CHAPTER 7

Oceanographic Influences on Larval Dispersal and Retention and Their Consequences for Population Connectivity

Robert K. Cowen

Division of Marine Biology and Fisheries
Rosenstiel School of Marine and Atmospheric Science
University of Miami
Miami, Florida 33149

I. Introduction

The larval stage of most coral reef fishes is spent in the pelagic environment, potentially well away from the reef proper. Survival of this stage is tenuous, being mediated by factors such as food availability, predator abundance, and physical conditions. The complex biological and physical interactions of these factors can result in a seemingly stochastic larval supply that drives temporal and spatial variation in recruitment intensity (Cowen, 1985; Roughgarden *et al.*, 1988; Choat *et al.*, 1988). This variation can be a major determinant of adult population sizes (Cushing, 1975; Rothschild, 1986; Sinclair, 1988). A growing awareness of this perspective has placed a premium on the need to study the early life history stages of marine organisms, forcing us to peer into the black box of larval biology and ecology. The following discussion will outline where advances have occurred in our understanding of how, and to what effect, coral reef fish larvae interact with the pelagic environment.

Without denying the importance of food and predation to larval survival (Houde, 1987; Bailey and Houde, 1989), it is clear that many species of coastal marine fishes are particularly dependent on directed transport to their juvenile or adult habitat. For example, coral reef fish larvae will not survive the dispersive stage of their life history without appropriate transport back to a reef (Leis, 1991a). Similar arguments can be made for many temperate species that are estuarine dependent or benthic oriented (Boehlert and Mundy, 1988). In contrast, many pelagic species do not require directed transport to complete their larval life, although some species may recruit only if their larvae are retained within a specific area [e.g., herring populations (Sinclair, 1988)].

Although fish larvae are often (erroneously) considered strict constituents of the zooplankton community, evidence suggests that many species exhibit some form of active behavior during their pelagic stage (Neilson and Perry, 1990; Leis, 1991b). Although some larval distributions can be explained purely through a combination of spawning sites and passive larval transport [i.e., constant buoyancy (Boehlert and Mundy, 1994)], other larval distributions are influenced by larval behavior interacting with the local current regime. The importance of vertical larval movements in affecting horizontal movements in estuarine systems (Boehlert and Mundy, 1988; Epifanio, 1988) or retention in bank systems (Werner *et al.*, 1993; Tremblay *et al.*, 1994) is well documented. There is also evidence of impressive horizontal swimming abilities in late-stage larvae (see Chapter 8). Thus there is a continuum of possible behaviors (e.g., passive to vertical to horizontal movement), as well as the timing of the onset or ontogeny of such behaviors. Such behavioral capabilities may strongly impact the survival and recruitment of coral reef fish larvae to benthic habitats.

The complexity introduced into biological systems by the physics of water movement contributes significantly to the variability associated with the recruitment of marine species. Variability in larval transport will

be determined by the interaction of water masses and the effects of external forcing such as winds and tides. Active behavior by larvae may modulate some of this variability, yet a strong change in the direction or intensity of flow of a particular water mass may result in a substantial change in larval supply to a given reef or island, or may carry larvae away from a suitable food environment. Because recruitment integrates the effect of physics across all life history stages, this variability is large and complex. Though it is unlikely that we will ever measure the importance of *all* processes contributing to variable recruitment patterns, we potentially can isolate the most important processes that are operating. By doing so, we stand a better chance of explaining observed recruitment patterns, predicting future recruitment, and ultimately forging a general theory of recruitment dynamics.

In such an effort, we also need to consider the evolutionary implications of how larvae have adapted to the physical environment to ensure their survival and successful transport or retention. How well can larvae match their behavior to the particular system in which they live? At face value this seems like an elementary question for any adaptationist; presumably a fish is adapted to the set of environmental variables it typically encounters. However, the larvae of a single species may encounter a broad range of coastal environments, ranging from continental shelves to island chains to isolated oceanic islands (e.g., most Caribbean or Indo-Pacific species), and therefore the question becomes one of how specific are the features to which larvae are adapted. If larval behaviors are adaptations to promote successful return to adult habitat, are these adaptations more likely to be keyed to the specifics of a particular location, or to features common to many systems? To address this, we need to determine the generalities of larval transport in terms of both the specific circulation features important to larval transport and the larval responses to these features.

In addressing the above topics, the emphasis here is on processes contributing to larval transport, although some discussion is devoted to processes contributing to survival as well. However, it is impossible to do full justice to this multifactor issue of larval survival in this chapter. To constrain the topic, this chapter is not a detailed review of physical oceanography, but there are sufficient citations to physical oceanographic studies that an interested reader can pursue the trail in greater detail. In most cases, the focus is on recent literature, particularly on those topics covered previously in Leis (1991a). Finally, although the primary focus is on coral reef fishes, the literature on temperate species is examined where necessary (see also Cowen and Sponaugle, 1997).

II. Scale

Embedded in any discussion of larval transport and its role in marine population dynamics is the issue of scale. Marine systems are highly dynamic largely because of the interaction of various physical processes operating on a variety of spatial and temporal scales (Haury *et al.,* 1978; Denman and Gargett, 1983; Mullin, 1993). Determining the relevant scales of physical processes will depend on the biological questions being asked as well as on the environments being studied.

The scale over which larval transport (or retention) occurs varies substantially among species and even among locations within a single species. For some species, larval dispersal is minimal and possibly nonexistent [e.g., the damselfish, *Acanthochromis polyacanthus* (Robertson, 1973; Thresher, 1985)], whereas at the other extreme dispersal can occur over thousands of kilometers [e.g., *Anguilla rostrata* and *A. anguilla* (McCleave *et al.,* 1987)]. However, for most coral reef fish species, with larval durations of weeks to months, transport will usually be on the scale of tens to hundreds of kilometers. It may ultimately be shown (see Section VII) that local physical effects aid retention, thereby placing a greater emphasis on smaller scale processes as influencing local population dynamics. If so, the sampling constraints that have led to focusing on smaller scales will have been fortuitously important in providing evidence of greater retention of young than was previously expected.

In addition to spatial scales, temporal scales are crucially important in the issues we study. For example, population exchange (or connectivity) is often indicated via population genetics studies (e.g., Lacson, 1992; Doherty *et al.,* 1995; Shulman and Bermingham, 1995; Planes, 1993, 1998). In general, these studies have suggested that a fair amount of genetic exchange occurs over rather extensive (thousands of kilometers) distances. Yet genetic exchange operates at a very different temporal scale, as compared to biological and physical processes contributing to larval transport. The level of exchange required to sustain genetic homogeneity is many orders of magnitude lower than that required to sustain a population ecologically (Avise, 1992; Lacson, 1992) because measurable genetic exchange occurs over many generations and often does so in a stepping-stone fashion. Knowledge of the extent of ecological time scale larval exchange is of fundamental importance to the study of population dynamics as well

as to the design of marine reserves. Decisions predicated on the assumption that larvae are widely dispersed may lead to erroneous actions if the assumption is wrong. However, lack of evidence of retention has generally resulted in the acceptance of the concept of well-mixed populations. This, in turn, has been interpreted to infer that mean current trajectories and larval duration may predict exchange between populations (e.g., McManus and Menez, 1997; Roberts, 1997b; but see Sale and Cowen, 1998; Bellwood *et al.,* 1998; Cowen *et al.,* 2000).

Thus, when examining processes affecting larval exchange, we need to examine time scales relevant to the ecological sustainability of coral reef fish populations: Larval stages last weeks; reproduction may occur once per year to daily; life-spans range from 1+ to 50+ years. A suite of physical processes fall within this temporal context, leading both to physical transport of larvae and to conditions directly affecting their survival. Recruitment of fishes with very protracted spawning seasons (e.g., year round) can be influenced by a broader spectrum of processes than is likely with fishes with short spawning seasons. A species that spawns over a very short period will exhibit interannual trends, whereas a species with more protracted spawning seasons will likely exhibit intraannual and even intraseasonal patterns as well. In the latter case, there is greater opportunity for small to mesoscale processes to introduce considerable variability.

On a larger spatiotemporal scale, maintenance of populations is affected by the longevity of individuals. Short-lived species will require more frequent input and survival of new recruits to sustain their populations than will long-lived species (Cowen, 1985; Warner and Chesson, 1985). The scale of important physical processes also depends on the type of environment being studied. Particular environments will determine which physical processes likely operate and, importantly, which do not operate. This effect of the physical characteristics of the system becomes particularly important when different types of environments are compared (e.g., shelf vs. oceanic environments). This latter point is often overlooked when attempting to compare among studies.

Another aspect of the temporal linkage between biological and physical processes relates to the capacity of organisms to respond to a given physical process. For example, availability of food obviously impacts all life-cycle stages, though it may do so in different ways. Increased nutrients may be rapidly transferred into potential prey ($1°$ and $2°$ plankton production) and therefore a relatively short-duration event associated with coastal upwelling or internal waves (e.g., Leichter *et al.,*

1996) may be an important contributor to the success of a cohort of larvae. Such short-duration, local nutrient pulses may not be immediately transferred into available food for adults, but longer (i.e., seasonal), more spatially extensive pulses may be, ultimately influencing reproductive output (e.g., Robertson, 1992; Clifton, 1995). However, if short-duration, localized nutrient pulses serve as an environmental cue for reproduction (i.e., ensuring food availability for newly hatched larvae, or recently settled juveniles), then similarly scaled processes may be important to both life history stages. In this case, the behavior of adults has increased the potential number of relevant scales over which physical processes may operate.

III. Biological Pattern

Much of the initial work on larval fishes focused explicitly on describing distribution patterns. More recently, the effort has shifted to identifying the processes contributing to the observed patterns of distributions, and, more importantly, trying to link these processes to observed patterns of recruitment variability. Below is a brief review of work on the horizontal, vertical, and temporal distribution patterns of coral reef fish larvae, with a strong emphasis on the factors contributing to the observed pattern.

A. Horizontal Patterns

Early work on the larval distributions of coral reef fishes described patterns with regard to the distances from shore certain taxa were distributed (see review by Leis, 1991a). To this end, Leis (1978) described three main assemblages of coral reef fish larvae with respect to proximity to shore: nearshore, neritic, and oceanic. Subsequently, a distinct fourth, and occasionally completely isolated, embayment (or lagoonal) assemblage was identified (Leis, 1986a, 1991b, 1994; Boehlert and Mundy, 1993; Leis *et al.* 1998). Leis (1991a) reviewed work on the horizontal distributions of coral reef fish larvae, demonstrating that taxon-specific spatial patterns exist for many taxa with respect to distance from shore. He concluded that such taxon-specific patterns clearly indicate that larval distributions are not merely the result of passive dispersion by currents; larval behavior must play an integral role.

Beyond determining that larvae of certain taxa typically are found at distinct distances from shore, several studies have been of sufficient spatial and/or temporal scope and resolution to identify larval assemblage

dynamics. These broad-scale studies have been coupled with detailed physical oceanographic data that indicate that far more complex mechanisms are operating in determining assemblage makeup and location than simply distance from shore. For example, Boehlert *et al.* (1992) identified high concentrations of pomacentrid/gobiid larvae nearshore of Johnston Atoll in the Pacific Ocean in the vicinity of an onshore flow. Though generated by different forcing mechanisms, similar nearshore distributions of pomacentrid/gobiid larvae were identified along the coast of Barbados, West Indies, where flow was directed onshore [at the depth of maximum larval concentration (Cowen and Castro, 1994)]. These same larval taxa were absent nearshore where such flow conditions were lacking.

It is now clear that larval assemblages are dynamic with respect to both the spatiotemporal distribution of and the species membership within each assemblage (Cowen *et al.,* 1993). Boehlert and Mundy (1993) review factors that may contribute to ichthyoplankton assemblages, noting that such factors may be separated based on their influence on the formation, maintenance, and/or disruption of assemblages (Table 1). Not only does this breakdown enable one to look at the causes

of patterns and dynamics of the assemblages, it also identifies the physical processes to which species may adapt.

First, the spatial (and temporal) formation of larval assemblages is strongly affected by the interaction of adult reproductive behavior with coastal currents. Regardless of whether optimal spawning strategies have evolved to maximize larval survival or minimize adult loss (Robertson *et al.,* 1990), the physical conditions present at the time and location of spawning will affect where the larvae end up. The location and time larvae enter the pelagic realm is further affected by egg development and any early swimming behaviors and/or buoyancy characteristics of the larvae. Second, the interaction of larval behavior with the physical environment enables assemblages to persist in time (Table 1). This may occur either through larvae seeking a particular environmental cue and/or prey, or via physical transport mediated by vertical larval movement. In either case, the larvae may be grouped by a variety of vertically structured features. Finally, assemblage membership may change over time (Cowen *et al.,* 1993). Quantification of such changes may provide insight as to how different larval behaviors may contribute to

TABLE 1   Factors of Potential Importance in the Formation, Maintenance, and Disruption of Ichthyoplankton Assemblages around Islands and Seamounts[a]

Type of factor	Influencing formation[b]	Influencing maintenance[c]	Influencing disruption[d]
Adult behavior	Spawning location Spawning time (tidal, diel, lunar, seasonal)	None	Predation (cannibalism) Influences on settlement
Egg development	Buoyancy (demersal vs. pelagic eggs, egg density) Incubation time Hatching location Hatching time	None	None
Larval behavior	Buoyancy at hatching Swimming ability at hatching	Habitat preference (temperature, salinity, light, depth) Vertical migration	Ontogenetic changes in vertical distribution Metamorphosis (settlement, schooling)
Biotic environment	Predation (absence will create "ecological safe sites")	Prey presence	Predation Prey absence (starvation)
Abiotic environment	Convergences Fronts	Eddies (Taylor columns) Upwelling Downwelling Internal waves Convergences Fronts	Diffusion Mixing Advection

[a] After Boehlert and Mundy (1993).
[b] Factors promoting spatial and temporal cooccurrence.
[c] Factors promoting integrity of assemblages over time.
[d] Factors causing eventual breakdown of assemblage structure.

their horizontal distribution within the same physical environment, and/or how larval behavior may facilitate the movement of larvae from one water mass (or flow feature) to another. Assemblages also may be disrupted by strong predation, the need to return to coastal, benthic habitat (i.e., settlement), or via strong diffusive and/or advective events [e.g., effect of transient, mesoscale eddies sweeping larvae away from the coastal environment (Cowen and Castro, 1994)]. Other recent studies of larval distributions (several of which include larvae of coral reef fishes) continue to shed light on the dynamic nature of larval assemblages (Sabatés and Olivar, 1996; Dempster *et al.*, 1997; Sanvicente-Añorve *et al.*, 1998).

Finally, the existence of predictable larval assemblages suggests that it should not be surprising to find multispecific recruitment events. Spatial coherence in recruitment events (especially over scales of tens of kilometers) has led to the suggestion of a single, mesoscale larval patch (Victor, 1986a; Williams and English, 1992; Thorrold, 1993). However, the behavioral and physical dynamics leading to larval assemblages, coupled with synchrony in spawning (and settlement) of many species (Robertson *et al.*, 1988, 1993; Milicich and Doherty, 1994; Sponaugle and Cowen, 1996a), may preclude the requirement that a single, mesoscale patch exist. At small scales, increased concentrations of larvae are often associated with frontal features (see reviews by Kingsford, 1990; Govoni and Grimes, 1992; Govoni, 1993; Olson *et al.*, 1994; Grimes and Kingsford, 1996). At larger scales, coral reef fish larvae have been found to be entrained in spin-off eddies (Limouzy-Paris *et al.*, 1997) and around offshore currents [e.g., Loop Current (Richards *et al.*, 1993)], or in jets of water steered by topographic features (Cowen and Castro, 1994). Such physically driven distributions can interject significant variability into general patterns of onshore/offshore distribution.

B. Vertical Patterns

Attempts to explain the above observed horizontal distributions of larvae have often required invoking an interplay between the vertical distribution of larvae and the physical environment. Although we have some evidence for vertically mediated larval transport for a few species of coral reef fish (Hare and Cowen, 1991; Cowen *et al.*, 1993; Cowen and Castro, 1994), there is a surprising dearth of information on the detailed vertical distribution of larval coral reef fish, particularly with respect to both diel and ontogenetic vertical migrations or movements. This is largely due to sampling capabilities that have only recently enabled more than a coarse reso-

lution of vertical distributions (i.e., surface/nonsurface) and the problem of labor-intensive sorting and identifying of samples taken from multiple depths at each sampling station. In contrast, there is a substantial literature on larval vertical distribution of temperate species (see review by Neilson and Perry, 1990).

As with horizontal larval distributions, early work reviewed by Leis (1991a) described certain taxon-specific vertical distributions, though the relatively few available studies made it difficult to generalize. That same year, Leis (1991b) published the first detailed study of the vertical distribution of coral reef fish larvae from a vertically stratified sampling program of the upper 20 m over the Great Barrier Reef (GBR) lagoon shelf. His general findings indicated a stronger vertical pattern in larval distribution during the day than at night [a finding similar to that of Gray (1998) for more temperate larval fishes, but see also Olivar and Sabatés (1997)], with most taxa avoiding the upper 6 m during the day. Several species, however, were daytime inhabitants of the near-surface (i.e., neuston) layer, a finding that has been observed in other areas [e.g., in Barbados, late-stage dactylopterids (R. K. Cowen and C. Paris, unpublished data)].

Subsequent studies have incorporated various vertically stratified sampling protocols to examine the distribution of tropical fish larvae in coastal and insular environments with relatively narrow shelves. In these areas, sampling occurred in water that usually exceeded depths of 100 m. Working in the waters around Johnston Atoll in the Pacific, Boehlert *et al.* (1992) found coral reef fish larvae to be most abundant between 50 and 100 m, with high concentrations also in the upper 50 m. Cha *et al.* (1994) reported on the nocturnal larval vertical distribution patterns for a variety of fish families, including mesopelagic and coral reef fish families collected off of the Florida Keys reef tract (water depth >150 m). Generally, the highest diversity of taxa were in the upper 50 m, with a drop in diversity with depth to very few taxa collected below 175 m (though it is difficult to separate coral reef fish families from the others in this particular analysis). Of the more common taxa in their samples, they found labrids, carangids, and bothids to be most abundant in the upper 25 m, gobiids, serranids, and scorpaenids to be most common in the upper 50 m, and synodontids to be most abundant at depths greater than 50 m. Cowen and Castro (1994) and Castro (1995) found similar patterns. Of particular note was the linkage between the shallow larval distribution of carangids (especially a preflexion *Caranx* sp.) and their horizontal distribution associated with surface convergences to the southwest and northwest of the island (Fig. 1A);
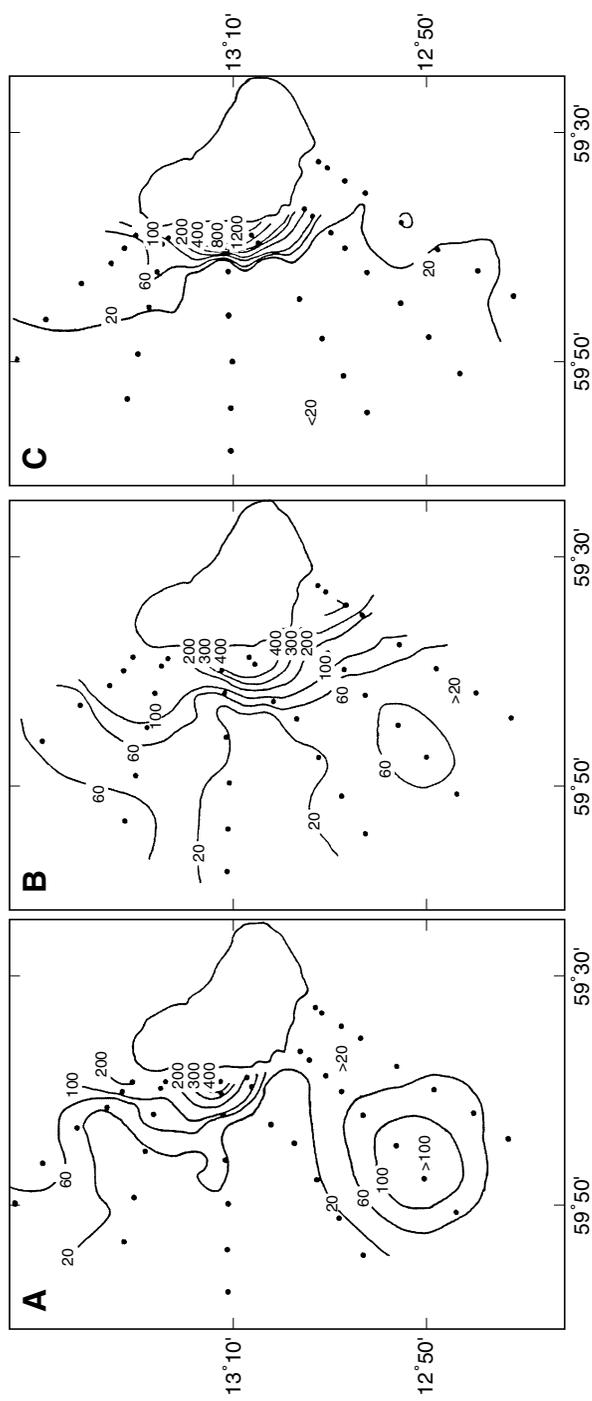
FIGURE 1 Distribution by depth intervals of larval coral reef fish (N per 1000 m^3) around the western side of Barbados during May, 1990. (A) 0–10 m; (B) 10–30 m; (C) 30–60 m. Modified from Cowen and Castro (1994).
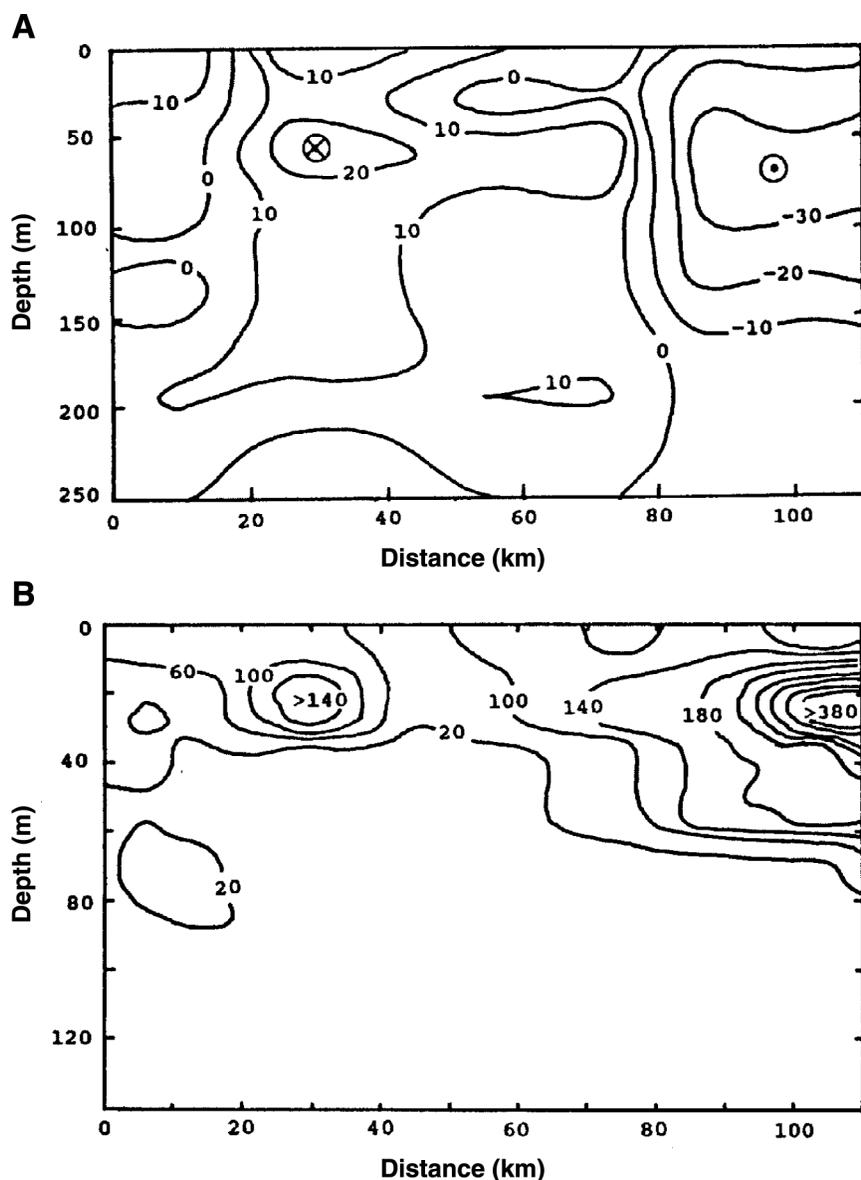
FIGURE 2 Vertical section of current (A) and coral reef fish larval density (B) of a section crossing the Barbados ridge, about 50 km northwest of Barbados. Currents are derived from a shipborne (bottom-tracked) acoustic Doppler current profiler; positive contours represent flow into the page, negative contours represent flow out of the page: Larval concentrations are N per 1000 m^3. The Barbados ridge is located centrally along the section (i.e., near 50 km) and has a minimum depth of 275 m. Modified from Cowen and Castro (1994).

pomacentrid and gobiid larvae were concentrated in the middepths (20–60 m) where onshore flow was evident (Fig. 1B,C). In general, few coral reef fish larvae were found deeper than 90 m, and a complex of coral reef fish larvae was associated as a vertically discrete (15–50 m) and horizontally stretched patch immediately above a jet of water that was streaming around the Barbados ridge (Fig. 2).

From a recent study of the vertical and horizontal distribution of larvae around Barbados, R. K. Cowen and C. Paris (unpublished data) have discerned a variety of taxon and ontogenetic (stage-specific) vertical patterns (Fig. 3). These preliminary data reveal that few coral reef fish larvae, even as early preflexion stage,

are found near the surface (i.e., less than 10–15 m), nor below 80 m. Of those species examined thus far, most occur between 15 and 60 m, the main exception being postflexion larval *Synodus* in slightly deeper water (50–80 m), a finding that is consistent with Cha *et al.* (1994). There were also several groupings of larvae, based on their ontogenetic vertical distribution patterns, for which (1) preflexion stage larvae are shallower than postflexion stage larvae (the most common pattern), with the difference in mean (center of mass) depth ∼10–20 m; (2) preflexion stage larvae are at the same depth as postflexion stage larvae, i.e., no ontogenetic change in vertical distribution; and (3) preflexion stage larvae are deeper than postflexion stage larvae
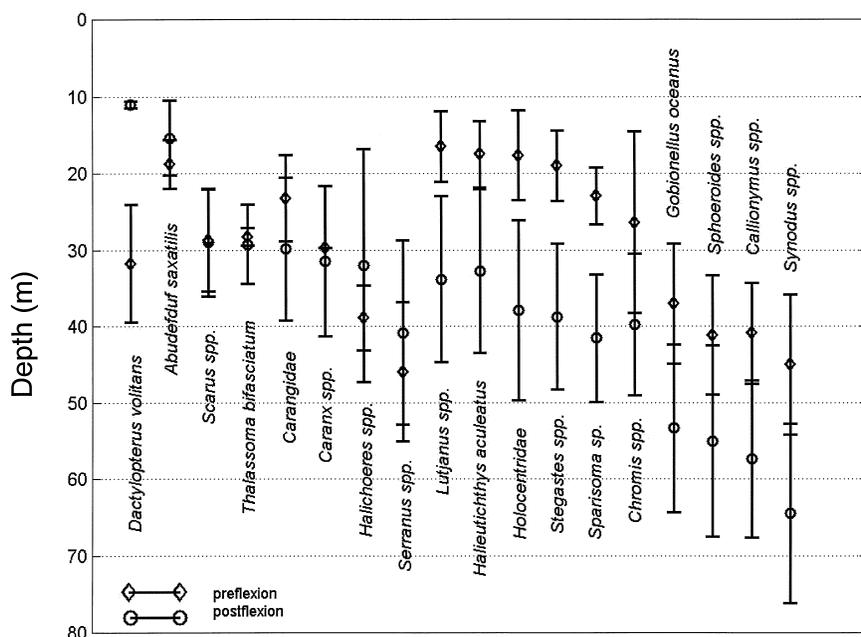
FIGURE 3 Stage-specific vertical distribution of a variety of a coral reef fish larvae from the eastern Caribbean island of Barbados (May, 1996). For each species, the mean (center of mass $\pm$ SE) is shown separately for the preflexion and postflexion stages. Larvae were collected with a 1-m^2 frame Multiple Opening/Closing Net and Environmental Sensing System, with nets fished at 0–20, 20–40, 40–60, 60–80, and 80–100 m. Data source: R. K. Cowen and C. Paris, unpublished data.

(obvious only in *Dactylopterus volitans*; later stage larvae of *D. volitans* move upward to the neuston).

We are still lacking examination of alternative explanations of the vertical distribution of larvae. For example, the 15- to 60-m depth range of many larvae around Barbados corresponds with the depth of mean onshore flow that may maximize local retention (Cowen *et al.,* 2000). Alternatively, this same depth range falls within the depth range of the chlorophyll maximum layer (R. K. Cowen and K. Lwiza, unpublished data), which could serve to concentrate potential food sources for the larvae. Similarly, for preflexion larvae to be concentrated between 20 and 40+ m suggests that preflexion stage larvae may either be swimming vertically and/or they are neutrally buoyant below the surface layer. If the latter is true, then periodic, low-salinity intrusions (Cowen and Castro, 1994; Kelly *et al.,* 2000) might alter the depth of preflexion larvae (i.e., they will move deeper) when low-density water is present in the upper 10–40 m. Obvious alternatives include that of seeking strata of high prey concentrations and/or avoiding predators. Also, and not necessarily mutually exclusively, is the potential need to avoid high ultraviolet (UV) levels in the upper layers (though this would probably require being only a few meters deep at most). There still are insufficient published data to assess these various hypotheses.

In summary, based on relatively few studies, several patterns of larval vertical distributions are emerging or have been confirmed. First, vertical stratification of larvae seems to be greater during daylight hours than at night (though additional studies directly assessing diel vertical migrations are needed). Second, there appear to be changes in vertical distribution with ontogeny for many taxa, the norm being that preflexion stage larvae are shallower than postflexion larvae, though notable exceptions exist. Third, most larvae appear to avoid the near-surface layer, whether over relatively shallow shelves (e.g., GBR) or in deep water. Fourth, most reef fish larvae are restricted to the upper 80 m.

C. Temporal Patterns

Few existing studies have examined the temporal pattern of coral reef fish larval abundance. However, there have been a number of studies examining temporal patterns of reproduction, which clearly translate into temporal patterns in larval abundance (at least for early-stage larvae). There have also been a variety of studies examining the temporal patterns in the abundance of late-stage larvae (i.e., presettlement) or recently settled coral reef fishes. Without pursuing an exhaustive review of reproductive patterns, it can be said that there exist several obvious patterns at seasonal, monthly (lunar/tidal), and daily time frames (e.g., Munro *et al.,* 1973; Lobel, 1989; Robertson, 1990, 1992; Robertson *et al.,* 1990; Colin and Bell, 1991; Hunte von Herbing and Hunte, 1991; Colin, 1992; Meekan *et al.,* 1993; Danilowicz, 1995; Crabtree, 1995; see review by Sadovy, 1996). An example of lunar periodicity in spawning is provided in Fig. 4 for the Caribbean pomacentrid, *Stegastes partitus*. This
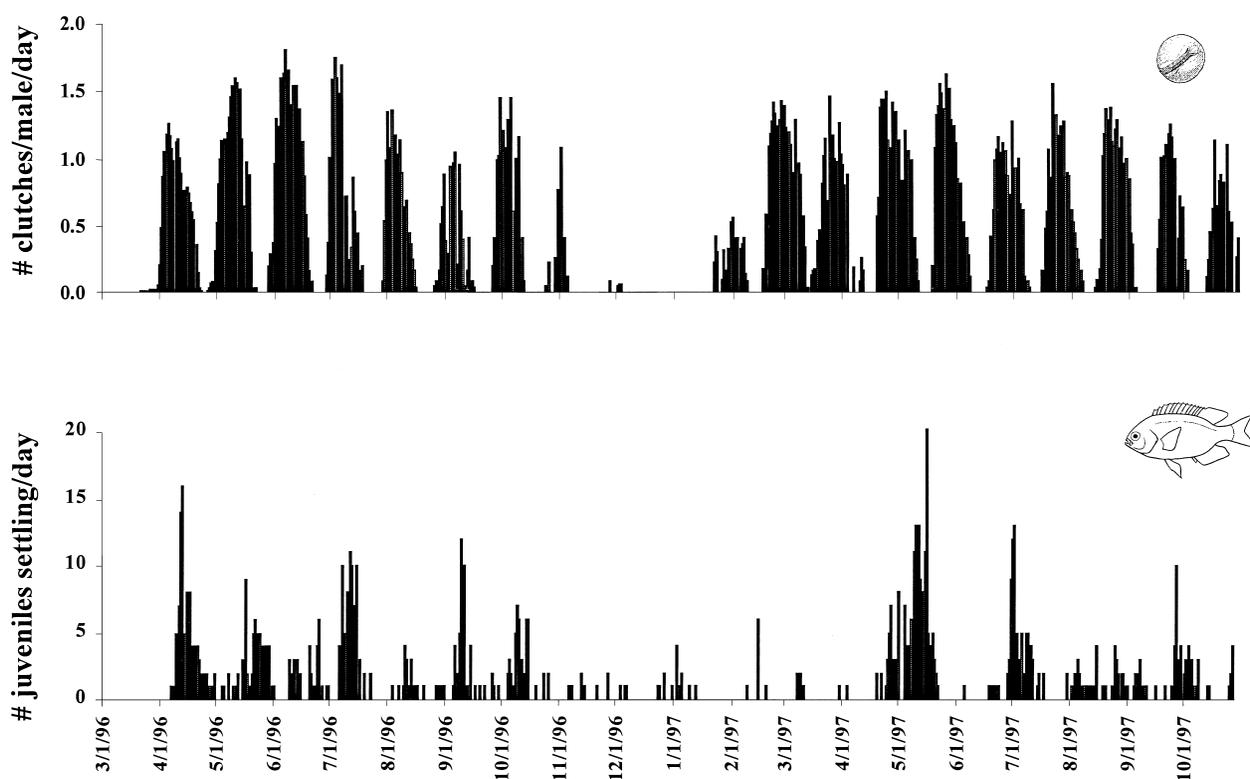
FIGURE 4   The 18-month time series of the daily pattern of spawning and settlement for the Caribbean pomacentrid, *Stegastes partitus*, at Barbados, West Indies. Daily spawning was estimated from 75 male nests and measured as number of egg clutches/male/day. Daily settlement pattern was back-calculated from otoliths of newly settled fish collected on biweekly surveys (*N* = 15 transects per survey). The time series was continual except during brief periods of extreme wave conditions. Also noted are two collection periods for offshore ichthyoplankton that corresponded with efforts to follow an entire cohort from hatching to settlement (∼28 days). Data source: S. Dorsey and R. K. Cowen, unpublished data.

species exhibits strong synchrony in spawning with the new moon and a seasonal signal is also evident. Cues to spawning include water temperature, lunar phase, tidal phase, and even wind (see Sadovy, 1996). These cues are prevalent throughout the range of all species, though the relative importance of each cue may vary, as will be discussed later.

Similarly, many species exhibit periodic settlement patterns synchronized with particular tidal or lunar phases (e.g., Dufour, 1991; Milicich *et al.,* 1992, Robertson, 1992; Shenker *et al.,* 1993; Meekan *et al.,* 1993; Sponaugle and Cowen, 1994, 1996a; Thorrold *et al.,* 1994b,c; Robertson *et al.,* 1999). Relationships to specific phases of the moon have been found for many species, with new moon peak settlement dominating in many regions (Dufour, 1991; Robertson, 1992; Meekan *et al.,* 1993; Thorrold *et al.,* 1994b,c; Sponaugle and Cowen, 1996a, 1997), but exceptions do occur. Peak settlement for certain labrids, scarids, pomacentrids, acanthurids, blenniids,

and gobiids to Barbados occurs on the third-quarter moon and with minimum-amplitude tides Sponaugle and Cowen (1994, 1996a,b, 1997). This third-quarter lunar and minimum-amplitude tidal periodicity also is shared by a variety of decapod crab larvae at Barbados (Reyns and Sponaugle, 1999). More unusual, on the full moons, two pomacentrids recruit to St. Croix (Booth and Beretta, 1994). A variety of workers also have identified semilunar periodicity (Hunte von Herbing and Hunte, 1991; Robertson, 1992; Thorrold *et al* 1994b,c). In general, the temporal patterns of settlement are more difficult to discern than are those in spawning due to substantial variability inserted during the pelagic period (see Fig. 4). Long time series are often needed to isolate patterns.

The tidal amplitude phase is closely linked to the lunar phase, thereby complicating the separation of lunar from tidal synchrony. Yet, several workers have discussed larval supply and settlement patterns of reef fishes in terms of tidal amplitude phase (Sponaugle

and Cowen, 1997; Robertson *et al.,* 1999), and some semilunar periodicity observed in larval supply (e.g., Shenker *et al.,* 1993) may be tied to the tidal amplitude cycle. Morgan and Christy (1994), Morgan (1995), and Reyns and Sponaugle (1999) discuss the linkage between lunar and tidal amplitude cues for marine invertebrates, particularly crab postlarvae (see below).

Finally, although a level of predictability occurs in the *timing* (and even spatial pattern) of the early life history stages of coral reef fishes, the *magnitude* of temporal patterns is not so predictable. This is due in large part to the overall influence of the processes operating during the pelagic phase. Many of the processes operating in the pelagic environment appear chaotic in nature and can decouple reproductive output from subsequent recruitment (Robertson *et al.,* 1988, 1993; Meekan *et al.,* 1993; Danilowicz, 1997) (see Fig. 4). However, when viewed in the appropriate context, these apparently chaotic processes may possess predictable characteristics that enable us to explain both variability in larval distribution and abundance, and adaptation by larvae to utilize specific physical processes.

IV. Physical Processes

A. Wind

Wind is the major driving force in the circulation of the ocean. As the wind blows across the surface, frictional forces drag the surface water along, albeit at approximately 3% of the wind speed. Similarly, this surface layer of water drags the next layer of water along, and so forth, with speed exponentially decreasing with depth until no additional wind-generated flow occurs. This wind forcing, coupled with Coriolis deflection (due to the rotation of the Earth), results in the actual direction of surface water movement to be at a 10–45° angle to the wind (clockwise of the wind in the Northern Hemisphere, counterclockwise in the Southern Hemisphere). Similarly, lower water layers move at an angle to the forcing layer above. This results in an "Ekman spiral," with the maximum depth of wind penetration effect called the Ekman depth (the mixed-layer depth). The depth of the Ekman layer is dependent on both the strength of the wind and the thermohaline structure of the water column. The stronger the stratification of the water column (i.e., the greater the change in density with depth due either to temperature and/or to salinity), the stronger the wind must be to affect flow to any given depth. The wind speed required to mix the water column to a particular depth is also dependent on the duration of the wind event; a long-duration wind event of a given speed will penetrate deeper, compared to a short-duration event.

In addition to the Ekman spiral, persistent winds blowing across the surface of the ocean can create small-scale circulation features called Langmuir circulation cells. These cells are parallel, typically penetrate 3–10 m depth, and are up to 50 m across and hundreds to thousands of meters long. Each cell has a spirallike circulation that alternates in direction from cell to cell, resulting in alternating zones of convergence (downwelling) and divergence (upwelling). The role of such features in generating plankton and larval fish distributions is discussed by Kingsford *et al.* (1991), Werner *et al.* (1997), and MacKenzie (2000).

Another wind effect of relevance to coastal areas is that the surface layer of water (typically the mixed layer down to the thermocline or halocline) can respond rapidly to changes in wind direction. Wind shifts are common along coastlines, where they may be affected by diurnal warming of the landmass (daily cycling), passage of meteorological fronts (weekly to monthly cycling), and seasonality. Where winds are offshore or poleward on an eastern coast (opposite on the western coast), the net effect is offshore flow of the surface layer, which may result in upwelling of deeper, cooler water near the coast. Conversely, where the wind is blowing onshore or equatorward on an eastern coast, the surface flow will be onshore. Where inlets to coastal embayments occur, such onshore flow may accentuate flow into the embayment. Where such inlets do not occur, the onshore flowing water may pile up along the coast, setting up a pressure gradient wherein the water tends to flow downgradient. This flow, in concert with Coriolis deflection, then turns right or left (hemisphere dependent) to flow along the coast, generating a coastal current. For reefs, winds may pile water up until it flows over the reef crest into the back reef (or moat), returning back out via reef channels (Yamano *et al.,* 1998). Such winds also force the buildup of waves, which may further induce inflow by overtopping of the reef crest (Roberts *et al.,* 1992; Symonds *et al.,* 1995). Response to a buildup or decrease in the winds can be immediate, whereas if sufficient wind-generated waves exist, the reduction in inflowing water over the reef crest may persist for some time after winds decrease or even reverse (Yamano *et al.,* 1998). Orientation of a particular reef or coastline to prevailing winds will therefore have important impact on flow conditions.

Larger scale circulations are also strongly affected by the winds, but these are predominantly on a

basin-wide scale largely associated with the major global wind bands (e.g., trade winds, westerlies, easterlies). Strong seasonal, interannual, decadal, or longer time scale variations in the wind can affect the intensity of current flows or even alter the direction of major ocean currents. The best example of such major changes is the effect of the El Niño/Southern Oscillation (ENSO) wind pattern on the equatorial currents of the Pacific Ocean (Philander, 1992). Although seasonal shifts in the wind patterns are relatively easy to capture in a typical study, longer time scale variations are not. Yet the importance of such variation cannot be overemphasized. Even if a single investigator cannot conduct long time series work [time series analysis typically requires a time series to be at least four times longer than the longest cycle being investigated (Chatfield, 1979)], when comparing among studies of 10+ years apart, potential differences in the meteorological and resultant oceanographic conditions must be considered.

Wind can have a positive effect when associated with delivery of late-stage larvae to shore. Shenker *et al.* (1993) found a strong correlation between the occurrence of two major recruitment peaks of the Nassau grouper (*Epinephelus striatus*) and two storm-related wind events that increased onshore flow during winter months. A similar positive relationship with wind was identified for other late-stage larval coral reef fishes passing through reef channels to benthic habitats on the Great Bahamas Bank (Thorrold *et al.,* 1994a). In this latter study (during summer months), a large, multispecific pulse of larvae was associated with a wind-relaxation event that resulted in a reversal of the coastal current and onshore flow. Studies on the GBR also have indicated that favorable winds generate strong recruitment pulses (Milicich, 1994; Kingsford and Finn, 1997).

Despite these positive results, the effects of wind on delivery of late-stage larvae to settlement habitat are not always temporally consistent. Whereas Shenker *et al.* (1993) found a positive relationship in supply with onshore (storm) winds, the reverse was true several years later (Grover *et al.,* 1998). Elsewhere, either no relationship between wind and recruitment has been found, or negative effects have been identified (e.g., Sponaugle and Cowen, 1997; Robertson *et al.,* 1999). Thus caution must be exercised when generalizing from one study to the next with respect to specific relationships between the wind field and delivery of young (late-stage) larvae to settlement habitat. These results suggest it is likely that onshore favorable winds may enhance the delivery of late-stage larvae to coastal habitats; however, such winds may serve to complement other behaviorally mediated onshore movements

(e.g., swimming, tidal flows), and are not necessarily a prerequisite for recruitment.

Wind can also influence initial dispersal of larvae. Appeldoorn *et al.* (1994) found that spawning of the bluehead wrasse (*Thalassoma bifasciatum*) cooccurred with periods of maximum wind-generated flow (on both a diel and seasonal basis), which rapidly carried the eggs off the reef patch. However, contrary to standard belief, the eggs were carried along and slightly toward shore, an area hypothesized (Johannes, 1978; Shapiro *et al.,* 1988) to result in high mortality of eggs by planktivores concentrated in coastal habitats. Similar evidence of primarily alongshore dispersal (versus offshore) of spawned eggs was obtained by Colin (1992) for the Nassau grouper (*E. striatus*) in the Bahamas. In the extreme, strong wind events associated with large storms may preclude successful spawning altogether due to extreme turbulence from large waves in shallow water (Petersen *et al.,* 1992; Robertson *et al.,* 1999).

Beyond transport, wind can affect food availability via upwelling, vertical mixing and even microturbulence. Several of these features may require time to manifest their impact on larval feeding conditions. For example, upwelling may inject surface waters with a pulse of nutrients, which is translated over several days into primary and secondary production. Other features, such as the effect of microturbulence enhancing prey encounter rates by larval fish (Rothschild and Osborn, 1988; MacKenzie *et al.,* 1994; Dower *et al.,* 1997; but see Dower *et al.,* 1998), may be almost immediately responsive to changes in wind conditions. Therefore, the relative timing of a wind event is likely important and can result in effects at a variety of time lags from settlement. Such interactions add to the complexity of the patterns of settlement, though utilization of nonlinear models with appropriate time lags may reveal linkages between recruitment and events occurring early in the pelagic phase (Dixon *et al.,* 1999). Spatial variability in such processes can be similarly visualized to lead to spatial patchiness in larval condition (Suthers, 1996; McCormick, 1998a) and, potentially, survival (Searcy and Sponaugle, 2000). Searcy and Sponaugle (2000) detected among- and within-cohort variability in the condition (measured as otolith growth) of newly settled labrids (*Thalassoma bifasciatum* and *Halichoeres bivittatus*) that appeared to be related to their survival potential through the early postsettlement days on the reef.

In summary, where winds are positively correlated with settlement, their effect may be important only in the final delivery of the young, not necessarily with respect to early retention or transport processes. For the

later stages, wind might enhance settlement but not be a prerequisite for successful settlement (e.g., cross-shelf transport may occur when larvae are rapidly advected across the shelf with favorable winds, but such transport may also occur in the absence of these winds). The same may be true for wind and for wave-generated flow across reefs (Roberts *et al.,* 1992; Symonds *et al.,* 1995; Yamano *et al.,* 1998) that deliver larvae into atoll lagoons (Dufour, 1991; Dufour and Galzin, 1993). Over longer time scales, seasonal winds may directly influence the settlement success, either by reducing spawning success during periods of high winds and turbulent conditions on the reef or by enhancing the likelihood of coastal retention during periods of minimal wind (Johannes, 1978; Lobel, 1989; Colin, 1992).

B. Tides

From shore, the changing tide is observed to bring water either toward or away from the observer. Yet the flow generated by tidal movement turns out to be much more complex (Barnwell, 1976). In its simplest form, a tidal current along a constant shelf bottom may result in elliptical movement, moving on scales of kilometers with each tidal cycle. If the water column is strongly stratified (such as near a river/estuarine outlet), flow along the bottom may move quite independently of the lighter, fresher surface water. However, coastal and island reef environments are not topographically simple, and therefore they impose a complex frictional (or topographic) effect on flow (Hogg *et al.,* 1978; Hogg, 1980). This effect is scale dependent, and results from water being forced from one area to the next, while being squeezed past obstacles (e.g., reefs, headlands). Along the bottom, the flow is reduced due to friction, which ultimately steers the water (typically along contours); closer to the surface, the water may accelerate because the same amount of water is passing through a reduced cross-sectional area (e.g., water flows out of a hose more rapidly when you place your finger over part of the opening). Once on the other side of the obstacle, the flow quickly slows (depending on the topography), resulting in adjacent areas of decelerated and accelerated flows. Water inshore of regions of flow deceleration will be pulled along by frictional forces. These frictional forces will also rapidly decrease the flow closer to shore, potentially setting up a zone of convergence between the fast- and slow-flowing water and even an eddy in the lee of the obstacle. What becomes particularly complex about tidal flows, however, is that the flow then reverses. Yet rather than just simply reversing this effect, the picture is further complicated by both the momentum of the water and (at nonequator

latitudes) Coriolis forcing. Numerical models demonstrate the overall effect of topography on tidal flow with these two added factors (e.g., Pingree and Maddock, 1980).

Tidal circulation around islands and headlands has been shown to generate occasionally strong, eddying motions that may serve to slow the offshore advection of larvae (e.g., Hamner and Hauri, 1981; Black and Gay, 1987; Wolanski *et al.,* 1984a, 1989; Black, 1994; Furukawa and Wolanski, 1998). Scaling effects, however, tend to limit tidally generated eddies [or phase eddies; sensu Black and Gay (1987)] to smaller islands and reefs in shallow water (versus larger, oceanic islands in deep water). Over time, these phase eddies grow and decay with changing tidal phases and, coupled with Coriolis effects, result in a nonuniform residual (net) flow around the island [anticlockwise in the GBR; reviewed by Black (1994)]. This asymmetry in flow results in potentially higher retention in certain regions around a reef, as opposed to others. Efforts to verify the retention of larvae in these eddies have been based on both field and model estimates, but largely for invertebrate larvae of relatively short duration, [e.g., coral and crown of thorn starfish (reviewed in Sammarco, 1994; Gay and Andrews, 1994; Black, 1994)].

Additional work suggests that retention of reef fish larvae around a reef (or small island) does indeed occur. Jones *et al.* (1999) marked the otoliths of prehatching pomacentrids at Lizard Island, GBR, then, after a lag phase for larval duration, collected presettlement larvae with light traps around the same reef. They successfully "recaptured" tagged larvae and estimated that between 15 and 60% of the hatched fish were retained, a rather remarkable finding! Missing from this study, however, is a mechanistic explanation of what retention mechanisms were responsible. Physical retention mechanisms associated with tidal and current flow past and around a reef may well have played a strong role by slowing or countering the outward advective and diffusive flow of the shelf currents. Also, late-stage larval behavior (Stobutzki and Bellwood, 1994; Leis *et al.,* 1996; Leis and Carson-Ewart, 1999) and sensory capabilities interacting with tidally generated frontal features (Kingsford *et al.,* 1991) may have served to augment any physical retention mechanisms.

Overflow of the reef crest also can occur with flooding tides (e.g., Parnell, 1988). Such overflow may serve as an important delivery mechanism of settlement-stage fish, especially in reef systems with few other avenues of entry to backreef/lagoon habitats [Dufour and Galzin, 1993; Dufour *et al.,* 1996; but see Sancho *et al.* (1997) for an example of larval acanthurids swimming upcurrent through a reef channel]. The relative importance

of this sort of tidal flow, as compared to wind- and wave-generated overtopping flow (sensu Roberts *et al.,* 1992; Kamano *et al.,* 1998), will clearly depend on local tidal ranges and reef orientation.

Tidal flows also may have strong impacts on reefal systems located near shelf edges via tidally mediated upwelling, which can occur in two different ways. First, tidal flows near the shelf edge can generate large internal waves that propagate toward shore. When formed where the thermocline is relatively shallow, larger amplitude internal waves (e.g., 5- to 10-m excursions) can move cooler, nutrient-rich subthermocline waters into shallow depths (Wolanski and Delesalle, 1995). When these internal waves break, nutrient-rich water may be mixed upward and carried onto the reef environment, as has been shown in the Florida Keys by Leichter *et al.* (1996, 1998). Second, tidal movement through narrow passages between reefs near the shelf edge of the GBR has also been implicated as a mechanism creating the upwelling of nutrient-rich deeper waters (and associated organisms). Such sources of increased nutrients, and associated zooplankton (see below), may serve as an important food source for planktivorous coral reef fishes, perhaps even influencing their reproductive success (Robertson *et al.,* 1990; Schultz and Warner, 1991; Tyler and Stanton, 1995).

In temperate systems, internal waves and tidal bores can transport larvae across shelf environments (Shanks, 1983, 1986; Kingsford and Choat, 1986; Pineda, 1991, 1994, 1999), but their importance as a cross-shelf transport mechanism has not been examined for coral reef fish larvae [but see Leichter *et al.* (1998) with respect to tropical zooplankters]. While early interpretations of internal wave-mediated surface transport invoked onshore movement of neustonic larvae in surface convergences, or "slicks" (Shanks, 1983, 1986; Kingsford and Choat, 1986), Pineda (1991, 1994, 1999) and Leichter *et al.* (1996, 1998) have proposed a more dynamic explanation with respect to how internal tidal bores function.

Of special relevance to some of the temporal settlement patterns observed for coral reef fishes, internal tides (and their associated tidal bores) may be lunar cyclic, but not necessarily in direct association with the spring-neap tidal cycle. Specifically, Pineda (1991, 1995) found that when the water column is stratified, peak internal tide activity occurred approximately 7–12 and 19–24 days after the new moon (i.e., on the quarter moons). Such timing corresponds to the third-quarter peak of settlement observed for a variety of coral reef fish species (Sponaugle and Cowen, 1994, 1996a, 1997) and decapod crab larvae (Reyns and Sponaugle, 1999) around Barbados.

Reyns and Sponaugle (1999) suggest that this temporal relationship at Barbados, but not, for example at Panama (e.g., Victor, 1986a; Robertson *et al.,* 1999), may be due to the relative importance of internal tides in the two locations.

In addition to direct transport and nutrient-related effects, tidal flows may also serve as important environmental cues for reproduction and timing of settlement. As discussed above, a variety of coral reef fishes exhibit lunar cyclic recruitment patterns, but there is evidence of geographic variation in terms of in which specific lunar phase the recruitment is occurring. Timing to lunar phase is therefore not likely a simple function of light/dark as has often been suggested (see Reyns and Sponaugle, 1999). Rather, flows associated with the tidal amplitude cycle may also be important, leading to complex interactions between recruitment patterns and lunar/tidal cycles (Morgan, 1995; Sponaugle and Cowen, 1997; Robertson *et al.,* 1999; Reyns and Sponaugle, 1999) (see Fig. 5). These patterns lead to an important final point: given the potential for geographic variation in the temporal pattern of reproduction, and especially settlement, sampling should encompass the *entire* lunar/tidal cycle rather than focus on specific phases, at least until the temporal patterns are definitively determined.

C. Freshwater Input

In the immediate vicinity of a river, both the low salinity and typically high turbidity of the outflowing water will have severe negative impacts on the survival of coral reef fish (and on the coral reefs). Yet, freshwater input is pervasive throughout the wet tropics, at least in a seasonal context, both from direct rainfall and as river runoff. Direct rainfall may lower surface salinity, but generally not by much because the rainfall is spread over a wide surface and mixed with the seawater (e.g., 100 mm of rain can mix with several meters of seawater without changing the salinity more than a few practical salinity units) (Andrews and Pickard, 1990). However, over a season, the input of freshwater may create a strong seasonal signal in lowered surface salinity.

The extent of impact of freshwater river input, outside of the extreme case mentioned above, is related to the outflow, local currents, and topography. Some rivers of small, local watersheds will input sufficiently small amounts of freshwater such that mixing with seawater will eliminate the signal even very close to the source. Other rivers, such as the Orinoco River of Venezuela, can be observed to spread their effect over very large areas ($>10^6$ km^2) (see Müller-Karger *et al.,* 1989). At varying distances downstream from such
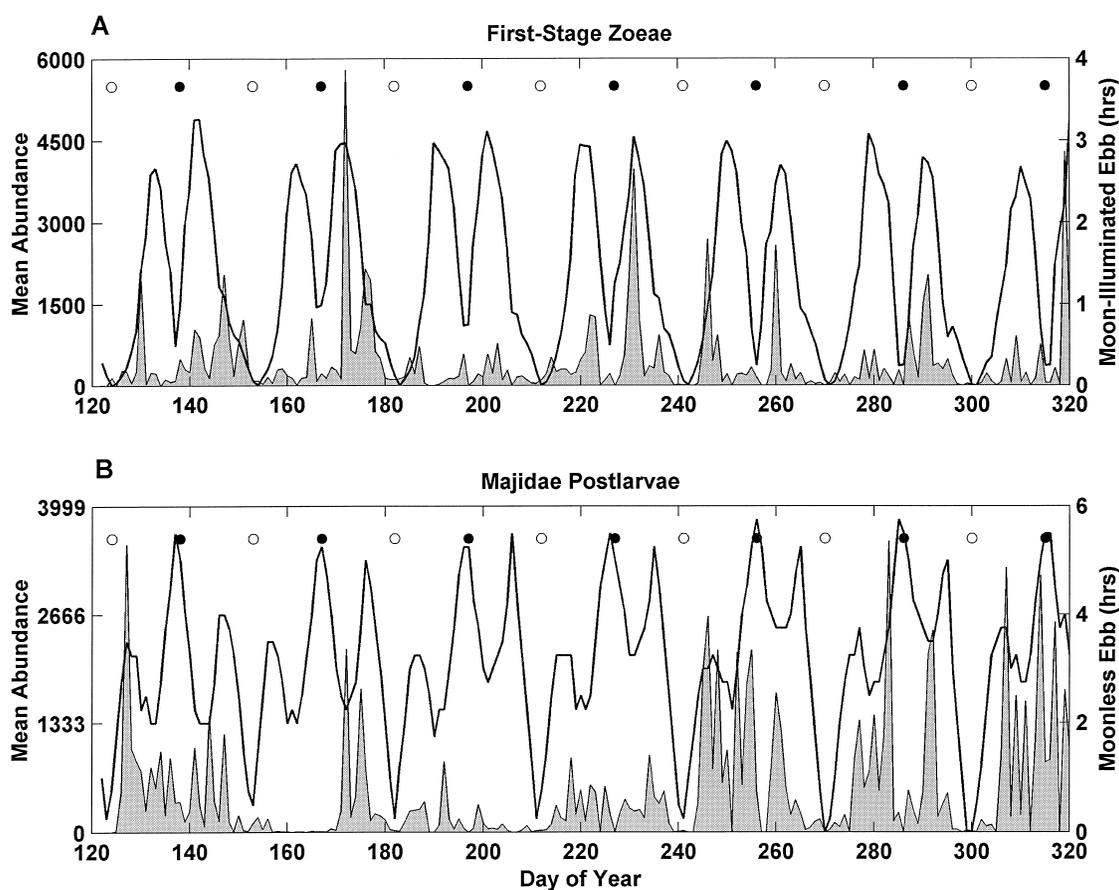
FIGURE 5 Time series (200 days) of the relationship between larval crab abundance (shaded) and proximate environmental cues (solid line) along the west coast of Barbados during 1996. Shown relationships are significant cross-correlations at $p < 0.05$. (A) Crab zoeae abundance vs. moon-illuminated ebb tides (i.e., the number of hours ebbing tides occur in relative darkness due to nightly change in moon phase). (B) Majid crab postlarve vs. moonless ebb (i.e., total darkness). Modified from Reyns and Sponaugle (1999).

freshwater sources, the river can be a positive nutrient source, possibly a long-distance transport process, or an episodic detriment to recruitment or coral reef fish survival. A recent example of the latter was the transport of a freshwater-borne pathogen to the southern Lesser Antilles Islands, apparently via an unusual turn of the Orinoco River toward the east (H. Oxenford, University of the West Indies, personal communication). This pathogen (*Streptococcus iniae*) has been implicated in extensive fish kills of coral reef fish around the islands of Tobago, Grenadines, Grenada, Dominica, and Barbados.

An important role of freshwater input into the coastal ocean is its effect on the baroclinic (thermohaline) circulation. Because freshwater is less dense than seawater, it floats on the surface, adding to the stratification of coastal waters. This can result in a plume of relatively fresh water flowing away from the source, in some cases hundreds of kilometers (or more) distant (Müller-Karger *et al.*, 1989; Gilbert *et al.*, 1996). Depending on the spread of such plumes, their impact on larval fish distributions (and corals) can range from minimal to great (Murray *et al.*, 1982; Roberts and Murray, 1983; Andrews and Gentien, 1982; Andrews, 1983; Wolanski and Van Senden, 1983; Wolanski *et al.*, 1984b; Sabatés and Maso, 1992).

Associated with such plumes are fronts, where the salinity changes rapidly and flow tends to converge. Fronts may serve to concentrate organisms either through convergent mechanisms or by the attraction of organisms to areas of high prey concentrations (e.g., Aldredge and Hamner, 1980; Denman and Powell, 1984; Mackas *et al.,* 1985; LeFerve, 1986; Wolanski and Hamner, 1988; Govoni *et al.,* 1989; Kingsford, 1990; Kingsford *et al.,* 1991; Govoni and Grimes, 1992; Olson *et al.,* 1994; see also review of Grimes

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and Kingsford, 1996). These processes have important implications for understanding the roles riverine and estuarine plumes, and their associated fronts, may have in determining the distribution and abundance of larval fishes. Despite the potential importance of riverine plumes, however, few studies exist that document the effect of riverine plumes on coral reef fish larvae [but see Govoni (1993), Grimes and Kingsford (1996), and Allman and Grimes (1998) for examples of plume effects on other fish species]. One exception is the study by McKinnon and Thorrold (1993) and Thorrold and McKinnon (1995) on a plume (resulting from heavy rainfall from Cyclone Joy) associated with river outflow into the GBR lagoon north of Townsville, Australia. They found very high zooplankton biomass associated with the freshwater plume that spread up to 20 km offshore (roughly into the middle section of the GBR lagoon). Coastal (offshore of the plume) species of larval fishes (e.g., some holocentrids and pomacentrids) were apparently aggregated at the front as the plume propagated offshore, though their numbers did not increase within the plume, per se. Whether these offshore taxa actually benefited from the increased food environment associated with the increase of zooplankton biomass and production is not clear, but is suspected. Though not explicitly examined, the vertical distribution of larvae is important, because these plumes do not generally penetrate to particularly great depths (e.g., less than 5 m). Except for the neustonic-oriented mullids (which were concentrated in the plume front), other typically deeper larvae may benefit from the vertical mixing of zooplankton-rich plume water as it passes over coastal waters.

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D. Ocean Currents

There have been many efforts to use long-term mean currents as indicators of larval transport potential and/or pathways of population connectivity. However, within ecologically meaningful time scales, there is really no such thing as a "mean" current field. Neither are there purely random motions of water. Rather, oceanic flows tend to be coherent and exhibit a variety of mesoscale features (Robinson, 1983). Organized flow results in a multitude of mesoscale features, including eddies and fronts that can act independently or may interact with topographic features or other currents potentially to enhance the retention or dispersion of larvae (e.g., Owen, 1980; Hamner and Hauri, 1981; Olson and Backus, 1985; Wolanski and Hamner, 1988; Okubo, 1994; Olson *et al.,* 1994). Kingsford (1990) has summarized manifestations of these interactions (as well as smaller scale features).

Our perception of the true nature of oceanic flow has changed over the past few decades (Fig. 6. See color insert). For example, the prevailing view of circulation within and through the Caribbean has been characterized by Wust (1964) based on mean estimates of ships' drift data (Fig. 6A). Such views continue to be expressed in terms of estimating larval drift pathways (e.g., Roberts, 1997b). However, over shorter time frames, flow is much more dynamic than that indicated by climatological (i.e., mean) data. From a Lagrangian perspective, based on drifter tracks released and followed over an 18-month period, it is clear that there is considerable flow variability within the Caribbean, often occurring either orthogonal or opposite to the mean flow (Fig. 6B). Particular pathways of individual drifters released from a similar location can end up thousands of kilometers apart after just a few months, whereas others may remain remarkably coherent where strong recirculations occur (e.g., in the Panama/Colombia gyre). Even at a single point of time, high spatial variability in flow is apparent (Fig. 6C). The circulation within the core region of the Caribbean is characterized by the presence of a variety of mesoscale features, including eddies and meanders ranging in size from 50 to 500 km. Further, closer to shore, it is apparent that the oceanic circulation features are interacting with coastal flow to create a variety of regions of nearshore recirculation.

How the coastal flow field is affected by the larger scale oceanic circulation is clearly illustrated in the work of Lee and others within the vicinity of south Florida and the Florida Keys. Their work over the past two decades demonstrates how interactions of physical flows over several scales result in a series of potential larval retention mechanisms (Fig. 7) (summarized in Lee and Williams, 1999). Briefly, warm, highly saline flow exits the Caribbean Sea through the Yucatan Straits into the Gulf of Mexico and transits northward. The flow then anticyclonically reverses direction to form the Loop Current, flowing south and exiting the Gulf through the Straits of Florida (SSF) to become the primary source of the Gulf Stream (Maul, 1977). Periodically (every 7–19 months), the entire Loop Current pinches off and is translocated westward into the Gulf of Mexico (Maul, 1977; Sturges, 1992; Maul and Vukovich, 1993). When this happens, water exiting the Yucatan Straits flows directly into the SSF. In either situation, the Florida Current (FC) follows the steep topography associated with the shelf break/slope occurring between 7 and 10 km offshore of the Florida Keys at a speed of 150–250 cm sec^{-1}.

When the Loop Current is present, its outer edge spawns smaller scale meanders and cyclonic eddies that
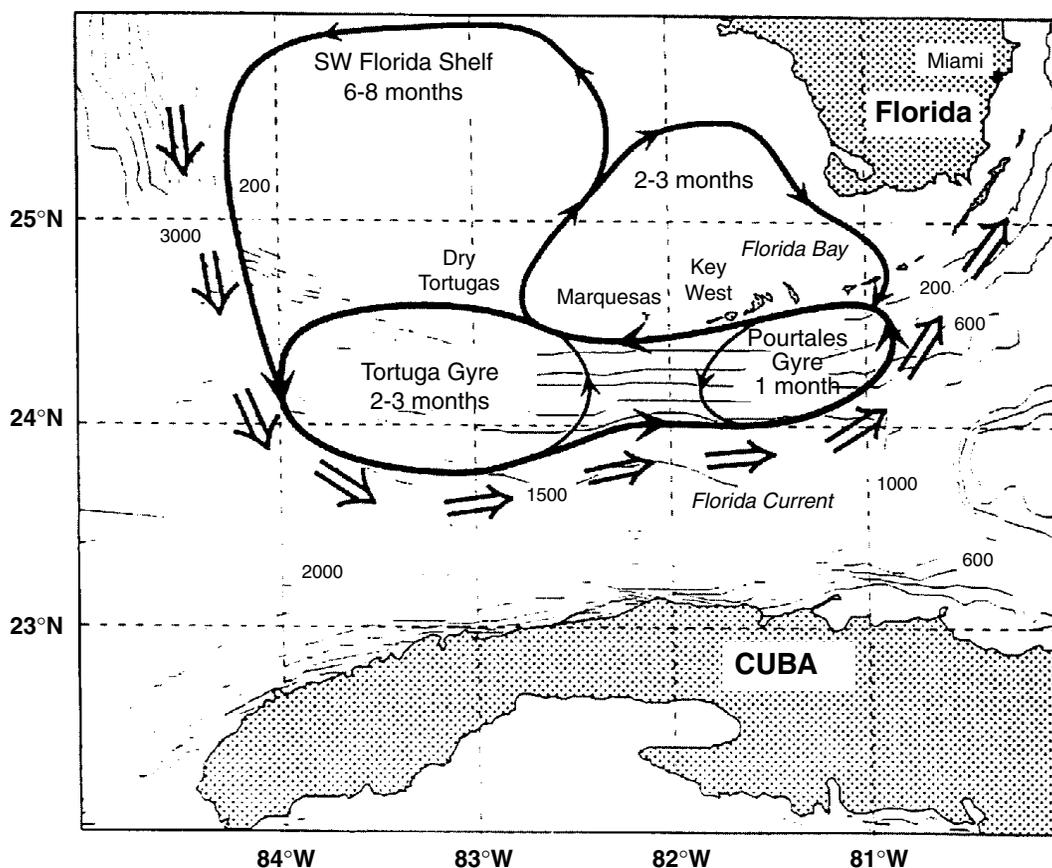
FIGURE 7 Hypothesized larval transport pathways of varying duration based on observations of circulation and hydrographic structure in waters south and west of the Florida Keys. After Lee and Williams (1999).

are carried anticyclonically around the Loop Current (Fratantoni *et al.,* 1998). Once one of these smaller eddies makes the full transit around the Loop, it may get trapped between the northern edge of the FC and southwest of the Dry Tortugas (westernmost key of the Florida Keys). These quasistationary cyclonic "Tortugas gyres" are of the scale of 50–100 km in size, and may reside for between 50 and 140 days, maintaining their position until being pushed out by the arrival of the next gyre transiting around the Loop Current. Once displaced into the Straits of Florida, the Tortugas eddies are deformed (and shrink) by the topography and the curvature of the Middle Keys as they propagate downstream between the shelf/slope topography and the FC at a rate ranging from 5 to 16 km/day. Circulation velocities of the gyres range from 20 to 50 cm sec^{-1} (Lee *et al.,* 1994) prior to being absorbed beyond the Pourtales terrace, where the shelf narrows and the FC moves close to shore.

The passage of a Tortugas gyre into the Straits of Florida contributes to cross-shelf flow (between the Florida Current and the shallow shelf) and is a potential source of enhanced nutrients in the Florida Keys system (Lee *et al.,* 1994). Further, the inshore flow associated with these eddies provides a countercurrent circulation to the strong FC. Their infrequent (up to two to three per year) (Fratantoni *et al.,* 1998) but relatively slow (∼months) passage (Lee and Williams, 1999) interjects considerable variability in coastal flow, which is counter to the flow conditions of the FC and may serve as a retention mechanism for coastal-derived larvae that would otherwise be carried away by the strong, unidirectional FC (Lee *et al.,* 1992, 1994; Lee and Williams, 1999).

At a smaller scale, submesoscale eddies (SMEs) are periodically trapped and advected along the inshore edge of the FC due to strong horizontal shears caused by the strong flowing FC encountering the steep topography of the Florida Shelf (Lee and Mayer, 1977; Lee *et al.,* 1991). These small, generally cyclonic eddies (∼5–10 km in diameter) are rapidly translated along the shelf break, bringing cool, upwelled water

onto the shelf (Lee *et al.,* 1991) and potentially aggregating larval fish and their prey (Limouzy-Paris *et al.,* 1997). The circulation associated with these SMEs and the larger Tortugas gyre has been implicated with the onshore transport (Limouzy-Paris *et al.,* 1997) and retention of locally spawned organisms (Yeung, 1996; Lee *et al.,* 1992, 1994; Criales and Lee, 1995; Porch, 1998), though direct linkages between these features and recruitment patterns are lacking.

Thus, the various mesoscale circulations associated with larger scale flows, and direct interactions of larger scale flows with coastal topography, can interject a strong influence on the coastal circulation. Such interactions create not only strong variability in the coastal flow, but also multiple mechanisms for retention (and nutrition) of coastal larvae that would not be apparent through consideration of mean (large-scale) currents alone. The variously scaled mechanisms exemplified in the Florida Keys system provide a variety of mechanisms that may promote localized retention of coral reef fish larvae (as well as larvae of other coral reef organisms such as lobsters, shrimp, and conch) (Munro *et al.,* 1968; Yeung, 1996; Criales and Lee, 1995; Stoner *et al.,* 1997; Limouzy-Paris *et al.,* 1997). Similar interactions of oceanic and coastal currents are indicated in other regions of the Caribbean [e.g., Barbados (Cowen and Castro, 1994) and Cuba (Lindeman *et al.,* 2001)], as well as other coastal regions [e.g., United States east coast (Hare and Cowen, 1991, 1996) and the western Australia coast (Hutchins and Pearce, 1994)], though none perhaps so well described in terms of the physics. Despite this detailed knowledge of the currents and supportive larval distribution data (e.g., Limouzy-Paris *et al.,* 1997; Criales and Lee, 1995), hypothesis-driven studies that link larval distribution and behavior to such retention mechanisms are still lacking.

E. Insular versus Continental Environments

Along the leeward side of many oceanic islands, a strong, nutrient-enriched patch of water may exist, termed the "island-mass effect" (Doty and Oguri, 1956; Gilmartin and Relevante, 1974). This effect has been attributed to local rainwater as either runoff or groundwater; local benthic production enhancing overlying, nearshore waters; wind-induced upwelling bringing up deeper, nutrient-rich water; and/or vertical oscillations from internal waves (Hamner and Haury, 1981; Sander, 1981). Theoretical studies, laboratory experiments, and field studies of flow around islands and seamounts have also indicated the effect of flow disturbances producing eddying motions capable of

upwelling nutrients above the thermocline (e.g., Hogg, 1972; Emery, 1972; Hogg *et al.,* 1978; Pingree and Maddock, 1980; Gorden and Hughes, 1981; Simpson *et al.,* 1982; Genin and Boehlert, 1985; Roden, 1987). Heywood *et al.* (1990, 1991) found field evidence of enhanced nutrient levels in the lee of a small island, Aldrabra, in the Indian Ocean. During periods of moderately high flow past the island, isopycnals were elevated in the lee of the island, suggesting the existence of a trapped eddy. However, during periods of slower ambient flows, no such conditions existed. Other studies (in addition to several of those cited above) have identified increased zooplankton biomass around islands (LeBorgne *et al.,* 1985; Hernandez-Leon, 1988, 1991; Rissik *et al.,*1997). Such effects on the primary and secondary production around islands may be important in providing adequate food sources for the larvae of island populations of coral reef fishes (Suthers, 1996), particularly in the highly oligotrophic oceanic waters surrounding many of these islands. Further, the doming effect of the nutricline, and related production, bring these potential prey sources into depths [e.g., 50–70 m (Rissik *et al.,* 1997)] that correspond to depths at which larvae are typically found (see Section III,B).

In addition to increased nutrients, these island effects can act to magnify the vertical stratification of the water column. For example, where winds generate upwelling, surface flows are typically directed in the opposite (offshore vs. onshore) direction from the deeper layers. Such stratified flows may be only a few tens of meters apart. Clearly, a larva could benefit by moving into deeper water to enhance local retention (e.g., Cowen and Castro, 1994). Even without enhancement of nutrients via upwelling, winds passing around and over an island can create a wind shadow close to the leeward shore (the offshore extent of this shadow is in part dependent on the size and altitude of the island). Such shadows in the lee of an island may serve to enhance local retention of larvae because of limited wind-generated flow (Barton *et al.,* 1998).

Wind-generated upwelling also occurs in noninsular areas. For example, where coastlines are irregular and/or headlands and hills occur, the windfield can be significantly interrupted, resulting in considerable variability in alongshore wind conditions. Variation in the coastal bathymetry will also have strong impact on how the wind field influences the flow of water. Additionally, orientation of coastlines relative to prevailing wind directions can create opportunities for seasonal upwelling (e.g., along the Caribbean coastline of Colombia and Venezuela). Where such upwelling occurs, surface flow is offshore within the field of the wind, yet "upwelling shadows" may form (sensu Graham *et al.,* 1992) in the coastal recess equatorward of the headland. The water

within the shadow remains nearshore and may form a sharp front, where it grades into the upwelled water. Depending on the persistence of the upwelling, the surface-oriented species associated with the upwelled water may be prevented from reaching the coast except during periods of relaxation (e.g., Wing *et al.,* 1995a,b). Conversely, larvae within upwelling shadows may experience reduced offshore advection and thus increased retention.

Island wake eddies, eddying motions in the lee of an island, have been implicated as important retention mechanisms for larvae (e.g., Boden, 1952; Sette, 1955; Sale, 1970; Emery, 1972; Hamner and Hauri, 1977, 1981; Pingree and Maddock, 1980; Lobel and Robinson, 1986; Black and Gay, 1987; Wolanski and Hamner, 1988). Generally forced by topographic influence on flow past the island, eddies have been identified in both deep-water (steep topography) and shallow-water (shelf) environments (e.g., Simpson *et al.,* 1982; Wolanski *et al.,* 1984b; Pattiaratchi *et al.,* 1986; Heywood *et al.,* 1990, 1991; Wolanski, 1994). Formation of such eddies is dependent on the Reynolds number, a combination of flow speed, island diameter, island shape, depth of surrounding seas, and water column stratification, which may lead to temporal and spatial variability in the presence and duration of island wake eddies (Batchelor, 1967).

Perhaps as a result of such variability, at least for oceanic islands, the evidence supporting the eddy-retention hypothesis is equivocal. For example, although a trapped, von Karman-type eddy was hypothesized for the island of Barbados (Emery, 1972; Powles, 1975), no such eddies were found in the lee of the island (Cowen and Castro, 1994; Bowman *et al.,* 1994; Stansfield *et al.,* 1995). Instead, the flow passing the island was clearly steered by topography, resulting in flow running predominantly parallel to shore, with nearshore, vertically stratified, onshore (at depth), and offshore (at surface) components (Cowen and Castro, 1994). Elsewhere, as reviewed by Leis (1991a), the importance of semipermanent eddies in the lee of several of the Hawaiian Islands (e.g., Oahu and Hawaii) (sensu Patzert, 1970) as retention mechanisms for coral reef fish is equivocal. Despite findings of a drifter being ejected from the eddy and back to the island (Lobel and Robinson, 1986), the waters around and within the proposed retention eddy contained very few coral reef fish larvae (see Lobel and Robinson, 1988). Finally, Farmer and Berg (1990) review a variety of mechanisms, including eddies, that have been hypothesized as facilitating retention of Bermuda's fish and invertebrate larvae. Although no direct evidence of trapped eddies exists for Bermuda, inferential evidence supports

the contention that local retention of coral reef fish larvae is the norm (Schultz and Cowen, 1994). Instead of topographically generated eddies, a variety of circulation features may contribute to larval retention around Bermuda. Thus, island-wake eddies may add, perhaps at the "event" level, some retention potential to locally derived larvae, but they are typically quite transient and likely do not serve as a major or permanent "retention" mechanism.

We may wonder whether the various physical processes affecting larval reef fishes differ in importance across different physical environments, in particular, insular versus continental coastlines. These are clearly different environments, yet, for example, most Caribbean coral reef fishes successfully exist (i.e., they recruit and survive to reproduce) in both classes of environments. Do the larvae of a given species rely on very different physical processes and/or respond in very different ways depending on their environment? To do so would require considerable local adaptation (with a bewildering array of both sensory capabilities and behavioral responses) to ensure successful onshore transport of larvae in many different environments. A more parsimonious alternative is that larvae are utilizing physical features common to a broad diversity of coastal environments. Despite the various forcing mechanisms operating in these different environments, the resultant flows (particularly the vertically stratified flows) may be quite similar. This would enable relatively simple sets of (or even a single) behavioral responses to result in successful cross-shelf movement of the larvae.

One example of how a species might utilize a simple vertical behavior to move onshore (i.e., across the shelf) in a variety of physical environments is that of the labrid, *Xyrichtys novacula.* The adult range of this species spans from Cape Hatteras, North Carolina, throughout the Caribbean to northern Brazil. Larval *X. novacula* are commonly found in a variety of different physical environments: around islands (e.g., Barbados) and in continental shelf environments such as the New York Bight (NYB) and South Atlantic Bight (SAB) (Hare and Cowen, 1991; Cowen *et al.,* 1993). Around Barbados there is an upwelling-generated subsurface onshore flow occurring at a depth of between 20 and 40 m. The NYB is often a three-layered system in the summer when larvae are present. During wind conditions that force the surface waters offshore and to the north, the offshore, warm salty Slope Sea water can flow onshore along the thermocline at middepth (20–40 m) over the very cold and dense remnant winter water, and under the relatively fresh surface layer. The SAB is essentially a two-layered system in which the water below the thermocline flows gently onshore. In

all three cases, an ontogenetic vertical migration from near-surface waters to middepths (e.g., 20–40 m) results in the onshore movement of larvae.

Some circulation features are ubiquitous across a broad spectrum of otherwise different physical environments. One such important and common feature are the relatively short vertical distances separating water masses flowing in different directions. As a result, a larva that is adapted to swim vertically (or alter its density) to utilize a specific flow feature at a particular stage of its development may be able to keep itself within a particular prey environment or be transported nearshore, whether it is located along a coastal headland of continental South America or near an isolated island such as Barbados. Variability in a specific physical feature may drive year-to-year variability in recruitment for a given species at various locations, but it is the general prevalence of that feature that results in species-adaptive behavior. Viewed from a different perspective, a species may persist best in those locations where there are similar physical features that either successfully retain larvae or aid in their transport to coastal habitats.

Studying the commonalties among transport processes, including the physical features involved, how external forcing influences these features, and, finally, how organisms (larvae and adult) behave in response to these features, may facilitate our understanding of how these processes can contribute to fluctuations in larval supply. The variable nature of recruitment to some populations may be a result of more frequent interruptions of specific flow regimes. This will be particularly apparent in areas that are near the upstream portion of the larval supply, where sporadic recruitment occurs only during significant alterations in typical flow patterns (Cowen, 1985) and populations persist on the basis of storage of strong year classes (Warner and Chesson, 1985). An improvement in our understanding of how larvae are transported can help us better predict when the conditions are favorable (or not) for recruitment, as well as improve our understanding of biogeographic relationships and stock maintenance (Sinclair, 1988). Although we risk overemphasizing physics in lieu of studying larval behaviors, it is important to search for general patterns in the interaction of larvae with their physical environment.

V. Biophysical Interactions

The preceding review of transport mechanisms demonstrates that our understanding of the physical regime and how it may influence the movement of larvae is considerable. The various mechanisms and processes discussed so far may all contribute to the successful survival, retention, and transport of larvae to appropriate settlement habitats. Many of the physical mechanisms can affect multiple biological factors such as reproductive timing, location and output, larval feeding and transport, and onshore movement leading to settlement. Currently, recruitment studies have been able to identify both temporal and spatial patterns in recruitment, and to a lesser extent, recruitment events have been correlated with specific physical features (e.g., wind, upwelling flow, eddies). Further, larval distributions have been identified that are best explained by the interaction of larval behaviors and physical mechanisms. Such interactions suggest that temporal and spatial patterns of larval distribution may be predictable.

Where we still have a large gap in our knowledge, however, is in explaining the magnitude of recruitment events with any predictability. Perhaps one reason we are still limited in our ability to predict recruitment strength is that particularly large (successful) events occur as a result of the cooccurrence in time and/or location of the full suite of (or some significant subset of) mechanisms favorable to recruitment. For example, onshore winds may enhance recruitment only when other factors (e.g., good food environment for larval survival, low predator field, favorable spawning conditions) all are conducive to forming a relatively large larval pool. In the absence of the winds, some low-level recruitment may occur, or vice versa; but in the absence of favorable spawning conditions, even with strongly favorable onshore winds, no measurable recruitment event will occur. The end result is only a partial explanation associated with the single variable, wind. The requirement of cooccurrence of multiple factors to elicit a strong recruitment event is akin to the "rogue wave" theory of Neill *et al.* (1994), whereby the factors affecting recruitment may vary with differing periods, but occasionally the cycles (and aperiodic factors) come together in favorable harmony to produce particularly large cohorts. Thus, our predictive abilities will be limited if we examine a reduced set of causative variables. This is clearly a multivariate problem spanning a broad range of physical and biological variables and scales.

VI. Modeling

A well-designed field study focusing on larval transport may define how biology and physics interact to explain a given distribution of larvae, but such a study is static. It is not realistic to conduct a field study under all possible field conditions at even a single site, let alone all possible sites and scales. For this, modeling

is required. The system we are attempting to understand (the pelagic world of larval fishes) is very complex, but not necessarily chaotic. This complexity, at least the dominant components of it, potentially can and needs to be modeled. Simple models can serve as conceptual frameworks or can demonstrate the sensitivity of a given process to particular conditions. However, more sophisticated models should be able to help us predict where, when, and how many larvae are going to recruit to a given shoreline or coral reef. It is important to stress, though, that modeling efforts require empirical field studies to provide parameterization and identify the important biophysical processes. Empirical studies should also serve as important field tests of model predictions.

Physical models are becoming more and more sophisticated. For example, general ocean circulation models that operate at the basin scale or larger (global) are remarkably high resolution (12–20 km); examples include the S-coordinate Primitive Equation Model (SPEM), the Princeton Ocean Model (POM), and the Miami Isopycnic Coordinate Ocean Model (MICOM) (Song and Haidvogel, 1994; Bleck and Chassignet, 1994). When applied to smaller spatial scale coverage, the resolution may become finer (e.g., 6 km), enabling the resolution of submesoscale features. For small-scale, shallow-water circulation studies, hydrodynamic models are available for resolution on the scales of tens to hundreds of meters (e.g., Black *et al.,* 1991; Wang, 1990). Just as for the descriptive oceanographer working at the interface between open ocean and coastal environments, the challenge for physical modelers is linking basin-scale ocean circulation models with coastal circulation models where complex topographic effects occur.

Biological models of various levels of sophistication exist that can be linked to physical models for a more complete biophysical understanding of larval dynamics. Such models can focus on larval behaviors (e.g., vertical distribution, directional swimming, or simply random walks) (Dutkiewicz *et al.,* 1993; Werner *et al.,* 1993; Wolanski *et al.,* 1997) or vital rates (e.g., growth and mortality rates) (Werner *et al.,* 1996; Hofmann and Lascara, 1998). These models can be relatively simple linear models (e.g., fixed, size-specific rates) or more complex (and realistic) models that incorporate a range of biological responses to environmental conditions [e.g., individual-based models (see also Eckman, 1996)]. For example, models that link larval growth and mortality rates to plankton productivity, which is responsive to the physical environment, can provide important means of coupling biological and physical processes toward an understanding of larval survival.

Linking such processes to a larval transport model would provide information on both the distribution and the abundance of a cohort of larvae.

However, these models are not perfect and there are, at times, considerable differences among models (e.g., see Wolanski, 1993; Black, 1995) that stem from either the model assumptions and/or how they are parameterized. Nonetheless, circulation models allow us to examine how larvae may be transported under a suite of physical conditions. Further, when coupled with biological models that are responsive to the physical conditions set forth by the physical model, these models allow us to examine the range of potential outcomes. We also can use models to make field-testable predictions (e.g., how rapidly larvae are dispersed away from a coastline or along a frontal feature, or how well larvae grow and survive under certain physical conditions), as well as to examine probabilities of the occurrence of certain events (e.g., the "rogue wave" situation—high food level, low predator level, and high larval retention level all at once). The overriding caution, however, is that all models must be field parameterized and field tested. All too often, models are utilized, even with caveats that certain "oversimplifications" were made for computational simplicity, without appropriate validation. The results of such exercises often are published and then all too readily accepted. The potential error in this approach can be exemplified in the model results whereby, for example, a slight change in (or inclusion of) larval mortality rates or diffusivity constants can have order-of-magnitude effects on the model outcome.

VII. Implications for Population Connectivity

Work in a variety of systems has indicated that larval export may not be as widespread as previously thought (e.g., Schultz and Cowen, 1994; Polovina *et al.,* 1999; Jones *et al.,* 1999; Swearer *et al.,* 1999; Cowen *et al.,* 2000). This issue is particularly relevant on the ecological time scales over which most recruitment studies are conducted. Further, when considering the management of fished or otherwise impacted stocks, knowledge of the source of new recruits is of paramount importance. Yet, until recently, the general paradigm was that coral reef fish populations (like most marine populations) are broadly open due to the potential for long-distance dispersal by larvae (Thorson, 1950; Scheltema, 1986). Such perceptions have been reinforced by simple models of larval dispersal by mean currents and mean pelagic larval durations (e.g., McManus and Menez,

1997; Roberts, 1997b). Further, many genetic studies have found limited genetic heterogeneity among local populations (Shaklee, 1984; Lacson, 1992; Planes, 1993; Shulman and Bermingham, 1995; Doherty *et al.,* 1995) except in highly isolated oceanic islands (Johnson *et al.,* 1994; Planes *et al.,* 1998a,b).

One cause of this dichotomy is the mixture of relevant scales. Population genetic studies measure gene flow, which requires only very limited exchange to reduce greatly the genetic differential between local populations, whereas the levels of exchange required to sustain *ecologically* a "downstream" local population from some given source population is many times greater. The other main cause is that the oversimplified models (mean flow and primary layer depth) significantly overemphasize the true level of exchange [by about nine orders of magnitude (Cowen *et al.,* 2000)]. On an even more basic level, it does not make biological sense to send all of one's larvae downstream, because there is no means of evolutionary feedback of selective pressures to the source population required to generate specific life history traits (Strathmann, 1982).

This review describes how a variety of biophysical processes may operate to slow significantly the loss of larvae away from the local population. The interaction of deep-water mesoscale and coastal flows creates high variability in local flow conditions. Within this variation are common features, e.g., vertically stratified flows, to which larvae may respond behaviorally, resulting in enhanced retention relatively close to shore and to the source population. Nearshore environments may also convey increased probability of survival via increased productivity. Thus the biophysical processes are in place to favor local retention and survival over long-distance dispersal. This is not to say that larvae are not dispersed long distances, rather that such dispersal may be relatively minor in comparison to the number of larvae that are retained, or the frequency with which they are retained. Resolving this issue will require a multipronged approach, including larval transport dynamics, population genetics, and larval tagging (e.g., elemental fingerprinting; see Chapter 11, this volume).

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VIII. Future Directions

Though there have been some significant excursions into the larval black box over the last decade, it is still dusk inside the box. By exploring the details of larval behavior, in conjunction with the physical world, we have made significant strides in understanding the dynamics of the pelagic system and how larvae have adapted to survive this pelagic stage. We also continue

to be rewarded with examples of behavioral and sensory capabilities that were beyond belief only a short time ago (e.g., see Chapters 6 and 8, this volume). Similarly, that there are more and more examples of rather restricted larval exchange should not be surprising, given what we know of the pelagic stage in the life history of coral reef fishes. Linking the dynamics of this stage to recruitment and population dynamics overall, however, continues to be a challenge.

There are directions of research, as well as applications of new technologies, that will continue to shed light into the box. First, there is a need to continue to explore all aspects of the biology and ecology of larvae in the pelagic environment. One immediate approach should be to expand taxonomic coverage. For tropical species, most effort, particularly that tied to late-stage settlement/recruitment dynamics, has been focused on labroids, specifically, labrids and pomacentrids. Several recent efforts have expanded on the number of taxa studied to include mullids, acanthurids, and gobiids. Further, given their economic importance, more work is being focused on haemulids, lutjanids and serranids. This trend must continue. With greater taxonomic coverage, more general theories of larval dynamics and ecology can be forged. There is also a need to study all stages of development. Most plankton studies collect preflexion and early postflexion larvae, but relatively few (or no) later stage postflexion larvae. Light traps have added significantly to our knowledge of late-stage larvae at or near settlement, and recent behavioral studies of these late-stage larvae have revealed some remarkable swimming capabilities. Similar insights will likely be gained when statistically meaningful quantities of all stages of larvae are successfully collected.

There is also a clear need to continue to study the full range of potential larval behaviors. We need to know under what conditions they are expressed and how they interact with the physical conditions in a given system. The potential range of larval vertical behaviors of different taxa is just beginning to be understood. There is still much work to be done to understand how such behaviors change under different physical conditions (e.g., changes in hydrographic conditions), and to what cues larvae are responding and how sensitive larvae are at detecting these cues. Finally, within the context of larval biology and ecology, a more thorough examination of all factors controlling larval and juvenile survival is needed. For example, how does survival differ under different prey conditions? This information is required to comprehend fully biophysical interactions that determine recruitment success. Merely demonstrating that a particular larval advective pathway is feasible does not mean that

larvae might survive the trip. We do not know whether oceanic (versus coastal) conditions can provide sufficient food to grow and survive to metamorphosis (see Searcy and Sponaugle, 2000).

Such studies (as described above) will require more extensive sampling, and as sampling frequency or duration increases, so does the effort required for processing the samples. A separate problem is that it is difficult to catch older and larger larvae with conventional nets because their density decreases and their swimming capability increases. Development of real-time or near real-time sampling technologies would be incredibly beneficial in efforts to couple synoptic physical surveys with biological studies. The Video Plankton Recorder (VPR) of Davis *et al.* (1996) shows some promise in this direction, though its field of view is still too small to sample adequately the volume of water required to quantify larval fishes. Tied to such rapid sampling techniques is the requirement for rapid identification of larvae to the species level. The state of knowledge in this regard is still limited, even with the significant progress being made (e.g., Leis and Carson-Ewart, 1999; Richards, 2001, and the many contributors to these volumes). With the advent of rapidly evolving molecular techniques (mitochondrial DNA, molecular probes, microarray techniques), rapid and potentially semiautomated, identification and eventually quantification may be possible.

Other technologies are worth exploring or developing to further enhance our ability to examine larvae *in situ*. For example, S. Sponaugle and J. S. Jaffe (personal communication) are exploring the use of new three-dimensional sonar technology (Jaffe *et al.,* 1995) to "visualize" the interaction of larvae with their environment. This technology allows individual larvae and zooplankton to be tracked in a three-dimensional volume, enabling the observation of *in situ* swimming behaviors and predator–prey interactions during the transition from pelagic to benthic environments. Technologies also exist that will enable the identification of larval sources and transport pathways. These include tracking of larvae via dye injection to track water mass movement (e.g., Houghton and Visbeck, 1998), release of larvae artificially tagged with either otoliths marking (e.g., Secor *et al.,* 1995b; Jones *et al.,* 1999) or molecular marking (Hitchcock *et al.,* 2002), using natural tags (microchemistry of constituents of otoliths; see Chapter 11, this volume), and using new molecular genetic techniques such as microsatellite DNA (O'Reilly and Wright, 1995; O'Connell and Wright, 1997; Carvalho and Hauser, 1998).

Once we are able to address these questions, it will be possible to make significant advances into the larger issues of recruitment and population dynamics. Our current advances have greatly enhanced our understanding of the mechanisms creating temporal and spatial patterns in larval distributions and settlement. Moreover, details of biophysical processes have contributed to our ability to explain larval retention and the realization that marine populations may not be as "open" as previously thought. Linking new techniques with knowledge of these biophysical processes should lead to a better explanation and prediction of settlement amplitude, especially when coupled with studies of postrecruitment processes, recruitment variability, and ultimately population dynamics.

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