthic" when removed from the trap in the morning, and refuse to swim in the pelagic environment (Leis *et al.*, 1996). What other, more subtle, alterations may have taken place in other species while in the trap, or while being held in the lab, remain to be determined.

Modified light traps that direct their catch to a nearby reef can enhance recruitment by two- to three-fold (Munday *et al.*, 1998). This is potentially useful not only in experimental work, but also in management of reefs. Interestingly, the taxa that recruited on the reefs differed in proportion from the catch in nearby conventional light traps. This might be the result of habitat selection at settlement by the larvae, as indicated by Munday *et al.* (1998), or an indication that among the taxa attracted to the light, entry into the trap is more selective than is settlement (Choat *et al.*, 1993). Light traps may have still other innovative uses not anticipated by their designers.

B. Larval Rearing

In the past 10 years aquarists and researchers have managed to rear a wide range of tropical reef fishes, over 100 species from at least 24 families. In some instances this may have reduced some of the pressure from aquarium collectors on the reef communities. Excitingly, a handful of dedicated researchers have reared reef fishes in sufficient quantities to allow the description of larval development and exploration of larval processes under controlled conditions.

Some success has been obtained by rearing larvae collected from the wild midway through their larval phase (e.g., McCormick and Molony, 1992, 1995), but most workers have had to rear larvae from eggs of captive brood stock. Initial success was with species, such as clown fishes, that spawn benthic egg clutches. Additional success has been achieved in Japan with the commercially important broadcast spawner, the coral trout, *Plectropomus leopardus* (Masuma *et al.*, 1993), and a number of wrasse species (Kimura and Kiriyama, 1993; Kimura *et al.*, 1998). Although some of the damselfishes, particularly the clown fishes, have been reared for decades, it is only recently that rearing has been used to elucidate important processes in the larval stage. Much of the work that we review was based on these studies. The ability to rear larvae from known parents, under manipulated environmental conditions, will undoubtedly yield our most detailed insight into the black box in the decade to follow.

C. *In Situ* Studies of Behavior

An approach that has proved fruitful in casting light into the black box of reef fish larval biology is the *in situ* observation of behavior. Divers can simply look for larvae and observe them. This has been successful in temperate waters (Breitburg, 1991, and references therein), but not generally in coral reef waters (but, see Kaufman *et al.*, 1992). However, wild larvae can be captured either by light trap or by fixed net, and then released and observed individually by divers in the pelagic environment, either in lagoons, over the continental shelf, in open ocean conditions, or in more shallow waters adjacent to reefs (Leis *et al.*, 1996). One diver concentrates on and follows the larvae, and does nothing else, while the other diver follows and notes depth and direction every 30 seconds and measures distance traveled with a flowmeter. Thus, three-dimensional trajectories of individual larvae can be constructed. When released near reefs, the reaction of the larva to the reef and its residents, and its settlement behavior, can be observed. In addition, "unplanned" observations on predation on or feeding by the larvae can be made. Many, but not all, species are amenable to this approach. Most species are seemingly not bothered by the nearby observer divers: they swim at a speed far below their maximum, and alter it to suit different situations, undertake no obvious avoidance behavior, frequently feed, may retreat to the shelter of the observer diver when threatened, occasionally try to "settle out" on the diver or his/her gear, and deliberately and carefully examine and often reject potential settlement sites over the reef before swimming

on (Leis *et al.*, 1996; Leis and Carson-Ewart, 1997, 1998, 1999).

This methodology has limitations: not all species are amenable to its use, it is very labor intensive, any bias in behavior of the larvae caused by the presence of the divers is unknown, it cannot be applied at night, and safety considerations limit *in situ* observations to depths less than 20 m. To date, the number of taxa examined *in situ* in this manner is relatively small, being largely a subset of the relatively small number of species captured by light traps. Capture of wild larvae by other methods that do not share the biases of light traps, or use of reared larvae *in situ*, can help overcome the first limitation. The method is inherently labor intensive, so only alternative methodologies can solve this problem. The use of high-tech equipment such as the "fish TV" sonar (Jaffe *et al.*, 1995) could help to assess diver induced bias. Because such equipment can be used at night and in unlimited depths, this should help to resolve some of the other limitations.

IV. Off the Reef and into the Blue

A. Egg Loss: Benthic versus Pelagic Spawners

There are two broad modes of spawning among coral reef fishes: benthic spawning of eggs followed by varying levels of parental care, and broadcast (or pelagic) spawning whereby eggs are released directly into the water column, with no subsequent parental care. Spawning mode does not appear to influence female fecundity or traits that may affect larval survival. Thresher (1984a) showed that pelagic and benthic spawners do not differ in fecundity when adjusted for size. Cowen and Sponaugle (1997) reviewed the available evidence supporting the idea that egg and larval traits are related to which spawning mode is adopted. They found no support for the suggestion that benthic spawners should have larger eggs than pelagic spawners, or shorter larval durations.

Spawning mode does appear to influence the initial mortality of the eggs prior to the embryos dispersing from their natal reef. The mortality levels of eggs from broadcast spawners is typically low immediately after egg release. Detailed observations over 2 years at a spawning site on Johnston Atoll showed that only 0.6% of broadcast spawnings were preyed on by planktivores (out of a total of 7448) (Sancho *et al.*, 2002). Observations suggest that planktivores are attracted to the gamete cloud for only a few seconds immediately

after a spawning rush and interest is lost soon after as the eggs are quickly dispersed by the prevailing water currents (e.g., Colin and Bell, 1991). Patterns of predation vary among localities on the same reef, from none (out of greater than 1000 observed spawning ascents) to low levels at other sites where pomacentrids were a more common component of the fish assemblage (Colin and Bell, 1991). Although generally low, the impact of planktivores on the gamete clouds was also found to vary for different species of spawners at the same site (Colin and Clavijo, 1988). Whether spawning is conducted in pairs or groups also influences the rates of gamete predation, with lower levels of predation after group spawning events (Sancho *et al.*, 2000a). Cannibalism can also contribute greatly to the loss of gametes immediately after release in some species of broadcast spawners. One field study on found that males of two of three species of razor wrasses (*Xyrichtys*) eat ova from 40% of spawnings (Nemtsov and Clark, 1994).

The only predation study that has come to our attention measured predation rates on the eggs of damselfishes, benthic-spawning reef fishes (*Pomacentrus amboinensis*), at Lizard Island (Emslie and Jones, 2001). As in many benthic spawners, the male guards the egg clutches until they hatch (4.5 days after spawning). Daily censuses of mapped clutches indicated that predation by fishes on eggs was high and varied among sites around the island. The mean egg loss from 20 monitored nests in each of four sites ranged from 14 to 40% per clutch, suggesting that for at least some benthic spawners, egg predation can be an important source of offspring mortality.

B. Out in the Blue: The Pelagic Biology of Reef Fish Larvae

1. WHAT INFLUENCES LARVAL SURVIVAL?

Although studies of temperate fisheries species have placed emphasis on the early life history traits that affect the ability of larvae to acquire food and avoid predation, most research on recruitment variability in coral reef fishes has focused on abundance patterns of larvae and the processes responsible for delivering them back to the reef (reviewed by Leis, 1991a). Recent research suggests that early life history traits, such as growth and length of larval life, influence recruitment variability in coral reef fish species as they do in temperate fish species.

Most mortality occurs during a pelagic phase that may range in duration from 8 days in some anemone fishes to greater than 120 days in some wrasses (Victor, 1991). It is well known that small changes in this initial

mortality rate can lead to large changes in the numbers of larvae surviving to settle to the reef population, even if reproductive output remains constant (Houde, 1987; Underwood and Fairweather, 1989). Any factors that influence these mortality rates will have an influence on the magnitude of recruitment of that cohort. It is becoming apparent that a complex of interacting factors determines the mortality schedules of a larval cohort. The quality of the eggs will influence the viability of the larvae. Larval growth rates have been shown to have a direct bearing on mortality schedules, with growth being influenced by features such as egg quality, larval density, food availability, water temperature, and the number of predators for the ontogenetic stage in question. Research on temperate species has stressed the importance of some of these factors for decades, but it is only recently that a handful of researchers started to explore their importance to the dynamics of tropical reef fishes.

a. Maternal Characteristics Influence Larval Quality Egg quality may have a profound influence on subsequent larval growth rates and mortality schedules. Very little research has been done on the importance of egg quality in coral reef fishes. Many of these fishes are protogynous hermaphrodites that are serial spawners, meaning individual females spawn numerous times during a spawning season. Many of these fishes are remarkably fecund, releasing hundreds of thousands to millions of eggs in a single spawning season (Sale, 1980). Breeding ambon damselfish females, *Pomacentrus amboinensis*, spawn every second day of an approximately 3-month spawning season, laying a monolayer of ~6600 eggs (Kerrigan 1994; Kerrigan and McCormick, 2001).

It is unknown how the nutritive quality of the eggs changes through the spawning season. However, information from following the egg output of individual *P. amboinensis* throughout the main portion of the 3-month spawning period suggests that there may be a general trend for a reduction in the size of eggs over the spawning season (Fig. 2). Interestingly, there was no reduction in clutch size over the same period, suggesting that clutch size was being maintained at the expense of egg quality in this species (M. I. McCormick, unpublished data). The trend for reduced egg sizes later in spawning season has been found for serially spawning temperate fish species such as the Atlantic cod, *Gadus morhua* (Chambers and Leggett, 1996).

The size of larvae that hatch from benthic embryos can vary considerably among local populations of a coral reef fish. McCormick (1999b) and Kerrigan and McCormick (2001) showed that the size of newly

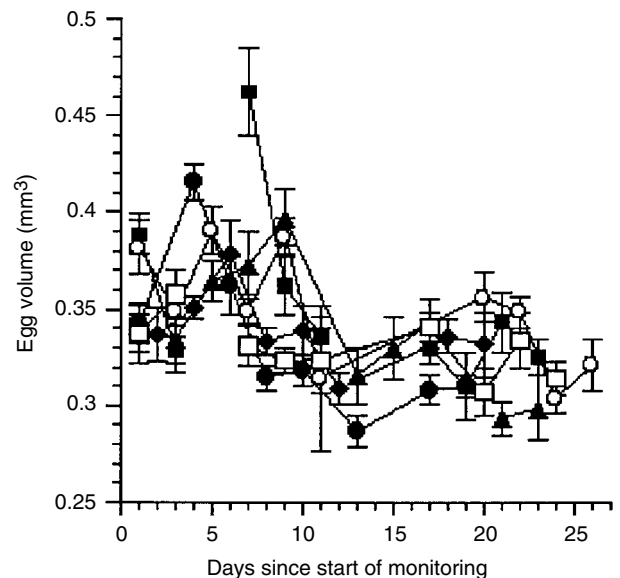


FIGURE 2 Trends in mean egg volume (\pm SE) among consecutive clutches for five females of the damselfish *Pomacentrus amboinensis* over a 4-week period in the middle of the breeding season.

hatched larval *P. amboinensis* ranged between 2.56 and 3.39 mm SL (mode 3.1 mm), with more variability attributable to differences among clutches within a location (47%) than within individual clutches (29%) or differences among localities (24%). Similarly, yolk sac size at hatching varied over a threefold range (0.04–0.13 mm²), with most variability found at the local scale and attributable to differences within clutches (64%) and among clutches (35%) rather than to those at the locality level (2%). Much of the variability in these qualitative attributes of early stage larvae can be attributed to differences (among individuals) and changes (within an individual) in the maternal energy investment in offspring.

The nutritional condition of the mother at the time of gametogenesis can influence the quality of the offspring she produces, and this will directly influence larval mortality rates. Kerrigan (1997) experimentally manipulated food availability for a 4-week period for two size classes of breeding female *P. amboinensis* at Lizard Island. To enable the egg output to be quantified, these polygamous damselfishes were placed in breeding pairs on isolated patch reefs. Kerrigan found that, regardless of female size, supplementary fed females produced larvae that were larger at hatching and possessed larger nutritive yolk sacs than did nonsupplementary-fed females. Although supplementary-fed females produced larger and more nutritively rich offspring, clutches of eggs were the same size as nonsupplementary-fed

females of the same size. Maternal liver size, the metabolic powerhouse, was found to be the best predictor of size of the larvae that the females produced (Kerrigan and McCormick, 2001).

The behavioral interaction the mother experiences during egg production profoundly influences the characteristics of her offspring. Kerrigan (1997) found that when an additional female, restrained in a glass container, was introduced into the patch reefs occupied by a pair of breeding *P. amboinensis*, then the unrestrained females produced larger offspring, regardless of whether the females had been supplementary fed. Maternal behavioral interactions appear to influence progeny characteristics through alterations in the maternal hormonal system. Maternal hormones play an important role in development of fish offspring, as they do in other vertebrates (Clark and Galef, 1995, 1998). Developmental hormones aliquoted to the egg during gametogenesis govern developmental rates prior to the production of these hormones by the embryo. Current evidence suggests a direct link between hormones in the maternal plasma and the eggs the female produces, with developmental (e.g., thyroxine, triiodothyronine), reproductive (e.g., testosterone, estradiol), and metabolic (e.g., cortisol) hormones transferred passively (Schreck *et al.*, 1991; Hwang *et al.*, 1992; Mylonas *et al.*, 1994).

All the behavioral interactions and environmental alterations are interpreted through the fishes' sensory systems and then transformed into hormonal signals by the action of the hypothalamus and pituitary gland. Hormones associated with sensory responses and body maintenance form a potent cocktail that is transported through the plasma of the circulatory system and is in direct contact with the developing oocytes in the ovary during egg formation. During gametogenesis these hormones are incorporated into the yolk sac, which forms the nutritive store prior to the start of larval feeding. Two steroid hormones that are of particular ecological interest are the corticosteroids cortisol, which has been used as an endocrinological indicator of stress (Pankhurst and Van der Kraak, 1997), and testosterone.

Cortisol can directly influence larval morphology. McCormick (1998b) found a correlation between levels of cortisol in the ovaries of breeding females and the size of their larvae in a natural population of tropical damselfishes. In this instance, female cortisol levels appeared to be elevated by high densities of egg predators around the nest site. Elevation of maternal cortisol to levels within the natural range for a species, using cortisol implants, resulted in the production of smaller larvae. Detailed laboratory experiments con-

firmed this and found that cortisol directly affects larval growth and developmental rates (McCormick, 1999a, also unpublished data). Further, a small increase in the amount of testosterone in the eggs increase the size of the yolk sac at hatching (McCormick, 1999a). It is thought that testosterone may improve the efficiency with which nutrients within the yolk are used. The importance of these hormonal mechanisms in influencing variability in larval characteristics is highlighted by the finding that larval morphology can be made to span the whole range of natural variability in body attributes by simply altering the levels of cortisol and testosterone that embryos are exposed to, within naturally occurring limits (McCormick, 1999a).

Maternal condition appears to have an important and as yet poorly studied influence on the initial morphology of coral reef fish larvae. Many questions remain unanswered. Is this variability accentuated over the rest of the larval phase by the selective forces, such as size- or growth-selective processes (see Chapter 10, this volume)? Are there long-term post-settlement effects on individuals? Studies of terrestrial vertebrates, such as rodents and birds, suggest that the embryonic hormonal regime influences important milestones, such as size at maturity, success in competing for mates, and overall reproductive fitness and survival (e.g., Clark and Galef, 1998; Price, 1998). Studies are currently being conducted by Mark McCormick to determine the extent to which maternal characteristics influence postsettlement events in coral reef fishes.

b. Importance of Larval Growth The theory that larvae that grow and develop faster have higher survival and enhanced recruitment (i.e., "stage-duration" hypothesis, Chambers and Leggett, 1987; Houde, 1987; Hare and Cowen, 1997) is now supported by several field studies of temperate species (Campana, 1996; Meekan and Fortier, 1996; Fortier and Quiñonez-Velazquez, 1998; Meekan *et al.*, 1998) and by recent work on tropical species. Bergenius *et al.* (2002) back calculated larval growth history from daily collections of newly settled Caribbean surgeonfish, *Acanthurus chirurgus*. They found a strong correlation between the growth rate immediately after the start of the first feeding and the magnitude of the settlement pulse ($r = 0.76$; see Fig. 3). This period, between 9 and 12 days after hatching, is the period of exponential growth for this species and appears to represent a "critical period" in the larval life history. Average larval growth rates in the Caribbean damselfish, *Stegastes partitus*, accounted for 83% of the variability in the magnitude of light-trap catches of this species on a monthly basis (Wilson, 2000).

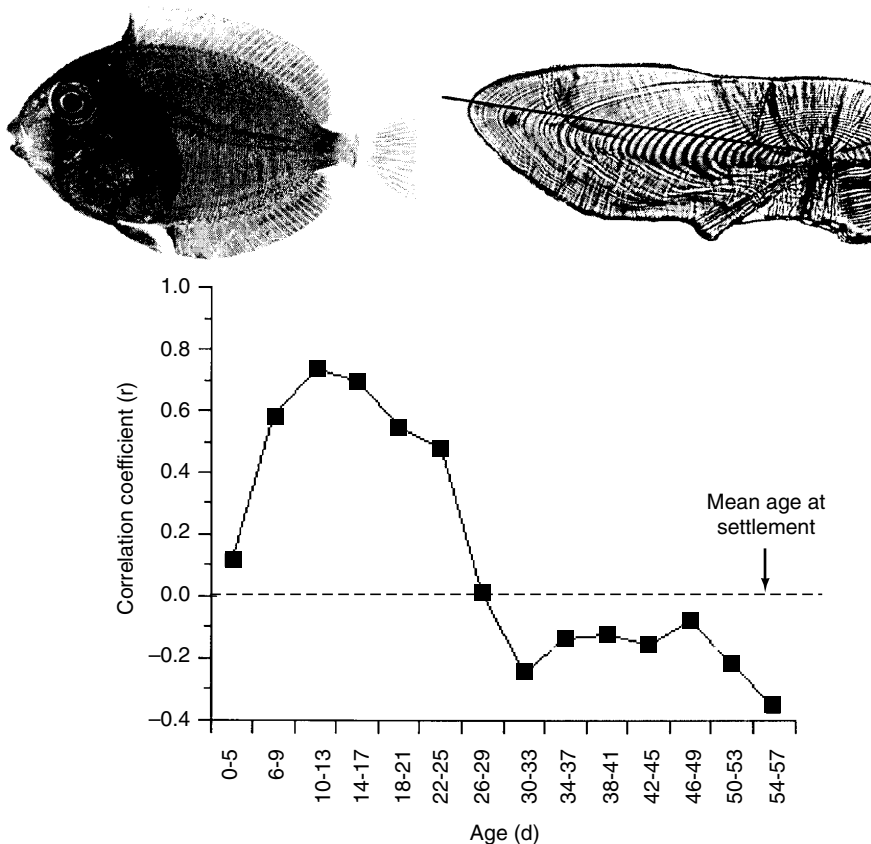


FIGURE 3 Importance of larval growth to survival. Coefficients (r) from correlation analyses between average growth rate during 4-day intervals of pelagic life and monthly settlement of a Caribbean surgeonfish, *Acanthurus chirugus*, to a San Blas (Caribbean) reef. Newly settled fish were collected over 44 consecutive lunar months (1984–1987) and their growth history was determined using the microstructure of their sagittal otoliths (adapted from Bergenius *et al.*, 2002).

To date, these are the only attempts to examine the influence of growth history on larval mortality rates. The use of otoliths to delve into the larval growth history of tropical fishes is a useful and underutilized approach (see Chapter 11, this volume). Decades of larval research on temperate fisheries species have led to identification of a number of key or critical periods in the life phase that may prove to be useful foci for tropical larval research. Critical periods have been identified at first feeding, during swimbladder inflation, and during metamorphosis at the end of the larval phase (Blaxter, 1988b).

Starvation has been suggested as a potentially important source of larval mortality in nutrient-poor tropical waters. To date, however, very little information is available on the influence of food availability on larval performance and mortality schedules. This is in part because of the difficulty of identifying tropical larvae to species. The only study to illustrate that starvation can be an important source of mortality in tropical larvae was conducted on three scombrid species in the Panama Bight (Margulies, 1993). Using a combination of field and laboratory studies, it was shown that susceptibility to starvation was stage specific and that preflexion larvae could suffer significant daily losses ($62\text{--}63\% \text{ day}^{-1}$).

Food availability influences growth rates and larval duration in reared larvae. Laboratory-based larval rearing experiments that have manipulated food availability into three or four levels have been conducted using a tropical goatfish [*Upeneus tragula* (McCormick and Molony, (1992))] and two damselfishes [*Amphiprion melanopus* (Green and McCormick, 1999) and *Pomacentrus amboinensis* (M. I. McCormick and B. Green, unpublished)]. For all species, greater access to food increased developmental rate (reduced pelagic larval duration) and increased the size of fishes at metamorphosis. Furthermore, when exposed to the same densities of prey, larvae from the high-food-density treatments fed at a higher rate than did larvae from the low-food-density treatments. This suggests that feeding history influences both how a larva will react when it encounters food and the larva's subsequent growth potential. It is presently unclear how feeding history influences metabolic efficiency, but this will undoubtedly be an important feature linking food intake to somatic growth and development.

Interestingly, McCormick and Molony (1992) found that if given the opportunity, midway through their pelagic stage, larvae that had been starved almost to the point of no return were able to compensate for poor growth. Larvae of the goatfish, *Upeneus tragula*,

starved for 3 days and then fed *ad libitum*, settled at the same size, weight, and lipid content as compared to fishes that had been continuously fed. Evidence suggests that these fishes are physiologically well suited to coping with a patchy food resource. Starved fishes did, however, have a lower developmental rate and overall growth rate as compared to the fully fed fishes, suggesting that the former may have sustained lower survival if mortality was growth or size-selective in the field.

Water temperature has a direct influence on larval growth and developmental rates in both temperate and tropical fishes (Benoît *et al.*, 2000). The only study of the effects of temperature on larval developmental rates in a tropical reef fish (McCormick and Molony, 1995) supported the large body of information on the influence of temperature on vital rates in temperate fishes (e.g., Chambers and Leggett, 1987; Francis, 1994; Brander, 1995; Rutherford and Houde, 1995; Hunte von Herbing and Boutilier, 1996). Higher temperatures sped up development, leading to shorter PLDs. Moreover, of the tropical goatfish studied, when food was unlimited, water temperature did not affect the nutritional condition or muscle development at metamorphosis.

Wind has been suggested to affect the feeding ability of larvae and therefore to have secondary effects on larval growth (MacKenzie *et al.*, 1994; Gallego *et al.*, 1996; Dower *et al.*, 1997). Dixon *et al.* (1999) found a dome-shaped relationship between wind speed (4 to 8 m sec⁻¹) and the numbers of competent larvae of damselfishes (*Pomacentrus amboinensis*) caught in light traps around Lizard Island. There was a 16-day lag between wind stress and impact on larvae. This relationship is believed to be a product of wind-generated turbulence [a cubic function of wind speed (Oakley and Elliott, 1982)]. Turbulence above or below a certain optimum reduces the effectiveness of prey capture and consequently results in reduced growth (Dower *et al.*, 1997).

2. SWIMMING ABILITIES

The late larvae of coral reef fishes are strong, “effective” swimmers, capable of sustained speeds higher than ambient currents and of swimming nonstop for tens of kilometers over tens of hours. Further, they are much faster than larvae of temperate species of similar size, particularly the well-studied Clupeiformes and Gadiformes. This surprising information on settlement-stage larvae is the result of laboratory swimming chamber (or flume) measurements of swimming endurance [51 species of 9 families (Stobutzki and Bellwood, 1994, 1997; Stobutzki, 1998)] and *in situ* speed measurements of free-swimming larvae [over 50 species of

15 families (Leis and Carson-Ewart, 1997)]. A comparison of the two approaches is found in Leis and Stobutzki (1999). Speeds mentioned herein are sustained speeds, unless otherwise stated.

Temperate fish larvae of 1–2 cm apparently swim at 1–5 BL sec⁻¹ (Blaxter, 1986; Miller *et al.*, 1988; Meng, 1993; Williams *et al.*, 1996b), whereas similar-sized larvae of coral reef fishes swim at a mean speed of 13.7 BL sec⁻¹ with some as fast as 34 BL sec⁻¹ (Leis and Carson-Ewart, 1997, 1999, 2001). Put into perspective, a freestyle swimmer capable of 13.7 BL sec⁻¹ would swim the 100-m race in 3.6 seconds; the Olympic record is 48 seconds. The actual speeds of reef fish larvae average 20.6 cm sec⁻¹ with some as fast as 65 cm sec⁻¹. This is faster than the average ambient current speed in the study area, so the average reef fish larva near the end of its pelagic stage is indeed an “effective” swimmer. As an aside, we note a tendency for biologists to assume that average currents are stronger than they really are. For example, Barlow (1981) considered 5 km hr⁻¹ (1.38 m sec⁻¹) to be a “typical” current speed. This is a typical speed for the Gulf Stream, and perhaps tidal jets, but average speeds in the vicinity of coral reefs where propagules are actually put into the water are rarely more than 10–20% of that value (e.g., Andrews and Pickard, 1990; Burrage *et al.*, 1994; Young *et al.*, 1994). This means that effective speeds are often lower than is widely assumed.

Just as remarkable as their swimming speeds, these larvae have great endurance, being able to swim an average of 40.7 km (some up to 140 km) in the lab unfed and without rest before exhaustion (Stobutzki and Bellwood, 1997). The mean time to exhaustion was 83.7 hours (maximum 288.5 hours). On a per-size basis, this is equivalent to a human swimming roughly 4000 km. The *in situ* swimming speeds of these larvae are strongly correlated with their lab endurance ($R^2 = 0.60$ to 0.77 , depending on whether the comparison is at the family or species level) (Leis and Stobutzki, 1999), indicating that good swimming performance is independent of the means used to characterize it.

Swimming far and fast may simply increase the possibility of encountering a reef by chance alone, but pelagic reef fish larvae in blue water may be able to detect and orient to reefs (see Section IV,B,5). Orientation combined with effective swimming abilities would greatly increase the capacity of larvae to find a reef. In either case, this capacity would vary among species because swimming abilities vary among species.

In settlement-stage larvae both swimming speed and endurance are positively correlated with the size among taxa (Stobutzki and Bellwood, 1997; Leis and Carson-Ewart, 1997), although the relationships are not strong—explaining less than half the variation in

swimming performance among taxa. However, it must be emphasized that swimming performance is known for only a small fraction of reef fish species or families (Leis and Stobutzki, 1999). For example, we have no information on larvae of eels, scarids, labrids, most blennioids, and most gobioids. These groups are among the most speciose on coral reefs, so this represents a large hole in our understanding of swimming performance (and other behaviors) of larvae, and in our attempts to generalize. Even within families for which some data are available, the numbers of species studied are usually small. Approximately 20 species of the lutjanid subfamily Lutjaninae (shallow-water tropical snappers) occur in the Great Barrier Reef region (Randall *et al.*, 1997), but only three species are frequently caught in light traps, and one of these is unsuitable for study (J. M. Lies, unpublished). Equivalent numbers for serranid groupers are 50 and 3. Aside from the Pomacentridae and Apogonidae, the situation is similar for other studied families in the Great Barrier Reef region. Finding a means to obtain and study underrepresented taxa would be very valuable.

Larvae begin their pelagic phase as plankton (weak, ineffective swimmers, with little or no control over trajectory, except, perhaps, vertically) but end it as nekton (strong, effective swimmers, with great control over trajectory). Here we have key question: When during the pelagic phase do the larvae change from plankton to nekton? Nearly all information on swimming abilities currently available is on late- or settlement-stage larvae. Leis and Carson-Ewart (1997) reported that small (6–8 mm SL) pomacentrid (*Pomacentrus?*) larvae about midway through development, but with caudal fins formed, had *in situ* swimming speeds of 3–7 cm sec⁻¹ (about 6 BL sec⁻¹). This is higher than speeds of temperate larvae of similar size, but not “effective” near Lizard Island, where average current speeds are 10–15 cm sec⁻¹ (Frith *et al.*, 1986). Unfortunately, obtaining such small, wild larvae in good condition for *in situ* studies is very difficult, and it is likely that the answer to the key question of phase change will be provided with laboratory-reared larvae. However, swimming abilities of lab-reared larvae and wild larvae must be compared, because it is by no means assured that they are equivalent (Duthie, 1987; Cobb *et al.*, 1989). Based on laboratory measurements of reared larvae, Fisher *et al.* (2000) provided the first report of swimming ability development in reef fish larvae. They found that swimming speed increased steadily with age, but that swimming endurance increased abruptly, and that both swimming performance and the timing of improvements in it varied among the three species they studied. The two pomacentrids had attained swimming

ability sufficient to “significantly influence dispersal” only 1–2 weeks following hatching (about 70% of the way through the pelagic phase). The apogonid was a much poorer swimmer.

Swimming ability is more dependent on state of development than it is on size per se. Fisher *et al.* (2000) found this to be the case. This is also suggested from the fact that the mean *in situ* speed of settlement-stage *Chromis atripectoralis* and *Chromis viridis* (7–9 mm) was 19–24 cm sec⁻¹, whereas the swimming speed of similar-sized but less developed (not settlement stage) *Pomacentrus* (?) larvae was 3–7 cm sec⁻¹ (Leis and Carson-Ewart, 1997). Many larvae are much larger than this at settlement, and it is tempting to predict that they will be “effective” swimmers for most of their pelagic stage, i.e., that portion of development following full development of their fins. Fins are essentially fully developed in most reef fish larvae at 5–10 mm (Leis and Carson-Ewart, 2000). Although growth rates during different portions of the pelagic phase are not well known, it appears the majority of the pelagic phase of most reef fish species occurs after the fins form. However, the data required to test this prediction are essentially lacking and the critical factor might be muscle development rather than fin development, per se. According to Matsuoka (1998) “true sustained swimming can occur only after the stratification of the red [muscle] fibres.” Development of red muscle can vary among species. There are no studies of muscle development in reef fish larvae, but in temperate sparid and serranid larvae, pink muscle formed “towards the end of the larval life” (López-Albors *et al.*, 1998) and red muscle “at the end of larval development” (Ramírez-Zarzosa *et al.*, 1998). In a subtropical sparid, red muscle appeared at 7 mm (TL), and only three to four layers were present at 11.2 mm (Masuda and Tsukamoto, 1996). In contrast, in a subtropical carangid, red muscle appeared at 4.3 mm (TL), there were five to six layers at 8 mm, and 10 layers at 12.4 mm (Masuda and Tsukamoto, 1996, 1998). Because of accelerated muscle development, the carangid should be a better sustained swimmer than the sparid is at all sizes. Histological studies of muscle development in larval reef fishes might shed considerable light on the question of swimming ability. Because of their superior swimming performance, we expect that reef fish larvae would develop red muscle at a small size, and would rapidly add muscle layers with growth.

At least some species rapidly lose some of their swimming abilities on settlement (Stobutzki and Bellwood, 1994). Juveniles of three pomacentrid species a few days following settlement were able to maintain top speeds [critical speeds; see Leis and

Stobutzki (1999)] that were on average only 69% of those of settlement-stage larvae. This implies large changes in muscle physiology and probably morphology over a very short time. Settlement stage reef fish larvae are fast enough that they should cruise swim in an inertial hydrodynamic environment (i.e., high Reynolds number, as do adults), whereas smaller larvae cruise swim in a viscous environment (low Reynolds number) (Webb and Weihs, 1986). However, the somewhat lower viscosity of seawater at tropical temperatures might lower the size at which larvae move from a low to high Reynolds number (Fuiman and Batty, 1997). This is supported by Fisher *et al.* (2000), who conclude that only the smallest reef fish larvae operate in a viscous environment. This means that reef fish larvae, because of their rapid development and high swimming speeds, pass into the more energy-efficient realm of inertial swimming when younger and at smaller sizes than do temperate larvae. This might result in greater growth efficiencies that would further accelerate development rates. It also might mean that the high-drag "chaetodontiform" shape [truncated, gibbose body; see Webb and Weihs (1986)] of many late-stage reef fish larvae does not carry a high cost in swimming efficiency.

Not only does swimming speed differ among taxa, and within taxa ontogenetically, but it can also differ among different environments or with swimming directions. Reef fish larvae are flexible and adopt different swimming speeds in different situations. Larvae of the coral trout (Serranidae: *Plectropomus leopardus*) swim two to three times faster when leaving the vicinity of a reef than when approaching the reef (Leis and Carson-Ewart, 1999). They also swim at the higher speed in open water >1 km from a reef. Similar differences were evident in the swimming speeds of butterfly fishes and damselfishes (J. M. Leis and B. M. Carson-Ewart, unpublished data). The damselfish, *Chromis viridis*, swims 26% faster in an atoll lagoon than in the open ocean 1 km outside the atoll (Leis and Carson-Ewart, 2001). However, two other species show no difference in swimming speed in either of the two environments. This flexibility shows how much control these late-stage larvae have, and indicates that modeling of swimming will be complex, and dependent on where the larvae are and even in which direction they swim.

3. SCHOOLING

Schooling in clupeoids, carangids, and some other temperate species begins at sizes smaller than those at which many reef fishes settle (Leis, 1986b; Blaxter, 1991; Kingsford and Tricklebank, 1991; Masuda and Tsukamoto, 1996, 1998), and the clumped distribution

of newly settled reef fishes has led to speculation that schooling by reef fish larvae prior to settlement is likely (see Leis, 1991a). The observations of mass movement of acanthurid larvae along the reef bottom by Sancho *et al.* (1997) also imply schooling prior to settlement. Presettlement, pelagic schooling occurs in mullets, and in at least two species of pomacentrids, a microdesmid, and a caesionine lutjanid (McCormick and Milicich, 1993; Leis and Carson Ewart, 1998). One of the settlement-stage pomacentrids was schooling at 7–10 mm. All these species school to some extent as reef-associated juveniles, so schooling prior to settlement should not be surprising. In contrast, limited observations on chaetodontid larvae showed no tendency to school (J. M. Leis, unpublished). In addition, larvae of several temperate reef and coral reef fishes school pelagically (Kingsford and Tricklebank, 1991) and epibenthically prior to settlement (Breitburg, 1991; Lindeman *et al.*, 2001), so this could be a widespread behavior. In principle, because fins, eyes, and other sensory systems are present, schooling seems morphologically feasible for much of the pelagic period of reef fishes. An unanswered question is how the larvae in the pelagic environment find each other, to begin to school. Average densities of larvae are low in tropical waters (Leis, 1991a), so on average, huge volumes of water must be searched before a larva will encounter a conspecific. Perhaps the concentration of larvae at physical interfaces (e.g., the surface, thermoclines, the shoreline) or in hydrographic structures such as fronts or convergence zones plays a role in initiation of schooling.

Presettlement schooling by larvae, if widespread, has obvious implications for patterns of settlement and recruitment, for our interpretation of these, and for sampling design. Not the least of these is that settlement of a schooling larva would not be independent of the other individuals in the school (Breitburg *et al.*, 1995). Schooling in larvae might also have the antipredator advantages that are normally attributed to schooling in adults, and could act to enhance the orientation of larvae (many sets of sense organs may be better than one) and, therefore, the ability of larvae to locate reefs and settle onto them.

4. VERTICAL DISTRIBUTION

The vertical distribution of fish larvae largely determines the physical and biological conditions in which they actually live, because gradients in these factors are frequently stronger in the vertical plane than in the horizontal. Currents differ in both direction and speed with depth, and because currents influence distributions of larvae, it is important to understand by which currents the larvae are actually affected.

Similar arguments apply to food concentrations, predator abundance, light levels, and a host of other factors. Leis (1991a) noted a paucity of information on the vertical distribution of reef fish larvae, particularly in the open ocean, but progress has been made in this area, especially in studies using plankton nets and midwater trawls (see Clarke, 1991; Boehlert *et al.*, 1992; Cha *et al.*, 1994; Cowen and Castro, 1994; Boehlert, 1996; Boehlert and Mundy, 1996; Cowen and Sponaugle, 1997). Such towed nets capture primarily younger larval stages (Choat *et al.* 1993).

Light traps have the potential to measure vertical distribution of older, larger larvae that are poorly sampled by towed nets, but only at night. A single study using this methodology has been published (Doherty and Carleton, 1997). Deep traps captured an assemblage of larvae distinct from that found in surface traps, and this was primarily due to differences in the relative abundance of clupeoids, monacanthids, and a pomacentrid (*Dascyllus*). Larvae of most species were more abundant in surface traps, although the picture was complicated by differences in ontogenetic stage between surface and deep catches. Large settlement-stage individuals of several species in at least five families were captured only in deep traps.

Studies of vertical distribution of larvae using *in situ* behavioral methods reveal both species-specific behaviors and behavioral flexibility (Leis *et al.*, 1996; Leis and Carson-Ewart, 1999, 2001). This approach complements towed-net studies by providing data on late-stage larvae, and light-trap studies by providing daytime data.

The most striking thing evident to date from the *in situ* work is the flexibility in vertical distribution behavior. In one study, larvae of four species of four different families selected shallower depths in an atoll lagoon than they did in the ocean 1 km offshore (Fig. 4) (Leis and Carson-Ewart, 2001). Similarly, larvae of a serranid and a chaetodontid swam much deeper 1 km off the windward side of an island than they did 1 km off the leeward side (Leis and Carson-Ewart, 1999, also unpublished). The serranid swam at similar depths in the immediate vicinity of both windward and leeward reefs, a depth that was similar to that chosen 1 km off the leeward side of the island. It is not obvious why swimming depth differs among locations, although one influence may be the light regime. In the areas where swimming depth was great, there was little upwelling light, either because of depth (the ocean) or because of dark bottom color (algal beds on the bottom off the island). In the areas where swimming depth was less, sandy bottoms resulted in upwelled, reflected light, even when the bottom could not be seen. In contrast, in the

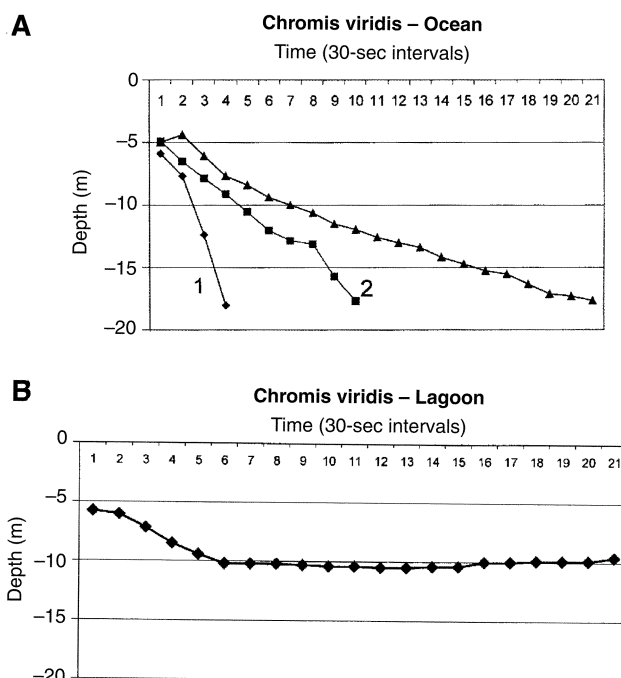


FIGURE 4 Comparison of *in situ* vertical swimming behavior of the pomacentrid, *Chromis viridis* at Rangiroa Atoll, Tuamotu Islands (from Leis and Carson-Ewart, 2001). All fish were released at a depth of 5 m and were followed for 10 minutes. (A) In the ocean, 1 km from the reef crest on the north side of the atoll, at a water depth of ~300 m. Lines are trajectories of individual larvae, and larvae were not followed below 18–20 m. Between lines marked 1 and 2 are 13 other lines not shown. (B) In the atoll lagoon, 1 km offshore, at a water depth of ~25 m. The line is the mean trajectory of 16 larvae. The standard error of each point on the line varies from 0.5 to 0.8 m.

lab, larvae of a temperate clupeid have a different vertical distribution behavior when placed in estuarine water as compared to ocean water (Forward *et al.*, 1996), implying a change in behavior due to a chemical sense. Further investigation is clearly warranted, and other factors such as directional stimuli emitted by the reefs (see below), or variations in turbulence due to wave action, should not be ignored. Turbulence affects the vertical swimming behavior of temperate crab larvae (for example, Welch *et al.*, 1999).

Variations in vertical distribution behavior among species are evident (Leis *et al.*, 1996), as studies using towed nets would lead one to expect. Some species at least in some situations had highly predictable vertical distributions (Fig. 4), whereas other species had large variations among individuals. What is perhaps less expected was the variation in depth range (amplitude) that individual larvae displayed. Amplitudes of >9 m

for individuals were not uncommon, as were numerous descents and ascents of several meters during the 10-minute observation period (Leis *et al.*, 1996; J. M. Leis, unpublished). This highlights one of the shortcomings of traditional vertical distribution studies using nets or even light traps: they measure population vertical distributions, without any means of identifying what individual larvae are doing (Pearre, 1979). For example, if 60% of larvae are captured at a particular depth, traditional studies provide no information as to whether the same 60% of individuals remain at that depth, or if there is movement of individuals among depths. The *in situ* studies suggest the latter may be the case, and that vertical movement of individuals may be large and frequent. However, it is also possible that such vertical excursions are limited to older larvae, and not found in the smaller, younger larvae that dominate net samples (but not light-trap samples). Such excursions could be a means of determining if the bottom is suitable for settlement, a means of locating vertically stratified concentrations of food, or even a means of obtaining orientation cues. The last could involve ascent to assess sun angle, descent to evaluate movement over the bottom, or both to locate vertically stratified water masses that could differ in a variety of physical, chemical, or biological cues or in flow characteristics.

Larvae may also occur near the bottom, in or near the benthic boundary layer, and if so, this would greatly limit passive dispersal. Epibenthic larval distributions have been identified by *in situ* observations in temperate systems (Breitburg, 1991), but there is little information on them in coral reef systems. Few larvae actually swam near the interreefal bottom for anything but very short periods (<1 minute) before attempting to settle near Lizard Island (Leis and Carson-Ewart, 1998). No larvae of coral reef fishes were identified as being in high abundance near the bottom in net tows taken in the same area (Leis *et al.*, 1989). Predation rates on larvae are high in the epibenthos near Lizard Island reefs, with lizard fishes particularly active (Leis and Carson-Ewart, 1998, also unpublished). This could explain why the scant available information indicates that few coral reef fish larvae have epibenthic distributions.

The visual capabilities of larvae can influence vertical distributions. In the laboratory, visual sensitivity in larvae of three apogonid and four pomacentrid species increased with age, and the apogonid larvae had greater sensitivity than did the pomacentrids (Job and Bellwood, 2000). This means that younger larvae should be restricted to shallower depths than older larvae, and that pomacentrid larvae should be restricted to shallower depths than apogonid larvae. This is broadly

in accord with the vertical distributions of these taxa found in the field. Pomacentrid larvae are typically most abundant at very shallow depths (references above), such that during the day have considerably higher light levels than the minimum required for feeding as identified by Job and Bellwood (2000). The results of such studies should not be expected to predict the details of vertical distributions, but they should specify depth floors below which larvae would not be anticipated because they do not have enough light to feed.

5. ORIENTATION IN THE PELAGIC ENVIRONMENT

Orientation is required if a pelagic reef fish larva is to find a reef by other than chance, and orientation requires not only cues and the sensory means to detect reefs, but also the ability to determine the direction from which the cues emanate. The existing information on the swimming behavior of reef fish larvae in the pelagic environment indicates that larvae do orientate rather than merely cruise about randomly. What cues they can detect and use to achieve this is less clear.

Settlement-stage larvae in open water tend to have roughly linear horizontal trajectories (Fig. 5), or at least trajectories that are significantly different from random (Leis *et al.*, 1996; Leis and Carson-Ewart, 1999, 2001). For example, 89% of over 100 *Chromis atripectoralis* larvae released in open water near Lizard Island had nonrandom trajectories (J. M. Leis, unpublished). In the vicinity of reefs, trajectories are more complex. Larvae that swim away from reefs when released adjacent to them most commonly had linear trajectories. More complex trajectories that are clearly influenced by the structure of the reef and the distribution of reef habitats and resident fishes are noted in larvae swimming toward or over reefs. Some individuals swim away from the reef, out of sight of it, and then return (Fig. 5) (J. M. Leis, unpublished). This behavior implies either a good memory for reef location, or the ability to detect a reef remotely and return to it.

Thus far, studies of trajectories of larvae in open water have not clearly shown that larvae can detect remote reefs. At Lizard Island, Leis *et al.* (1996) analyzed the open water trajectories of a group of larvae of several species, each released individually, and showed that individual trajectories of most were nonrandom, and that on average the trajectories differed among three locations on different sides of the island, and were offshore at each location. This implied that the larvae could sense the island from >1 km offshore. At an oceanic atoll, nearly all trajectories of four species were nonrandom and usually linear regardless of location (Leis and Carson-Ewart, 2001). However, a difference

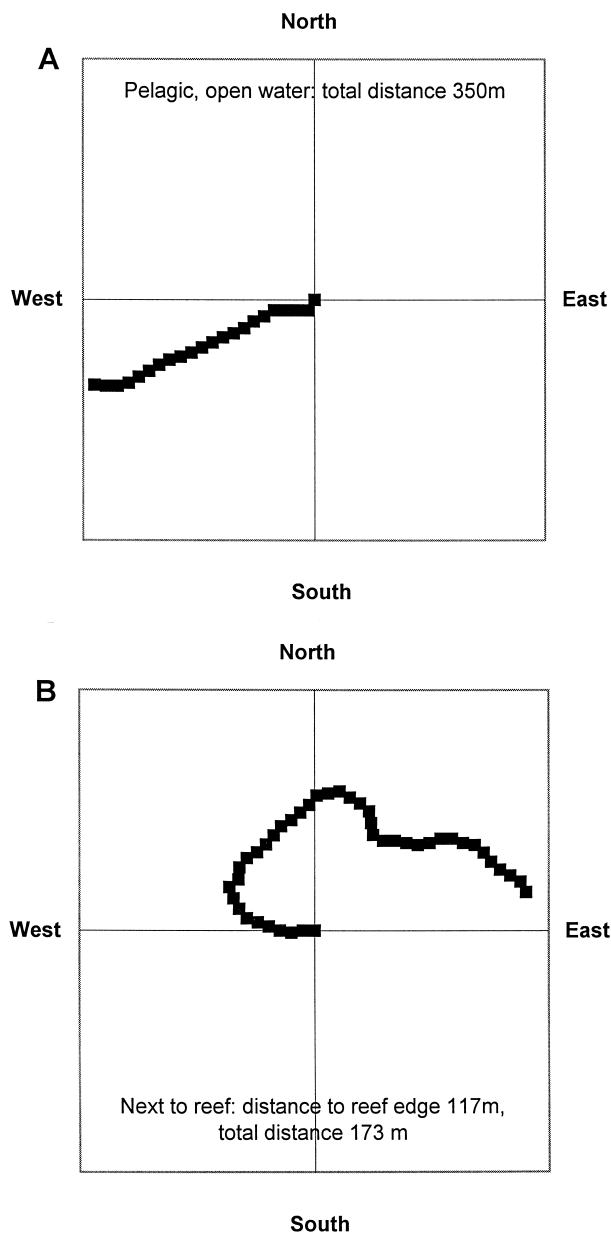


FIGURE 5 *In situ* horizontal swimming trajectories of reef fish larvae. Constructed from bearings taken every 30 seconds and plotted assuming constant speed throughout. Trajectories are relative to a possibly moving water column, not relative to the bottom. A and B not to same scale. Fish released at the origin. (A) A linear trajectory of a larval acanthurid, *Acanthurus triostegus* (~25 mm), in the open, pelagic environment in the lagoon of Rangiroa Atoll, Tuamotu Islands. Total distance swum was 350 m (average speed, 58 cm sec⁻¹). (B) A complex trajectory of a larval pomacentrid, *Chromis atripectoralis* (~9 mm), adjacent to and over a reef at Lizard Island. Slow current was running to the north. Larva released over sand bottom about 5 m to the west of the reef edge, which ran approximately along the north-south axis. Larva initially swam offshore, possibly in response to a school of fusiliers,

in swimming direction between the atoll lagoon and the ocean north of the atoll was not detected, nor was the distribution of average swimming directions significantly different from random at either location for any species. Other investigations specifically aimed at the orientation of larvae in open, pelagic waters are underway at Lizard Island (J. M. Leis, unpublished).

Somewhat more equivocal support for long-distance orientation by larvae comes from studies of distribution utilizing light traps. The distribution patterns of late larvae of coral reef fishes detected by light traps in the vicinity of a coral reef led Doherty and Carleton (1997) to suggest that "habitat discrimination begins while reef fish are still in the plankton." They speculated that sound was the most likely orientation cue. In contrast, Doherty *et al.* (1996) speculated that warm surface plumes emanating from a lagoon of another reef provided the cues that enabled larvae of a pomacentrid to avoid that lagoon (as shown by their light-trap catches).

Closer to shore, Stobutzki and Bellwood (1998) moored "behavioral cages" >50 m off the Lizard Island reefs at night, and showed, in both pomacentrids and apogonids, that most (64–67%) larvae swam toward the reef, regardless of the location of the cage. Based on the position of the cages, Stobutzki and Bellwood (1998) suggested that the larvae were attracted by reef sounds. Other attempts to combine larval swimming and orientation behavior with hydrography are promising, but show how far there is to go. Porch's (1998) numerical study of the southeast Florida coast showed that orientated swimming by larvae at even low speeds (1–10 cm sec⁻¹) resulted in 3- to 10-fold increases in reef fish settlement. Armsworth (2000) modeled the swimming responses of weak- and strong-swimming larvae (ineffective and effective swimmers, respectively) responding to current-dependent (e.g., odor) and current-independent (e.g., sound) cues emanating from a reef. He concluded that larval swimming and sensory abilities are far more important than the fine-scale detail of circulation in determining enhancement of settlement. Strong

out of sight of the reef. It then swam clockwise back to the reef, crossing the reef edge after 9 minutes (117 m swum; average speed, 22 cm sec⁻¹). From there, it swam over the reef for another 12 minutes, closely inspecting three coral heads, and was chased away from settling into a school of conspecifics at the first by a resident *Dascyllus auranus* (56 m swum; average speed, 8 cm sec⁻¹). Observations ceased at 21 minutes, with the fish still swimming over the reef. Note that due to the difference in speed before and after crossing the reef, these two portions of the trajectory are not to the same scale.

swimmers are able to utilize both current-dependent and current-independent cues for orientation, although the latter result in higher levels of settlement enhancement. Finally, Armsworth (2000) concluded that weak swimmers, in contrast, are able to employ only current-independent cues to navigate to reefs, and the enhancement of settlement due to these cues is less than that in strong swimmers. These results will be useful in directing future research effort.

Wolanski *et al.* (1997, 1999) and Wolanski and Sarenski (1997) combined numerical models of circulation with various scenarios of larval behavior, and concluded that only directed swimming by settlement-stage larvae beginning 2–3 km upstream of a reef could duplicate the distribution of larvae they observed with light traps (they assumed response to the sound of waves breaking on the reef). If the larvae were assumed to be passive, the model-predicted distributions were very different from observed distributions. When Wolanski and co-workers assumed larger larvae swam at 20 cm sec⁻¹ whereas smaller ones swam at half that speed, the model predicted different distributions around the reef for faster larvae than for slower larvae. They then attributed the observed differences found between the distribution of two large (~14 mm) *Pomacentrus* species and two smaller (~10 mm) species (*Chromis atripectoralis* and *Chrysiptera rollandi*) to differences in swimming abilities. This is an interesting result and an admirable attempt to incorporate behavior into physical models. However, a difference in body size of about 5 mm would be expected to result in an increase in swimming speed of only 4 cm sec⁻¹, not the 10 cm sec⁻¹ assumed, and, in fact, *Pomacentrus* spp. swim at 11–22 cm sec⁻¹, no faster than the other two, smaller, species (12 and 24 cm sec⁻¹ for *C. rollandi* and *C. atripectoralis*, respectively) (Leis and Carson-Ewart, 1997). Clearly, more than just numerical models of currents combined with predictions of swimming speed based on body size are required to explain the differences observed between the distributions. However, more significant for such an interdisciplinary approach, other numerical models of circulation around the same reef led to different results. The other models predicted that passive larvae would have distributions similar to those observed by Wolanski and co-workers in the field (Black and Moran, 1991; Black, 1988, 1998), therefore supplying no support for long-distance orientation. Biologists cannot be expected to choose among such extremely complex numerical models of circulation, but, obviously, the veracity of the numerical model predictions is critical to the outcome. Where the modelers disagree (see also Wolanski, 1993; Black, 1995), the biologists are left in the lurch. This

makes all the more significant Armsworth's (2000) conclusion that details of circulation are less important than larval swimming and sensory abilities.

Many possible cues associated with reefs could provide clues for orientation. These include smells and sounds emanating from reefs; differences in wind- or wave-induced turbulence; gradients in abundance of fish, plankton, or reef detritus; and differences in temperatures of lagoonal or reef flat water flowing from a reef. In some cases, a magnetic compass or sun compass could aid in increasing chances of larvae encountering a reef (e.g., a larva in the Coral Sea would increase its chances of encountering one of the reefs on the Great Barrier Reef by swimming to the west), but it seems unlikely either could assist orientation toward a particular reef. One possible exception is that a magnetic sense could allow a larva to detect an oceanic basalt island (or, some volcanic islands on continental plates) on which reefs were growing, because basalt islands have a magnetic anomaly (Smith, 1981; F. L. Sutherland, personal communication). Although fish can sense via the lateral line that they are moving through water when swimming, unless they have an external reference, such as a view of the bottom, they will be unable to determine that they are being moved by and with the water, as when being carried along with a current (Leis *et al.*, 1996; Montgomery *et al.*, 1997). Therefore, currents are potentially detectable using vision near the bottom or near a reef, but it is unlikely that currents or movement by them will be detectable in "blue water," and thus they are unlikely to be an aid to orientation. Some of these possibilities seem inherently more general, and therefore more likely in an evolutionary sense to have been utilized (see Chapter 6, this volume). For example, sound is virtually current independent, travels in all directions from the source, and propagates over long distances, so it could be a very general cue (Popper and Carlson, 1998). In contrast, smells are current dependent, must travel with water movement, and would be of little use "upcurrent" of any reef (Armsworth, 2000). However, where currents are weak, each reef might be surrounded by a diffusion-maintained "halo" of smell that could provide cues that a reef was near, and a similar halo could be established by current reversals such as those caused by tides. Magnetic anomalies are current independent, and more likely to be associated with reefs on oceanic islands than with continental-shelf reefs. Most reef fish species have wide distributions and live on a variety of island and shelf habitats, and in a variety of current regimes that differ in their predicability over many scales. In addition, changes in sea level over time can result in radical changes in reef systems and associated currents. Therefore, it seems likely that any

cues to which reef fish larvae have become adapted to use in finding reefs would be general ones, useful over much or all of the range of the species. Such predictions based on theoretical arguments should be treated with caution until they can be tested with reef fish larvae. Researchers have been misled by similar theory-based predictions in the past.

Another important consideration is the scale of the orientation involved. Vision is critical to settlement and close approach to the reef (see Section IV) (Leis and Carson-Ewart, 1998, 1999, also unpublished), but this is at scales of meters to perhaps tens of meters. Even at night, some light is normally available, although the minimum levels necessary for larvae to see, and to what distance, are generally unknown, except for feeding (Job *et al.*, 2000). It is unlikely vision plays a role in orientation toward reefs at a scale of hundreds to thousands of meters unless orientation using sun angle or polarized light is involved (see below). Similarly, olfactory cues are important for some species over the same scales as vision. Unlike vision, olfaction has the potential to operate over larger scales, as with salmon (Helfman *et al.*, 1997). If odors are transported by currents and structured by fronts between water masses, olfaction operating at a small scale could result in orientation over larger scales (M.J. Kingsford, personal communication). Similar arguments apply to temperature differences (Doherty *et al.*, 1996). Reefs are noisy places (Cato, 1978, 1992) and sound has the potential to provide orientation cues over a wide range of scales (Popper and Carlson, 1998). The lateral line is sensitive to water movement, but is capable of detecting this over only small distances, on the order of 1–3 body lengths (Popper and Carlson, 1998), unless augmented by connection to other systems (e.g., the “laterophysic connection” in some butterfly fishes, Webb, 1998). A magnetic sense could potentially operate over a variety of scales, from very large (oceanic), as shown in tunas and salmon (Walker, 1984; Walker *et al.*, 1997), to relatively small (local), as shown in hammerhead sharks (Klimley, 1993). It is likely that different cues are used at different scales even by a single individual: a possible scenario is use of sound to locate the reef, vision and the lateral line to avoid predators near the reef, smell to locate the settlement habitat, and vision to locate the settlement site in the habitat (see Chapter 6, this volume, for an examination of the available evidence on the capability of larvae to detect and utilize such sensory input). It is fair to say that aside from olfaction, hearing, and vision, none of these has been shown to be used by reef fish larvae for orientation, and even with these, the use has been at either relatively small or unknown scales. However, the auditory, visual, and

olfactory systems of fish larvae are apparently functional by the time the fins form, so they should be available early in the pelagic phase of most reef fishes. Here, we explore some of the evidence on smell and hearing and the implications for orientation.

Field and laboratory experiments show that some pomacentrids utilize smell to locate settlement sites over relatively small distances. The only species so far shown to utilize such cues are three genera of pomacentrids (*Amphiprion*, *Dascyllus*, and *Pomacentrus*), two of which are either exclusively symbiotic, or have species that are symbiotic, with anemones (Sweatman, 1985b, 1988; Elliot *et al.*, 1995; Arvedlund and Nielson, 1996; Danilowicz, 1996; Holbrook and Schmitt, 1997, 1999). Are larvae of taxa that are symbiotic with anemones particularly good at using olfactory cues to select settlement habitat? Two points about these experiments are important: first, they show that olfaction can operate over scales of up to a few tens of meters; second, they were done over the reef habitat, and did not show that olfaction can be used in the pelagic environment in the find reefs. Olfaction is clearly important in the location of specialized habitats such as anemones or corals, and in the location of conspecifics or in the avoidance of heterospecific congeners, all over small scales within reef habitats. Use of olfaction for orientation by other than a few species of pomacentrids, or over larger scales, or in the pelagic environment, is a real possibility given the results to date, but this has not yet been demonstrated. The fact that anemone fish still in the egg stage (or just hatched) can be imprinted with the smell of the host anemone (Arvedlund *et al.*, 1999) opens a number of possibilities. These include the imprinting of larvae that hatch from nonpelagic eggs with the olfactory cues of either the natal reef, or a particular type of reef (outer shelf, for example). This could aid in retention near, or return to, a natal reef, or in location of a particular reef habitat for settlement, respectively.

The case for sound being used as a cue is, except for one study, mostly inferential, theoretical, or inconclusive. Several investigators have interpreted their field results to be best explained by sound orientation, but tests of this hypothesis are few. A field experiment (J. M. Leis, unpublished) to test the hypothesis that reef sounds enhance recruitment to artificial reefs >1 km from natural reefs was compromised by general recruitment failure of all but apogonids (mostly *Rhabdamia* species), and these were recruited in an extremely patchy manner. More reef fishes did recruit to the “sound-enhanced” reefs as compared to control reefs, but the difference, at $p = 0.11$, was inconclusive due to low power, so the null hypothesis of

no enhancement could not be rejected. Little is known of the abilities of reef fish larvae to detect or localize sound (see Chapter 6, this volume), but the larvae of two subtropical perciform fishes have a “startle response” to sound at a size of 5–8 mm, before all fins are formed (Ishioka *et al.*, 1987; Fuiman *et al.*, 1999). So, in at least some fish larvae, hearing is operational at a small size, but that is not equivalent to being able to use hearing for orientation. In an important study, Tolimieri *et al.* (2000) showed that larvae of tripterygiids (a family of blennioid fishes) of 20 mm mean length used reef sounds for orientation. Far more tripterygiid larvae were caught in light traps adjacent to areas from which recordings of natural sounds from rocky reefs were broadcast than were caught in light traps where no sound had been broadcast. Clupeid larvae, however, showed no such difference. This constitutes the first clear demonstration that reef fish larvae, albeit temperate ones, can use sound for orientation; however, there was no indication over what scale the orientation was taking place. Innovative means of studying sound as a cue are required, but working with sound as a cue for orientation in the laboratory is extremely difficult (Popper and Carlson, 1998).

6. PREDATION ON LARVAE

Due to the enormous disparity between numbers of eggs spawned and newly recruited juveniles, predation on the pelagic stages of reef fishes is assumed to be intense. Yet, there have been few data to support this quite reasonable assumption. Johannes (1978) speculated that predation was more intense over the reef than in open water, and suggested this was a major reason why reef fish larvae were found away from the reef in open water. Leis and Carson-Ewart (1998) observed a higher rate of predation on settlement-stage larvae in the vicinity of and over coral reefs than in open water. The absolute rates of predation they observed were not meaningful due to the bias introduced by the presence of divers, but the data were useful in a relative sense to make comparisons between regions. This relative difference in predation was the first empirical support for Johannes' hypothesis.

In open water, settlement-stage larvae of several families react to schools of potential predatory fishes at distances of 3–6 m, and similar reaction distances were seen in near-reef waters, generally with more solitary predators (Leis and Carson-Ewart, 1998, 2001). The reactions included changes in swimming direction or speed, changes in swimming depth, and retreat to the shelter of the observer diver. Leis and Carson-Ewart (1998, 2001) concluded that larvae were alert to the threat of predation and could detect larger fishes at a

distance of several meters. This distance is great enough that it was unlikely the larvae would have been seen, and this allowed them to react in ways that reduced their chances of coming close enough to the predators to be seen or attacked. In short, settlement-stage larvae in open waters behaved in a way that was effective in avoiding predators. The larvae reacted to the predatory fishes several meters away, so it was assumed the larvae detected these fishes visually, although detection by sound or mechanosensory means could not be ruled out. Whether the larvae reacted to visual or other stimuli, they did so at distances much greater than those reported in laboratory studies of subtropical fish larvae of similar size (e.g., Higgs and Fuiman, 1998b; Poling and Fuiman, 1999). In fact, the reaction distances observed *in situ* were much greater than the dimensions of the containers used in those laboratory studies. This type of close reaction reported in the lab is thought to indicate that larvae avoid predators by dodging at the last moment, when the predator is too close to react effectively (Blaxter, 1991). This may well be an effective last-ditch defense, but the *in situ* observations combined with the lab results imply that larvae may have a layered defence. One set of behaviors operates at distance to take advantage of the small size and low visibility of the larva to decrease the likelihood of being detected by the predator, and the other set of behaviors operates at small separation distances if the first set fails and the larva is detected. This implies considerable behavioral sophistication by the larvae, but no more than many adult fishes possess. Blaxter (1991) suggested a similar layered defense in herring larvae, with the key difference in herring being that passive, rather than active, behavior in the outer layer reduced detection. Further, Blaxter suggested that the outer, passive layer of defense was predominant in “small” larvae, whereas the active, inner defense was predominant in older larvae. In fact, in the field, a temperate mugilid, when small (<9 mm), reacted to disturbance by aggregation, and, when larger, by scattering at high speed (Kingsford and Tricklebank, 1991). Neither fits comfortably in the layered defense model, which indicates that species-specific behavior may play a strong role.

Over the reef, Sancho *et al.* (1997) reported predation by eight fish species on settlement-stage acanthurids swimming along the bottom of the reef or on just-settled individuals in caves and crevices. Predation on pomacentrid larvae approaching the reef was primarily by synodontids and labrids and predation rate differed among species (Leis and Carson-Ewart, 1998). This difference was attributed to the swimming behavior of the larvae: species that swam more or less directly toward a settlement site on the seaward edge of

the reef suffered more predation than did species that swam high above the reef before descending to examine settlement sites, or than species that turned and swam offshore. Predation on settlement-stage serranid larvae as they approached the reef was also primarily by synodontids and labrids and differed in intensity between locations (Leis and Carson-Ewart, 1999).

Predation on and near the reef is generally thought to be highest during crepuscular periods, intermediate during the day, and lowest at night (Hobson, 1972, 1991; Johannes, 1978). It is argued that this diel predation pattern shapes the diel patterns of many other activities, including settlement of larvae (e.g., Hobson, 1991; Victor, 1991). However, this assumption has been tested only once, and the results were not in accord with the predicted diel structuring of predation. Predation rates on juvenile grunts (Haemulidae) that were 3–4 cm TL, the settlement size of some other species, were highest at night and dusk and lowest during the day (Danilowicz and Sale, 1999). As pointed out by Danilowicz and Sale, this brings into question the argument that temporal patterns in larval settlement on the reef are driven by temporal patterns in predation, but the reality is that diel patterns of settlement are not well known (see Section V,C).

V. Back to the Reef: The End of the Pelagic Stage

A. Connectivity: Dispersal or Retention?

The dominant view among biologists is that reef fish populations are demographically open, meaning that settlement and recruitment of propagules are overwhelmingly not back into the natal population (Sale, 1991b; Caley *et al.*, 1996), but this is rarely tested. Some have tried to test this by indirect methods, such as attempting to match spawning cycles to recruitment cycles (e.g., Danilowicz, 1997), thereby introducing assumptions that are difficult to evaluate. Indirect biochemical genetic methods have also been used. Where these show differentiation, and they often do (e.g., Planes, 1993; Planes *et al.*, 1998b), important demographic boundaries among populations are identified. Where these genetic methods show no population differentiation (panmixia), there is great relevance at evolutionary or biogeographic scales, but little relevance at the scale of most ecological or demographic questions (Shulman, 1998). Genetic panmixia does not indicate that demographically significant connectivity exists. This is because the amount of larval connection between populations required to eliminate genetic

differences detectable by most methods is so low [an average of a few individuals per generation (Shulman, 1998)] as to be demographically meaningless. Neither a fishery nor a marine reserve is likely to be maintained by such a low level of recruitment input. In other words, management must be done at ecological and demographic scales.

Models of larval connectivity typically make the “simplifying assumption” that larvae are passive (Roberts, 1997b), and utilize hydrographic models, usually of far-field currents, to estimate where propagules will end up at the end of “average” pelagic larval durations. At ecological and demographic scales, it is appropriate to use average PLDs, whereas at evolutionary or biogeographic scales, the appropriate measure is maximum PLD (Leis, 1991a). Unfortunately, such models ignore the reality that reef fishes do not normally spawn into far-field currents, and that reefs are more or less “buffered” from contact with far-field currents by hydrographic complexity at micro- to mesoscales. For example, Black (1988, 1995, 1998; Black and Moran, 1991) showed that retention of even passive larvae in the immediate vicinity of reefs can be remarkably high for periods of several days, and that this varies with depth. At a larger scale, the reefs of the Florida Keys are “buffered” from direct contact with the Florida Current/Gulf Stream system by a set of gyres with periods of several days to several months (Lee and Williams, 1999). Because of this, even passive larvae may take several days to weeks to come into contact with far-field currents. It is in the first few days of the pelagic period that the “simplifying assumption” of passive drift is most likely to apply due to the ontogeny of swimming abilities, and least likely to involve far-field currents. As shown above, the assumption of passive behavior by larvae is untenable. Therefore, the simplifying assumption of passive drift in far-field currents looks less defensible with time (see above).

Cowen *et al.* (2000) modeled dispersal of reef fish larvae from Barbados and concluded that long-distance dispersal is unlikely to be demographically relevant. They showed that at the scale considered (hundreds of kilometers), the twin effects of mortality and diffusion act to ensure only very small numbers of passively dispersed larvae ever reach downstream settlement sites. Further, the species-specific PLD limits the opportunity for a given species to settle at any reef intersected by a larval trajectory. Larvae must first be “competent” before they can settle on any reef they encounter. This study shows that the numbers of larvae reaching a distant reef are likely to be too small to be able to support a fishery or a reserve.

In some special cases, particularly atoll lagoons, it can be shown directly that the entire life cycle is completed in the vicinity of the natal reef, thus indicating that the population is closed, at least at the scale of the lagoon (Leis, 1994; Leis *et al.*, 1998; J. M. Leis, unpublished). However, in such cases, although the numbers of larvae are large, the number of "completer" species is small and is confined to a few families (often only one or two species in each), particularly Apogonidae, Blenniidae, Callionymidae, Carangidae, Clupeidae, Gobiidae, Hemiramphidae, Microdesmidae, Mullidae, Pomacentridae, and Schindleriidae. Similarly, in more open waters, larvae of some taxa may be retained over or near natal reefs, and although long-shore dispersal cannot be entirely ruled out in such cases, the populations are probably relatively closed (Leis, 1986a, 1993; Brogan, 1994b). On the Great Barrier Reef in such conditions, retained taxa (Leis, 1986a) were a subset of the "lagoon completers," and in the Gulf of California they were bythitids, blennioids (four families), and gobiocids (Brogan, 1994b). Most of these "completer" taxa spawn nonpelagic eggs (only the carangids, callionymids, and mullids do not). Other than these few completer taxa, lagoon species either spawn elsewhere or seem incapable of completing their pelagic larval phase in atoll lagoons if they do spawn there, and this is particularly true of species that spawn pelagic eggs. Although they hatch from pelagic eggs, there are indications that larvae of some haemulids and reef-associated sciaenids may never leave the vicinity of the natal reef, possibly by staying near the bottom (Lindeman *et al.*, 2001). If so, this would enhance the likelihood of self-recruitment and more closed populations for these species, although self-recruitment remains to be shown.

Some flexibility in life history pattern and a resultant geographical variation in population openness is evident in the extreme case of an atoll lagoon cut off from the ocean (Taiaro Atoll), where some species that do not normally either spawn or complete their pelagic phase in lagoons did so (Galzin *et al.*, 1998). At Taiaro, genetic evidence indicated that an acanthurid and a chaetodontid were completing their life cycles in the lagoon (Planes *et al.*, 1998c). The concentration of pelagic fish eggs in the lagoon was at least as high as that in the nearby ocean, indicating substantial spawning in the lagoon (Leis *et al.*, 1998), in contrast to other atolls (J. M. Leis, unpublished). Finally, the presence of a range of sizes (although not the full range) of scarid and labrid larvae in the lagoon indicated that some species of these two families may complete their pelagic phase in Taiaro Lagoon, again, in contrast to other lagoons. In addition, some taxa that

complete their life cycles in other lagoons were absent as both adults and larvae at Taiaro: most notable were a blennioid, a carangid, a microdesmid, and a schindleriid. Such flexibility indicates that an oceanic pelagic stage is facultative in a number of reef fishes, and that these species can achieve life cycle closure in lagoons, at least in extraordinary situations. If this is possible, then it might occur in other, less extreme, situations. Perhaps the pelagic stages of these species survive better in the ocean than in the lagoon, and this is a factor driving behavioral adaptations that normally place propagules outside the lagoon. However, survival, albeit at a lower level, may still be possible in the lagoon.

A more general direct test is to measure the proportion of self-recruitment that takes place at given reefs. Open populations, by definition, have low levels of self-recruitment, so significant levels of self-recruitment would indicate a population that is not totally open demographically. One such test is simply the presence of endemic species at small, isolated islands. That there are a number of these, and that their life history characteristics do not appear to be out of the ordinary compared to other reef fishes, are proof of absolute self-recruitment of these species on the scale of the island, implying that the populations of other reef fish species at these islands may be similar (Robertson, 1999).

Two research programs using different otolith-based methods have directly demonstrated remarkably high levels of self-recruitment in two reef fish species. At Lizard Island, 15–65% of the settlement-stage larvae of *Pomacentrus amboinensis* approaching the island at the end of their pelagic sojourn originated at that same island (Jones and Milicich, 1997; Jones *et al.*, 1999). At St. Croix in the Virgin Islands, more than 50% of the recruits of *Thalassoma bifasciatum* during time of peak recruitment had not spent time outside of coastal waters, and therefore originated at St. Croix (Swearer *et al.*, 1999). The scales here are very different: the Lizard Island reef complex is about 7 km long, but many other reefs are present in a 20-km radius, some as close as 2 km away; St. Croix is about 35 km long, and over 50 km from the nearest island reefs. Given the surprisingly high levels of self-recruitment in two such different reef systems at two different spatial scales and involving species with different reproductive characteristics (demersal eggs in the pomacentrid and pelagic eggs in the labrid) and with mean PLDs that differ by 25–30 days, we may anticipate that these results are fairly general.

Indications from several different approaches are that reef fish populations are probably more toward the closed than the open end of the demographic spectrum, although this almost certainly varies among species and

locations, and probably temporally. This has important implications not only for our view of reef fish populations, but also for our attempts to manage them. The design of marine protected areas (MPAs) and the push for their use as conservation and management tools are both predicated on the open population paradigm. Although, ironically, if populations are more closed than open, MPAs might be more favorably regarded by local stakeholders (K. C. Lindeman, personal communication). If populations on ecological time scales are more closed than open, then populations are probably more spatially subdivided than previously suspected. This means that different designs of MPAs are required (i.e., for a given area of MPAs, more and smaller reserves may be optimal, although the optimal size remains to be determined) and that the “dual function” of MPAs—both to maintain biodiversity and breeding stocks within MPAs and to replenish exploited populations outside them—may be difficult to attain over anything other than small to medium scales. Sladek Nowlis and Roberts (1999) confront this dilemma when they conclude on one hand that “without larval transport [outside MPA borders], the potential for fisheries benefits from reserves is more limited” (the open population view), while on the other, that without self-recruitment, MPA “benefits to the management area are likely to be much more limited” (the closed population view). The success of MPAs in achieving either of the proposed benefits, let alone both, is critically dependent on the location of reef-fish populations along the open-closed continuum, the scales over which ecologically-relevant dispersal or retention operate, and the spatial design of the MPA. We agree with Sladek Nowlis and Roberts (1999) that “we need to understand the movement dynamics of larvae” for effective MPA design.

B. Timing of Settlement

Near the end of the larval phase fish reach a developmental stage when they are ready to leave the water column and join the demersal reef population, if environmental and biotic cues indicate that appropriate habitat is available. This developmental stage is known as “competence.” Thus reef fish have a larval phase made up of two parts: (1) a precompetent phase, during which rapid development and growth occurs, and (2) a competent phase, characterized by reduced growth and body maintenance. The relative contribution of each phase to the overall PLD is presently unknown because the identification of morphological and physiological characteristics that signify competence has proved elusive (McCormick, 1999b).

Some widely distributed families, such as the wrasse, surgeonfish, and flatfish, can apparently extend the period of competence, thereby delaying metamorphosis and settlement (Randall, 1961; Victor, 1986c; Evans and Fernald, 1990; Cowen, 1991; Jenkins and May, 1994; Cowen and Sponaugle, 1997; Sponaugle and Cowen, 1997; McCormick, 1999b). In doing so, they increase their chances of finding suitable settlement habitat. Evidence for the delay of settlement comes from two sources, one circumstantial, the other experimental. A number of studies have found reduced otolith growth in the late larval stages of individual fishes with greatly extended larval durations (e.g., Victor, 1986c; Cowen, 1991; Jenkins and May, 1994; Fowler and Short, 1996; Masterson *et al.*, 1997; Sponaugle and Cowen, 1997). McCormick (1999b) provided the first experimental evidence that the convict surgeonfish *Acanthurus triostegus* could delay settlement once a period of competence was reached. He caught late-larval-stage fishes at night as they colonized a reef and placed them in one of two treatments: benthic cages in the shallow backreef, or fine monofilament cages suspended between 3 and 6 m in a 50-m water column on the outer reef slope. Fishes in benthic cages attained a juvenile pigmentation and shape within 5 days. In contrast, 24% of fishes in pelagic cages (8 out of 34) retained their pelagic body shape and remained transparent.

Of the studies that have shown some evidence of delayed settlement, most have found that larval durations well beyond the average are rare. Victor (1986c) and Masterson *et al.* (1997) found that less than 1% of the bluehead wrasse *Thalassoma bifasciatum* examined had extended larval durations. The majority of coral reef fish species examined to date display low variability in larval duration (Cowen and Sponaugle, 1997), and this may be a function of either the small sample sizes on which larval durations are based for many species, or indicative that their period of competence is short and measured in hours rather than days. Another alternative is that by the time fishes reach competence most larvae have positioned themselves, through a combination of active and passive means, close to a suitable settlement habitat, so extensive delays are not required. In studies in which extended larval durations are more common, fishes have usually been collected far from their spawning grounds (Cowen, 1991; Jenkins and May, 1994; Fowler and Short, 1996) or have very specific temporal settlement cues [e.g., specific lunar phase (Sponaugle and Cowen, 1994)]. These studies indicate that there is a window of opportunity for settlement, with the lower bound governed by the rate of development and the upper bound

determined by the extent to which a delay of settlement is possible.

It is presently unknown for fishes whether there is a cost to delaying metamorphosis and settlement. Delays in metamorphosis of marine invertebrates are commonplace and at times extensive (Pechenik, 1990), but often there is a cost associated with them. This cost can be manifest as reduced growth once settled, delayed maturation, reduced reproductive output, or lower survival (Pechenik *et al.*, 1998). McCormick (1999b) found that the surgeonfish he induced to delay metamorphosis for 5 days had reduced survival in tanks compared to control fish, but this may have been a feature of the low sample size or an artifact of the experimental procedure. The low incidence of delays in teleost fishes found to date may be a product of the potentially high costs associated with delay, and consequently their low survival.

The extent to which settlement to a benthic environment and metamorphosis are linked in time is largely unknown for coral reef fishes, but appears to be species specific. Some reef fishes, such as the dartfish, *Ptereleotris euides*, settle in schools into shallow caves below the reef crest and have poor mobility and are much less developed than other reef fishes, even other *Ptereleotris* species, at settlement (McCormick and Makey, 1997). Metamorphosis occurs over an approximately 12-day period involving a major change in body dimensions and pigmentation (McCormick and Makey, 1997). At the other end of the spectrum, the sergeant major, *Abudefduf saxatilis*, undergoes a gradual metamorphosis while associated with floating debris in the neuston and joins the reef community at a variable age and size as a fully metamorphosed juvenile (Druce and Kingsford, 1995; M. I. McCormick, unpublished data).

C. Settlement: A Pelagic Fish Becomes a Benthic Fish

When a ready-to-settle larva encounters a reef, it may either attempt to settle or reject the reef and move away in search of a more suitable settlement site. Although it is widely considered that larvae show strong habitat selection at settlement (Victor, 1991; Roberts, 1996; Booth and Wellington, 1998), connectivity models usually assume that larvae settle onto the first reef they encounter once they are competent to settle. This assumption is probably made because of the difficulties of inserting any other settlement behavior into models, but recent work shows it is far from realistic. A substantial proportion of competent larvae released

adjacent to reefs during the day reject the nearest reef, and swim away into open water [no nighttime data are available, and, of course, results at night may differ (Leis and Carson-Ewart, 1998, 1999, 2001)]. For 14 species of pomacentrids, about 30% (range 0–50%) of larvae swam away offshore without reaching the adjacent reef (although many initially swam toward the reef before turning offshore), a further 12% (range 0–50%) swam over the reef edge, and some closely examined potential settlement sites, before swimming away offshore. About 2% (range 0–11%) of the pomacentrid larvae swam offshore and then turned back to the reef after offshore excursions of a few to several minutes, usually out of sight of the reef. This may be a means of testing another portion of the same reef for suitability. Similar values were found for a serranid (Leis and Carson-Ewart, 1999). The percentage of larvae of a particular species that rejects any given reef varies from zero to 100%, depending on species and reef. For example, 100% of *Caesio cuning* larvae reject leeward and windward reefs at Lizard Island, whereas about 50% settle on the first lagoonal reef they encounter (J. M. Leis, unpublished). At present, the reasons for such rejection are only speculative, but it appears that the presence of potential predators accounts for only a small percentage of this, although this may vary with species. Other apparent factors are aggressive resident fishes, which often “rush” settlers, or the reef type. In fact, at least during the day, aggressive nonpredatory resident fishes appear to discourage settlement at least as much as does the presence of predators. Whatever the reason for swimming back into the pelagic environment, one would not expect such a high percentage of larvae to do so if reefs were difficult to locate from open water.

Settlement occurs when a larva leaves the pelagic environment to become closely bottom associated. Although postsettlement issues other than metamorphosis are beyond the scope of our review (see Victor, 1991; Roberts, 1996; Booth and Wellington, 1998), it is worth reiterating that most reef-based studies of “settlement” or patterns resulting from settlement are, in fact, studies of some unknown combination of settlement and postsettlement processes (Richards and Lindeman, 1987) [for notable exceptions, see Holbrook and Schmitt (1997, 1999) and Schmitt and Holbrook (1999a)]. Studies of “settlement patterns” are often of juveniles weeks to months older than settlement-stage larvae and are made with no attempt to examine what really happened during those weeks or months. Such studies assume that larvae settle into the places where the “recruits” were observed, that there has been no postsettlement redistribution, and that any

postsettlement mortality has no effect on whatever is being studied. In fact, the assumption of no redistribution is rarely tested (but see Finn and Kingsford, 1996), and very little is known about this, or the related phenomenon of "relaunch," or reentry into the pelagic environment following settlement. Further, mortality can be very high in the first few days after settlement (Holbrook and Schmitt, 1997, 1999). More work on the early postsettlement interval is required (e.g., Kaufman *et al.*, 1992; Frederick, 1997; McCormick and Makey, 1997), but here we review studies that actually investigate settlement.

Most reef fish biologists apparently believe that the vast majority of, or even all, settlement occurs at night. So pervasive is this idea that evidence of daytime settlement is sometimes dismissed as methodological error (e.g., Robertson *et al.*, 1988), and vision is often dismissed as unimportant for orientation and habitat selection at settlement (see Chapter 6, this volume). However, the evidence supporting the notion of nocturnal settlement is actually based on very few studies involving few species—principally pomacentrids (reviews in Sweatman, 1985a, and Leis and Carson-Ewart, 1999). There is simply no information on diel settlement timing for the vast majority of species, genera, or families. When the timing of settlement has been carefully examined, the majority does seem to take place at night, but substantial portions of total settlement (up to 66%) frequently take place during the day. Nearly all studies report some level of daytime or crepuscular settlement, and many studies do not eliminate the possibility of crepuscular settlement, when substantial light is present. In fact, settlement-stage larvae of most of the families that are released within view of reefs during the day are likely to settle (Leis and Carson-Ewart, 1998, 1999, also unpublished). Larvae are relatively easily put off from their attempts to become reef animals during the day by potential predators or by aggressive reef residents and may swim away offshore (Sweatman and St. John, 1990; Leis and Carson-Ewart, 1998, 1999, also unpublished). This behavior is variable among species: for example, when a school of fusiliers is encountered off a reef edge, *Chromis atripectoralis* larvae are likely to reach the reef by ascending over the school, whereas *Chaetodon aureofasciatus* larvae usually swim offshore (J. M. Leis, unpublished). Most of the potential predators and aggressive residents are not active at night. So, it is possible that attempts by larvae to approach and settle on a reef are of equal frequency day and night, and that any difference in the amount of settlement between day and night is simply due to attempts that are foiled by interaction with residents (Leis and Carson-Ewart, 1998, 1999). An implication of this

is that patterns of settlement and subsequent recruitment could be strongly influenced by the distribution of predators, especially those in the "wall of mouths" that fronts many coral reefs, and of aggressive residents.

Observations of settlement behavior in several species show that settlement is a complex process, that larvae are frequently highly selective about where they will settle at a variety of scales, and that the larvae are behaviorally sophisticated. One approach is to take settlement-stage larvae (usually captured in light traps, but sometimes reared in the lab) into the laboratory and provide choices of settlement substrates (e.g., Öhman *et al.*, 1998a; Danilowicz, 1996). This enables good control of many possible confounding factors, but investigators are frequently forced to define settlement as the position of the larvae in the morning or some other convenient time, rather than where settlement actually first took place. This allows postsettlement redistribution over up to 10 hours to affect the patterns observed. Lab situations can duplicate only a limited range of field conditions and the bias this might introduce is unknown. For instance, *in situ*, larvae of the serranid *Plectropomus leopardus* settled only in depths greater than can be duplicated in most laboratories (Leis and Carson-Ewart, 1999), so the value of laboratory settlement selection experiments in this species might be questionable.

In the field, examination of distribution patterns in the morning has many of the same drawbacks regarding postsettlement processes as the lab situation, but without the same level of control of other factors. Remote video recording (Holbrook and Schmitt, 1997, 1999) enables studies of the actual settlement process at any time, at least on the scale of a few meters, without other confounding lab or temporal effects. A final approach is to release larvae adjacent to or over reefs and observe *in situ* the behavior of the larvae as they attempt to settle and to deal with predators or residents (Leis and Carson-Ewart, 1998, 1999). This can only be done during the day, so can provide only half the picture, and the presence of the divers adds unknown biases. Investigators may hold light-trapped larvae in aquaria for several to 36 hours before initiating an experiment. Given the rapidity with which the morphological and behavioral changes associated with settlement take place (Randall, 1961; Stobutzki and Bellwood, 1994; McCormick, 1999a), this holding delay could affect the results, but this has not been tested.

In the lab, settling pomacentrids of four species made distinct habitat choices that varied widely among species, and postsettlement redistribution was detected in some species (Öhman *et al.*, 1998a). *In situ*

observations of settlement behavior of three of the species reveal some differences from and some similarities to the lab study (J. M. Leis, unpublished). This indicates that use of multiple approaches to study settlement could help identify which results are affected by method-induced biases.

In situ approaches show remarkable selectivity by larvae of some species at settlement (J. M. Leis, unpublished). Larvae of the fusilier *Caesio cuning*, in contrast to congeners, rejected windward and leeward exposed fringing reefs, but settled with high frequency on lagoonal platform reefs (total $n = 38$). Further, they settled only into mixed-species schools of similarly sized (20 mm) juvenile planktivores on the reef edges. Interestingly, a light trap placed near, but outside and downstream of, the lagoon entrance captured many more *C. cuning* larvae than did a trap placed 2 km away, implying that some of the selectivity can begin at some distance from the selected habitat. Patterns of settlement abundance can show similar distributions: i.e., high settlement density of apogonids in lagoons and low density on outside reef slopes (Finn and Kingsford, 1996). In contrast, larvae of two species of butterfly fish (*Chaetodon*) settled on both windward and lagoonal reefs, but only into live coral, regardless of presence or absence of other species, and selected corals were located on all parts of the reefs (total $n > 70$). The damselfish, *Chromis atripectoralis*, settled on all tested reef types, but only into schools of similarly sized (10 mm) juveniles. The location of the school on the reef seemed unimportant (total $n > 50$).

There are indications that some acanthurids may initially leave the pelagic environment in deeper water and migrate upslope or through reef channels into shallow reefal waters, at times *en masse*, before settling into caves and crevices on the reef (Sancho *et al.*, 1997). Larvae of an acanthurid in oceanic conditions about 1 km off the reef crest usually swam rapidly downward, and this led Leis and Carson-Ewart (2001) to speculate that these larvae might have been attempting to find the reef slope bottom far below and to then follow this up toward the shallow reef, where they settle. More work on such behavior is needed, but if the indications are borne out, at least two possible advantages are obvious. This could be an effective means both of finding a relatively nearby reef and of avoiding predation by the "wall of mouths" (Hamner *et al.*, 1988) that exists off most shallow reefs, but predation by other fish on the larvae as they move over the reef surface can be intense (Sancho *et al.*, 1997). Such behavior also indicates that the location of initial "touchdown" on the bottom may be some distance away from where the larva finally shelters. Whether the time and site of initial touchdown or

the time and site of sheltering should be considered "settlement" is debatable, but it does illustrate the potential complexity of the transition from the pelagic to benthic environment. Not every species simply slips into juvenile habitat directly from the pelagic environment as does *Chromis atripectoralis*, for example.

Given the settlement selectivity shown by larvae and their readiness to leave the immediate vicinity of reefs and swim back out to open water, combined with their ability to swim great distances at relatively high speeds, it is entirely possible that these behavioral inputs alone can determine the mesoscale distributional patterns of adults documented in places such as the Great Barrier Reef (e.g., Williams and Hatcher, 1983). For example, an average larva that rejected the mid-shelf reefs at Lizard Island would need to swim about 20 km [or about 28 hours at the mean speed found by Leis and Carson-Ewart, (1997)] to reach the outer-shelf barrier reefs. This is well within the endurance values for larval swimming found by Stobutzki and Bellwood (1997). Thus, settlement of this "average" species into the outer-shelf fish assemblages (Williams and Hatcher, 1983) rather than the midshelf assemblage at Lizard Island is feasible (assuming the appropriate orientation) based on proved behavioral capabilities alone.

D. Metamorphosis

A species-specific change in body structure and physiology, called metamorphosis, occurs at or around the time of settlement, during which fish lose many of the characteristics that enhance survival in the plankton while developing other features suited to their new benthic environment (e.g., Randall, 1961; Norris, 1963; Markle *et al.*, 1992; Keefe and Able, 1993; McCormick, 1993, 1999b; McCormick and Shand, 1992; Shand, 1993, 1994a, 1997). Information on what metamorphosis represents is sparse for fishes generally, and for tropical reef fishes in particular. There has been surprisingly little advance in this field since Youson's (1988) review of the subject.

The classical example of metamorphosis in fishes is that of the flatfishes (Pleuronectiformes). Temperate species that have been studied undergo a dramatic metamorphosis involving a reduction in body depth, a change from being bilaterally symmetrical to asymmetrical (one eye migrates to the opposite side), changes in dentition and jaw structure, reductions in the lengths of spines, development of scales, and changes in body pigmentation (e.g., Markle *et al.*, 1992; Keefe and Able, 1993). The speed of this metamorphosis is temperature dependent (Chambers and Leggett, 1996; Keefe and Able, 1993) and can encompass a substantial

proportion of the larval duration of the species. For instance, off the Oregon coast, the Dover sole, *Microstomus pacificus*, may reach the start of metamorphosis with eye migration only 1 month into a larval phase that may last 2 years (Markle *et al.*, 1992). This is somewhat of an extreme case and more typically metamorphosis may encompass the last 50% of the larval phase for flatfishes (e.g., Kvenseseth *et al.*, 1996). Tropical members of this order undergo the same magnitude of change, although metamorphosis may occur over a less protracted size range (Leis and Carson-Ewart, 2000).

Members of the Elopomorpha (which includes tarpon, bonefish, and eels) have a long, ribbonlike leptocephalus larval stage that is followed by an elaborate remodeling stage. The bonefish *Albula* sp. loses half its body length during an 8- to 12-day period (Pfeiler and Luna, 1984). The gelatinous matrix that makes up much of the leptocephali is resorbed and development of the bone and muscle framework characteristic of the juveniles occurs. The Pacific tarpon, *Megalops cyprinoides*, has a 25-day leptocephalus stage and then undergoes similar shrinkage for 12 days. This is followed by a month of slow growth, including remodeling into the true juvenile form (Tsukamoto and Okiyama, 1997).

In general, the changes that occur in tropical reef fishes (mostly Perciformes, as noted above) at the end of the larval phase are not as dramatic and occur rapidly. The convict surgeonfish *Acanthurus triostegus* comes onto the reef as a transparent discoid-shaped larva (Randall, 1961; McCormick, 1999b). Over a 5-day period the mouth, which was terminal at settlement, orients ventrally to facilitate reef-associated herbivory. Concomitant with mouth migration is a 12% reduction in body depth (McCormick, 1999b). During this period alimentary-tract length increases threefold (Randall, 1961). The Caribbean blenny, *Ophioblennius atlanticus*, undergoes a substantial metamorphosis from being a pelagic predator with long fangs and a short gut to being a grazing herbivore with fine comb-shaped teeth for nipping and scrapping algal turf and bacteria, and a long, coiled gut (Labelle and Nursall, 1985). During this metamorphosis the head profile becomes steep, the eyes migrate dorsally, and the adult coloration is assumed. This change involves at least a 7% decrease in standard length (Nursall and Turner, 1985), but over what time is unknown.

McCormick and Makey (2002) used sequential video images to examine trends in the morphological change associated with settlement in 34 species from 13 families of tropical reef fishes. They found that within a family, the extent of morphological change var-

ied greatly among species, and this prevented generalization. Typically, changes over the first 4 days involved changes in pigmentation, snout angle, fin spination, and body depth. This emphasizes the species-specific nature of the magnitude of the changes that occur at the end of the larval phase and of the rates of those changes.

Limited evidence suggests that those species that undergo a substantial metamorphosis stop feeding during this period and survive on endogenous reserves. In bonefish, metamorphosis is fueled by the breakdown of triglycerides and nitrogen-containing compounds (Pfeiler *et al.*, 1998). Similarly, reared temperate bass larvae, *Morone saxatilis*, used stored lipids during a nonfeeding metamorphosis (Chu and Ozkizilcik, 1995). The Caribbean redlip blenny also stops feeding as it comes into the vicinity of the reef and its lipid stores fuel metamorphosis (Labelle and Nursall, 1985; Nursall and Turner, 1985). Randall (1961) collected the convict surgeonfish, *Acanthurus triostegus*, from tide pools on the day of settlement and found no food in their stomachs. How common this nontrophic period is and its duration are unknown for tropical reef fishes. It does suggest that the nutritional stores available to a fish at the start of metamorphosis may help determine its survival potential because as it enters the demersal phase of its life, nutrition influences growth and performance.

Little is known of the sensory changes that reef fishes undergo as part of the metamorphosis associated with settlement. The visual and gustatory systems of one coral reef fish species have received the most attention. The goatfish, *Upeneus tragula*, is common component of ichthyoplankton samples from the Great Barrier Reef. From early in the larval phase of this species, it forms schools with a broad size range of its own and compared to other goatfish species, and is diurnally active in the top few meters of the water column (McCormick and Milicich, 1993). During the late larval phase these fish have a double layer of cone photoreceptors in their dorsal retina and high bipolar (processing) cell densities. This may greatly improve vision in shallow water. Over a 6- to 12-hour period around settlement the retina undergoes extensive reorganization; one layer of cone cells slots into the other to form a monolayer, and cone and bipolar cell densities greatly reduce (McCormick and Shand, 1992; Shand, 1994a). Interestingly, the absorbance spectra of these cones showed an abrupt shift toward shorter wavelengths, losing red sensitivity, a characteristic typical of deeper bottom-dwelling fishes (Shand, 1993). Over the same period of 6 to 12 hours, the barbels, which are used to find and excavate benthic

prey, rapidly migrated toward the mouth, increasing in length by 50%, and the taste buds that cover the barbel surface doubled in size (McCormick, 1993). The speed and extent of these structural changes are remarkable. However, it is unlikely that sensory changes of this magnitude are typical at settlement. In three other species of reef fish (a damselfish, wrasse, and apogonid) changes in the densities of various cell types in the eye occurred earlier in development, and were not coincident with settlement (Shand, 1997). This emphasizes the species-specific nature of the timing and magnitude of changes that occur in the visual system during larval development.

In most reef fishes, settlement also coincides with a change in both the rate of growth of the earstones or otoliths and their axes of growth (Wilson and McCormick, 1997, 1999). Otoliths are an integral part of the membranous labyrinth system that is responsible for balance, orientation, and hearing, so these changes imply that the function of these senses may change slightly with the necessity for precise orientation in a complex three-dimensional reef environment.

VI. Future Research Directions

It is now well established that at least the later pelagic stages of many reef fishes are far from passive, and that they are real animals—not simply biological driftcards—that have complex behaviors and considerable ability to control where they are and where they will settle. The next step is to extend behavioral studies to a wider range of species, in particular such important groups as labrids, scarids, and eel leptocephali. The first two families have much smaller, apparently less-well developed larvae than do most of the groups studied thus far (Leis and Carson-Ewart, 2000), and it will be of interest to see how their behavioral capabilities compare. The marine larvae of freshwater eels have been intensively studied (e.g., Tsukamoto, 1992; McCleave *et al.*, 1998). There is reason to believe they have good sensory abilities and these could be present in the larvae of reef eels. However, the morphology, mode of swimming, and, apparently, physiology of these eel leptocephalus larvae differ considerably from those of other reef fish larvae, so some surprises may be in store. Otherwise, the most urgent need is to determine when during the pelagic phase larvae are sufficiently developed to begin to control their trajectory. It is difficult to see how this can be done with other than reared larvae, but measurements should not be confined to the lab, and *in situ* work is essential. In addition, means must

be found of ensuring that results on lab-reared larvae are representative of capabilities and performance of wild larvae.

The great gap in our understanding of the sensory capabilities of reef fish larvae, particularly in the areas of hearing and olfaction, must be filled (see Myrberg and Fuiman, this volume). This should probably proceed on both a morphological and a behavioral level. Because “the strength of the sensory facility” was *the* critical parameter in modeling of larval swimming responses to different cues, Armsworth (2000) concluded that determining the sensory abilities of larvae “must become a fundamental research objective of those involved in management of reef fish populations.” Innovative means must be found to study the behavior of larvae at night, both in open waters and over the reef. Attempts to integrate larval behavior with hydrological models should provide much insight into the realities of dispersal and retention. This is critically important to our understanding of population connectivity and to management decisions, including design of MPAs.

Hand in hand with the need to learn about sensory capabilities are requirements to understand the performance characteristics of larvae, their ability to detect and catch prey, and how these develop. More research should be devoted to the role that starvation plays in tropical waters, and this will require some researchers to revisit their oceanographic roots to explore the link between the patchiness of prey and fish larvae of all developmental stages. To understand the link between reef populations and larval settlement, information on mortality schedules are desperately needed. This will likely lead to the detection of critical intervals in the life phase that are marked by enhanced sensitivity to environmental or biological conditions. These will serve to focus future research.

From an evolutionary perspective, it will be of interest to determine whether larval mortality is size or growth selective and what processes influence which individuals survive the larval period. Conditions of the breeding population may influence larval mortality levels on a range of temporal and spatial scales through the influence of nongenetic contributions from the mother (i.e., maternal effects). Recent modeling has shown that maternally affected traits may have enhanced rates of mutation, may evolve in a direction opposite to that favored by selection, and may have faster rates of speciation (Mousseau and Fox, 1998, for review). This may be particularly pertinent given the high levels of self-recruitment found in some studies (Jones *et al.*, 1999; Swearer *et al.*, 1999). With advances in larval rearing,

we are now reaching a stage at which some of these influences on individual survival and success can be assessed in lab conditions, at least for a restricted group of species.

Cowen and Sponaugle (1997) and Kingsford (1998) point out that research on coral reef fishes has emphasized the retention/dispersal question, whereas studies of temperate fish larvae have focused on feeding and predation (mortality). Without decreasing work on the retention/dispersal question, increased work on feeding and predation would be welcome. Taxonomic work on the pelagic stages of reef fishes is still needed for most groups. Inability to identify larvae to the species level, particularly early stages, is a major impediment to understanding of distributions, feeding, condition, and many other subjects.

Leis (1991a) listed eight areas for future research on reef fish larvae, and in four areas there have been significant advances. Wolanski, Black, and others have made great strides in examining the fine scale of water circulation, particularly through the use of numerical models, and coupling this with larval distributions. However, there is an urgent need for better ground-truthing of numerical models, as pointed out by the different results of two of these for the same reef. Integration of larval behavior with this physical oceanographic input to understand dispersal will be challenging. Vertical distribution is now better known, but more knowledge is needed about what individual larvae are doing and how vertical distributions vary in different conditions. A better understanding of how smaller larvae interact with vertical structure in currents, other physical factors, and food distribution is needed. Much more is now known of the swimming capabilities of reef fish larvae, but only in the later portions of the pelagic stage, and some important taxonomic groups remain unstudied. Research on the ontogeny of swimming and sensory abilities is a top priority. Behavior of reef fish larvae is now understood as complex and flexible, but we have only just scratched the surface here, and, again, only with the later portions of the pelagic stage.

In contrast, the other four research areas identified by Leis (1991a) have received far less attention. The first question (Where and when are larvae put into the pelagic system?), aside from the intensive studies of Hensley *et al.* (1994) and Appeldoorn *et al.* (1994), remains largely unanswered. Future studies in this area need to be mindful of Warner's (1997a,c) cautions about studying adaptation. It may be profitable to focus on spawning aggregation sites, and to examine their characteristics. However, spawning sites are not necessarily chosen for their adaptive value (Shapiro

et al., 1988; Warner, 1988a), and many species do not participate in spawning aggregations. As to what generality there is among different regions and topographic situations, this has been largely ignored (again, see Warner, 1997a,c). The nature of the physical and biological requirements of reef fish larvae might be usefully approached by aquacultural methods (Tucker, 1998), by correlative studies between distributions of larvae and physical or biological variables, or by "hind-casting" studies based on potential information stored in the otolith. More work is required here, and cautions about extrapolation from aquacultural studies must be kept in mind (e.g., Olla *et al.*, 1998). The final question (Are distributions of larvae adaptive?) will remain unanswered until more is known about where the larvae that successfully settle on reefs have been, and this knowledge is compared with the distribution of "unsuccessful larvae."

Finally, we must point out once again that the majority of the available research is on pomacentrids. Although pomacentrids are common and are in many ways ideal subjects for experiments, it is highly desirable that future work includes a wider representation of the extreme taxonomic diversity found on coral reefs. Pomacentrids are certainly not entirely representative of the biology of the rest of that diversity. However, we do not share the view that research on "toy fishes" [i.e., small species, such as pomacentrids, not of direct commercial interest (Roberts, 1996; Polunin *et al.*, 1996)] is not of importance to fishery biologists and managers. Especially during the pelagic stage, all species are "toy fishes" and face the same problems of a small animal in a large pelagic environment: first, they must survive and grow, and second, they must find and make a radical transition to another very different environment.

VII. Conclusions

Recent research on the pelagic stage of reef fishes has given us a good look into the black box of larval biology. This look reveals that these pelagic stages are real fishes with capabilities in excess of the larvae of well-studied temperate fishes. This has changed thinking about the way larvae fit into the dispersal/retention concept that has dominated work on reef fish larvae. We now know that larvae and their behavior have a major influence on the positioning of reef fish populations along the open-closed continuum of population demography. In the foreseeable future, we should have a firm and defensible basis for design of marine reserves and of the geographical size of reef fish population units for management purposes, based on

an increased understanding of larval biology rather than the simplifying assumptions of the recent past.

Acknowledgments

We thank our colleagues for sharing their unpublished work with us, and the numerous people who helped us gain

the information reported here. We acknowledge ARC funding through Grants A19530997 (JML), A19804335 (JML), F19600180 (MIM), and A19701068 (MIM), which supported both the preparation of this manuscript and most of the unpublished work reported here. Thanks to S. Bullock and B. M. Carson-Ewart for help with editorial matters, and to M. J. Kingsford and K. C. Lindeman for constructive reviews.

