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PREDICTING SELF-RECRUITMENT IN MARINE POPULATIONS: BIOPHYSICAL CORRELATES AND MECHANISMS

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ABSTRACT

Mounting evidence suggests that some populations of benthic marine organisms may be less demographically 'open' than previously thought. The degree to which a population receives recruits from local sources versus other populations has important ecological and management ramifications. For either of these reasons, it is often desirable to estimate the degree to which a population of interest is self-recruiting. Although methods for actual estimation of population self-recruitment are limited and often difficult to employ, the presence of several biological and physical conditions may improve our estimates of self-recruitment for particular populations. Biological traits of benthic adults (relative fecundity, spatial and temporal patterns of spawning and larval release, parental investment), as well as pelagic larvae (stage of development at hatching, pelagic larval duration, vertical migration behavior, horizontal swimming ability, and sensory capabilities) influence where and when larvae are released, where and how they are transported, their ability to move actively in the pelagic realm, and finally, spatial and temporal settlement patterns. Physical variables potentially influencing self-recruitment include site isolation, coastal complexity and flow variability. Within these physical variables we discuss explicit mechanisms by which larvae may be retained in proximity to their natal population. We provide examples from specific locations such as coral reefs, isolated islands and seamounts, and semi-enclosed embayments such as lagoons and estuaries, as well as characteristic oceanographic features such as upwelling systems, fronts, moving convergences, eddies and counter currents. We evaluate direct and indirect evidence to predict the relationship between these biophysical variables and the degree of self-recruitment in benthic marine organisms. We conclude that physical factors that result in a departure from unidirectional, depth-uniform water flow provide the opportunity for retention of larvae, and therefore of self-recruitment. These physical factors are common in the ocean and vary in intensity among locations and times. Some enable retention of passive larvae (physical retention), whereas others lead to retention only with active behavioral input by the larvae (biophysical retention). Larval behavior that can contribute to or result in retention or return to natal sites ranges from simple vertical orientation (within the capabilities of the larvae of most taxa) to complex sensory abilities and strong swimming (known to occur in larvae of a few taxa, particularly decapod crustaceans and fishes). For all taxa, both the pelagic larval duration and the time to behavioral competency will have a strong influence on likelihood of self-recruitment. Understanding the biophysical mechanisms by which larvae are retained near or return to their natal population will be necessary before generalizations can be made. Examples highlight the importance of each variable to processes controlling self-recruitment. For most correlates, further study is clearly warranted. Although certain variables hold promise for predicting self-recruitment, complex, non-linear interactions among these biophysical variables must be considered.

Many benthic marine organisms have life histories that include a pelagic larval phase. Although many taxa exist in local populations (defined here as all the individuals of a species living and reproducing in a particular area naturally delineated by geography or oceanography, or artificially defined by human interest or economics), there has been a strong historical assumption of broad population connectivity via larval dispersal across such species' ranges. A refinement of this paradigm suggests that marine populations range from entirely *closed*, self-sustaining populations (e.g., endemic island species where 100% of recruitment is due to the settlement of offspring produced by that population) to fully *open* populations recruiting only a relatively small proportion of their own offspring back to the population (i.e., receiving a high number of recruits from other populations). This concept can be supported by a few examples from either end of the spectrum. However, there is much more uncertainty between these extremes and many benthic marine populations likely have only a portion of their recruitment "subsidized" (sensu Pascual and Caswell, 1991) from external sources. For these recruitment-subsidized populations, the question becomes: relative to a particular area or local population, to what degree is the population self-recruited or subsidized from elsewhere?

Ocean flow fields operating during the pelagic phase theoretically disperse larval propagules (e.g., Fulton, 1989) and enhance population connectivity. However, there have been a number of hypotheses (see Sinclair, 1988) and recently, new evidence (Jones et al., 1999; Swearer et al., 1999; Cowen et al., 2000; reviewed in Swearer et al., this issue) suggesting that, in fact, some populations of benthic marine organisms may be less 'open' than previously thought. The interaction of various biophysical mechanisms may fully or partially counter dispersion and enable the retention of larvae near their natal source. Particular species may be more or less likely to exist in open or closed populations depending on their life history traits (both adult and larval) or where their populations are located. For example, species with very short larval periods may be more likely to settle close to their natal source. For species with longer pelagic durations, local populations may be more or less open or closed depending on their immediate physical setting and behavior of the larvae. Not only are multiple variables important in determining relative connectivity, but the complex interactions of these variables likely has contributed to our inability to resolve connectivity patterns in nature.

Of critical importance to any discussion of population connectivity is the need to define appropriate temporal and spatial scales (see Warner and Cowen, this issue). In the ensuing discussion, emphasis is placed on processes contributing to the exchange of individuals (particularly larval stages) over ecologically meaningful scales. Specifically, for the purposes of this paper, self-recruitment refers to *levels of retention that substantially affect the abundance of a local population (i.e., populations exhibiting high self-recruitment are those whose numbers are significantly influenced by recruitment of their own offspring)*. Even with substantial self-recruitment, rates of exchange among populations are likely much higher than that required to maintain genetic homogeneity of a population. The processes responsible for exchange at ecologically meaningful levels are far more complex, and are likely the processes to which adaptation has occurred, rather than those associated with rare long-distance exchange events (see Strathmann et al., this issue).

Our discussion will focus on *local populations*, the dimensions of which will be defined by the biological traits of the organism and the physical setting as well as the scale of the question (i.e., whether of a management or ecological nature). Our focus is on

scales that are smaller than the geographic range of a species (e.g., single component population of a meta-population). For internal consistency, we consider the scale of a local population to be within the range of 1–100 km.

What follows is a short discussion of each of several critical biological and physical variables (defined in Table 1) and how they might contribute to the likelihood of a population exhibiting self-recruitment. Although many of the biological traits and physical processes clearly must interact either to retain propagules near or to return propagules to the natal region, for the purposes of our discussion, we first summarize each variable independently and examine it in terms of self-recruitment. The hypothetical relationship between each isolated variable and the proportion of self-recruitment a population experiences is then evaluated based on empirical evidence. Much supporting evidence is drawn from estuarine and coral reef case studies largely because the relationship between retention and biophysical processes may be easier to define in these relatively discrete habitats. However, examples also are drawn from other taxa in other systems such as continental shelves and open ocean gyres. Further, where appropriate, the discussion is broadened to include examples from non-benthic marine populations. In the section on physical processes, we include a brief summary of how different mechanisms may function in particular areas to retain larvae. As will be apparent, many predictions remain largely untested and serve as suggestions for future research.

In this paper, we cite review papers wherever possible to reduce the number of cited papers while at the same time providing the reader with an entry to the literature. Note that the issue of self-recruitment extends over multiple temporal scales from the ecological to evolutionary. These scales clearly overlap, but we have placed most of our emphasis on purely ecological scales. For further detail on how ecological processes discussed herein are translated to an evolutionary scale, see reviews by Bradbury and Snelgrove (2001) and Strathmann et al. (this issue).

BIOLOGICAL TRAITS

ADULT FECUNDITY

Adult reproductive characteristics clearly determine population replenishment, but only certain traits may be important to the degree of self-recruitment a population experiences. As a species-level trait, fecundity should not directly influence the likelihood of self-recruitment. If fecundity is similar among all populations of a species, all else being equal, the proportion of self-recruitment for each population should be the same (i.e., for different species, the percent of self-recruitment should be independent of a species' fecundity).

However, where individual fecundity varies among populations of the same species, fecundity may influence local self-recruitment. For example, a population of fishes in a protected area may attain a larger mean body size (e.g., Polunin and Roberts, 1993). Larger fishes typically have a higher reproductive output, thus this protected population would contribute relatively more offspring than other local populations of the species outside the protected area. Assuming complete mixing of propagules from all metapopulations, a higher number of the protected population's offspring should recruit back to the local population. Thus, as a population-level variable, increasing relative individual fecundity should directly enhance the likelihood of local self-recruitment.

Table 1. Definitions of biological and physical variables as correlates of self-recruitment.

Variable	Definition
A1 Adult fecundity	Number of propagules produced by a mature individual of a particular species; Variation among different local populations has more effect on self-recruitment.
A2 Spatial pattern of spawning/larval release	Directed movements by adults to place propagules in specific location; ranges from asynchronous spawning by sessile animals to highly synchronous spawning migrations.
A3 Temporal pattern of spawning	Timing of propagule release, ranging from asynchronous, random patterns to highly synchronous behaviors.
A4 Parental investment and larval stage of development at hatching	Amount of energy invested in reproduction; stage of development refers to the movement capabilities of the larvae (whether via active swimming or buoyancy control).
A5 Pelagic larval duration	Portion of a species larval development spent free of either parental care and/or contact with the benthos; period during which propagules are susceptible to physical mixing and advection.
A6 Vertical positioning behavior by larvae	Any vertical movement that results from a biological response (swimming and/or buoyancy control) of the organism, including diel, tidal, ontogenetic, and other cue dependent movements.
A7 Horizontal swimming ability of larvae	Active, directed movement by larvae in the horizontal direction.
A8 Sensory capabilities of larvae and environmental cue strength	Ability of larvae to detect and respond to cues of varying strengths emanating from the settlement or natal site.
B1 Geographical site isolation	Degree to which a site (local population) is physically isolated from other sites.
B2 Coastal complexity	Degree to which the coastline is convoluted with respect to bathymetric and topographic features acting to steer the prevailing current. Includes topographic complexity, embayments of several sizes, and water residence time.
B3 Flow variability and water column stratification	Integration of changes in direction of flow and intensity of flow in both horizontal and vertical planes, includes upwelling/downwelling, fronts, convergences, eddies, and counter currents.

ADULT MOBILITY AND SPATIAL PATTERNS OF SPAWNING OR LARVAL RELEASE

Adult mobility in marine organisms ranges from zero in sessile adults through animals undertaking basin-scale migration patterns (e.g., tunas). Mobility in general will be tightly coupled to the functional boundaries of a given population, so as such, should not directly influence self-recruitment. However, although adult stages presumably exist in an environment favorable to adult survival, this location may not be conducive to egg or larval survival or subsequent recruitment to the adult population. Some species undergo significant migrations to place their eggs in environments that may maximize offspring survival.

As early as a century ago, it was recognized that spawning locations were spatially more restrictive than the distribution of the population (Damas, 1909). Spawning sites of marine fishes have been hypothesized to maximize larval feeding potential (Lasker, 1975) or minimize predation on propagules by dispersing larvae offshore (Johannes, 1978). In addition, some species may spawn at sites where currents are predictable and geographically stable, allowing for the retention of larval aggregations for several months (e.g., Atlantic herring, Atlantic cod, and haddock: Iles and Sinclair, 1982; O'Boyle et al., 1984; Gagné and O'Boyle, 1984; Smith and Morse, 1985). Currents also may favor the transport of larvae to nursery areas, and the life cycle is completed when juveniles migrate to adult habitats (Harden Jones, 1968). For example, plaice larvae spawned at sites in the North Sea are carried by currents to nursery grounds (Cushing, 1975) and mature fish tend to return to the same spawning site year after year. Due to selection of spawning sites and the subsequent larval drift (Cushing, 1975) or larval retention (reviewed in Sinclair, 1988), North Sea plaice populations may show a substantial degree of self-recruitment. Other examples of spawning migratory behavior include pelagic armorhead (Boehlert and Sasaki, 1988), southern bluefin (Davis et al., 1990), snapper and grouper (reviewed in Domeier and Colin, 1997), and American eels (McCleave and Kleckner, 1987).

Smaller scale migrations are also evident: grunion and capelin enter the intertidal zone to lay their eggs on beaches (Thompson, 1919; Frank and Leggett, 1981); and lingcod spawn in nests close to the topographically complex rocky shoreline so that negatively buoyant larvae hatch into water with reduced alongshore flow (Shaw and Hassler, 1989). However, other small-scale migrations may facilitate offshore transport of eggs: spawning at reef promontories is a common behavior for pelagic-spawning reef fishes (Johannes 1978).

Adult invertebrates generally are less vagile than fishes, and long migrations to release offspring are less common. There are notable exceptions, such as the migrations by lobsters (*Panulirus* spp., *Jasus* spp., *Homarus* spp.) on the continental shelves of Australia and the east coast of North America (Rebach, 1983; Campbell, 1986), the onshore spawning migrations by *Cancer* spp. crabs in the North Sea and northeast coast of North America (Nichols et al., 1982; Rebach, 1983), aggregated spawning by the squids *Loligo opalescens* along the coast of California (Cailliet and Vaughan, 1983) and *Illex illecebrosus* along the eastern U.S. coast (Trites, 1983). As with some fish migrations, alongshore adult migrations by adult blue crabs, *Callinectes sapidus*, may compensate for the displacement of larvae by coastal currents and increase the chances of self-recruitment (Oesterling, 1977; Provenzano et al., 1983; McConaugha, 1988; Steele, 1990).

Although these spawning migrations are most often thought to place the larvae in optimal locations for survival it is entirely possible that the locations also enhance retention (e.g., Atlantic herring; Iles and Sinclair, 1982). By enabling more control over where and

when offspring are released, increased adult mobility and selection of particular spawning locations could enhance self-recruitment.

TEMPORAL PATTERNS OF SPAWNING AND LARVAL RELEASE

Physical conditions at the time of larval release or spawning establish the initial conditions for larval dispersal. Thus, when offspring enter the water column at appropriate times, dispersal may be greatly reduced. Offspring release commonly is synchronized to meteorological conditions, short-term environmental cycles (tidal, light-dark) and long-term seasonal cycles. For example, it is hypothesized that coral reef invertebrates and fishes may spawn during months when gyres form, thereby enhancing the probability of larval retention (Johannes, 1978; Lobel, 1978; 1989) and self-recruitment. On shorter time scales, the timing of spawning has been hypothesized to reduce larval transport away from the parental site (Berry, 1986), as well as enhance fertilization (Oliver and Babcock, 1992), or enhance larval survival by swamping local predators or reducing larval encounters with predators (Johannes, 1978; Morgan, 1990).

Lunar and semi-lunar patterns of spawning and larval release are common and may be related to the importance of the tidal amplitude cycle in larval transport. For some reef fishes and corals, spawning coincides with neap tides, when lower rates of offshore flow may enhance initial retention of eggs and larvae near natal reefs (e.g., Babcock et al., 1986; Gladstone and Westoby, 1988; Robertson et al., 1990; Reyns and Sponaugle, 1999). Spawning synchronized to the tidal amplitude cycle also may be related to the frequency of internal waves or bores that may eventually transport larvae and zooplankton shoreward (Shanks, 1983, 1988; Barnett et al., 1984; Pineda, 1991; Leichter et al., 1996, 1998).

In a great many other cases, spawning and larval release coincides with spring tides, when strong currents enhance initial transport of eggs and larvae from shorelines (Korringa, 1944; Johannes, 1978; Taylor, 1984; Morgan 1995a). For example, some Indo-Pacific reef fishes and intertidal crabs and fishes worldwide synchronize their ovarian cycles with local tidal cycles and spawn or hatch larvae at times that would promote offshore transport (e.g., Hoffman and Grau, 1989; Taylor, 1984; Colin and Bell, 1991; Morgan, 1995a; Sancho et al., 2000). Eggs and larvae released during strong ebb tides may be rapidly transported away from reefs and shorelines, where predators abound, to safer open waters (Johannes, 1978; Hovel and Morgan, 1997).

Opposing strategies that favor initial retention or seaward transport are sometimes even evident in closely related species. Although the abalones, *Haliotis rubra* and *H. kamtschatkana*, spawn during periods of little water movement (Breen and Adkins, 1979; Shepherd et al., 1992), resulting in limited larval dispersal and high self-recruitment (*H. rubra*; Shepherd et al., 1992), *H. discus hannai* spawns during typhoons when large waves flush the surf zone and sweep larvae out to sea (Sasaki and Shepherd, 1995), reducing the probability of self-recruitment. In a similar manner, the tubicolous polychaete *Phragmatopoma californica* spawns in response to destructive storms (Barry, 1989), a strategy that would appear to promote dispersal rather than self-recruitment. However, due to the coupling of physical re-circulation systems and larval behaviors, this short-term dispersal away from reefs and shorelines may reduce predation by reef organisms without necessarily leading to widespread transport. For example, some storm events are coupled with downwelling conditions (Winant, 1980), so that larvae swept from the surf zone may be retained nearshore.

In summary, greater temporal synchrony of spawning suggests greater control over the survivorship and potential fate of larvae, thus greater synchrony generally should contribute to higher self-recruitment. In some cases this is clearly evident in the biophysical retention of animals near the natal source. In other cases, additional constraints such as predation may lead to the initial dispersal of young away from the natal site.

PARENTAL INVESTMENT AND LARVAL STAGE OF DEVELOPMENT AT HATCHING

A classic ecological paradigm states that higher parental investment (larger eggs; longer parental protection) leads to larger, more developed larvae that are able to settle after a short pelagic larval duration (Barlow, 1981; Strathmann, 1985). High parental investment (e.g., reef fishes guarding demersal eggs, Thresher, 1984; external and internal brooding by invertebrates, Levin and Bridges, 1995) should enhance egg, larval and even juvenile survival, as well as enhance self-recruitment by retaining young in the vicinity of the parent for an extended period. Furthermore, if these large, well-developed larvae do not settle in a short time, they often are able to exhibit some form of active swimming behavior (Bell and Brown, 1995; Fisher et al., 2000), which also may enhance retention of larvae near the parental population. In most marine environments, active swimming, either vertically or horizontally, can increase the chances of larval retention near the natal population (e.g., Bousfield, 1955; Wood and Hargis, 1971; Hill, 1991; Morgan, 1995b; Paris and Cowen, in prep.). Support for this contention can be found in the frequently observed nearshore distribution of larvae of reef fish species hatching from benthic eggs (e.g., Marliave, 1986; Kingsford and Choat 1989; Leis, 1991; Boehlert et al., 1992; Brogan, 1994; Cowen and Castro, 1994). Larvae of many species of invertebrates hatch from egg capsules or brood chambers at advanced stages of development. For example, among species with a larval stage, many gastropods hatch as advanced veligers that settle after a brief pelagic period. After being introduced to several islands in the South Pacific, two Southeast Asian gastropods (*Trochus* spp. and *Turbo* spp.) rapidly established viable local populations, suggesting a high degree of self-recruitment (Nash, 1993; Yamaguchi, 1993).

In contrast, the larvae from pelagic-spawned eggs are presumably smaller, less active and less capable of remaining near the source population, as suggested by the prevalence of pelagic-spawned reef fish species well offshore (Leis, 1991; Boehlert et al., 1992; Cowen and Castro, 1994). However, of the two reef fishes for which a high proportion of self-recruitment was measured, one spawns pelagic eggs and the other species spawns benthic eggs (Swearer et al., 1999; Jones et al., 1999), calling into question this paradigm (see also Cowen and Sponaugle, 1997). Thus, high parental investment that produces well-developed hatchlings should increase self-recruitment, but high rates of self-recruitment are still possible for pelagic spawners.

PELAGIC LARVAL DURATION

Time spent in the water column (PLD) is perhaps the most often cited biological variable potentially affecting self-recruitment. In simple model predictions of population connectivity, PLD is coupled with mean current flow to predict the degree of population exchange (e.g., Spratly Island fish populations: McManus and Menez, 1997; reef fishes in the Caribbean: Roberts, 1997). Even in more complex models factoring in diffusion and mortality, PLD remains a central variable contributing to the degree to which populations can self-seed (Cowen et al., 2000).

At first glance, the prediction (that population connectivity is inversely related to PLD) seems relatively straightforward and substantiated by both field and modelling studies. Coral planulae, sponge larvae, and larvae of bryozoans and ascidians with PLDs of \leq d hours to several days ('anchiplanic' larvae sensu R. Scheltema in Levin and Bridges, 1995). Clearly, the probability that a larva will settle within the local population boundaries is greatly increased with a very short pelagic larval duration. At the opposite extreme are organisms with very long larval durations ('teleplanic' larvae with durations between 60 to 365+ d, sensu Scheltema, 1971) such as the veligers of several gastropods and bivalves, lobster phyllosoma, and anguillid and muraenid (eel) larvae (McCleave and Kleckner, 1987; Hourigan and Reese, 1987; see review by Levin and Bridges, 1995). Given the complexity of the ocean over long time frames and assuming adequate survival over the open ocean, it is intuitive that exchange over long distances is more likely for organisms with long PLDs. This relationship is particularly relevant for organisms with larvae that are comparatively passive for at least a significant portion of their larval period.

A large number of organisms (if not most) exhibit active behavior during some portion of their larval period, and therefore, patterns of population exchange may be more complex than that predicted for relatively passive larvae. In a comparison of dispersal distance for larvae with PLDs of minutes to months, Shanks et al. (in press) found a significant correlation between PLD and dispersal distance. However, a number of organisms dispersed substantially shorter distances than would be expected due to active behavior that limited their dispersal (e.g., moving down into the benthic boundary layer). Reef fish larvae with relatively short PLDs (e.g., pomacentrids with PLDs of 24–29 d) may remain near source populations (Jones et al., 1999) using simple vertical migration behaviors (Paris and Cowen, in prep.). However, fishes with longer PLDs also may recruit back to source populations (Swearer et al., 1999), suggesting similar interactions with other variables. Active behavior on the part of adults (see above) or larvae can effectively reduce the dispersal of a number of taxa with varying PLDs.

Another mechanism that enables taxa with longer PLDs to recruit successfully to the natal population is plasticity in PLD. For example, a longer, more variable PLD may provide the flexibility to respond actively to favorable environmental cues which are temporally variable (Sponaugle and Cowen, 1994) increasing the chance of return to the natal population. The ability to delay metamorphosis (Victor, 1986a; Cowen, 1991) and tolerate slow growth (Pechenik et al., 1996a,b; Searcy and Sponaugle, 2000) also may be beneficial to organisms recruiting to relatively restricted adult habitats. For several endemic fishes (which represent repeated self-recruitment over long time scales), PLD's are particularly long and highly variable (see Bell et al., 1994 for a diadromous Caribbean goby; Randall, 1961 for a Hawaiian surgeonfish; and Cowen and Sponaugle, 1997 for compilation of data from Victor, 1986b and Thresher et al., 1989 on endemic versus non-endemic Hawaiian labrids) lending support to the contention that long PLD's may contribute to, or at least not preclude self-recruitment. A recent study also found that endemics were not characterized by any particular PLD (Robertson, 2001). Half of the endemics from seven small, isolated islands had PLDs \leq 30 d and half had PLDs between 1–3 mo long. All endemics clearly experience successful self-recruitment.

In summary, the prediction of an inverse relationship between PLD and self-recruitment may hold for species with larvae that are relatively passive during a portion of their PLD or larvae with very short PLDs. However, there are many exceptions to this relation-

ship and these exceptions are due to active behavior. Active larval behavior may entail rather simple vertical migrations or more robust and directed horizontal swimming (see below). The interaction of behavior with physical processes results in a breakdown of the predicted relationship between PLD and dispersal distance such that the converse is not necessarily true for taxa with active or long-lived larvae.

VERTICAL POSITIONING BEHAVIOR BY LARVAE

Larval movements need not be extensive or elaborate to enhance self-recruitment. The simplest behavior is vertical movement. The flow field in most coastal water columns is vertically stratified, and consequently, relatively simple vertical positioning by larvae can be an important determinant of larval transport. Even in vertically-mixed water columns, flow in the benthic boundary layer is slower than in the remainder of the water column, and wind stress can establish an Ekman spiral (i.e., frictionally-driven flow with directionality of the flow rotating slowly with depth). Because velocity differs among depths, larvae may position themselves vertically to move horizontally in different directions or speeds.

Classic studies in estuaries have documented three types of vertical migration that mediate horizontal transport of larvae: ontogenetic, diel, and tidal. Strong evidence exists in support of ontogenetic (Bousfield, 1955; Wood and Hargis, 1971; Sandifer, 1975a) and tidal (Weinstein et al., 1980; Cronin and Forward, 1982; Dittel and Epifanio, 1982; Fortier and Leggett, 1983; Hoss, 1984; Laprise and Dodson, 1989; Christy and Morgan, 1998) migrations facilitating self-recruitment. Theoretically, diel vertical migrations also may facilitate retention in estuarine circulations (Hill, 1991; Morgan, 1994; see below).

Beyond strictly estuarine systems, simple upward swimming by larvae may lead to their capture by frontal circulations (Epifanio, 1987; Franks, 1992; Govoni and Grimes, 1992). If the time scales of the fronts approach the larval duration for even relatively passive larvae (or the passive portion of the larval phase for species that become active prior to settlement), such features (see below) may locally retain larvae. Upward movement also has been shown to facilitate onshore transport due to wind (e.g., blue crabs, Epifanio, 1995) and internal waves (Shanks, 1986). Similarly, changes in vertical position with ontogeny have been shown to promote onshore transport of larval fishes and invertebrates by moving larvae into onshore flowing strata (Shanks, 1983, 1986; Cowen et al., 1993, 2000; Pineda, 1999; Shanks et al., 2000; Paris and Cowen, in prep.). Such onshore movements might be used as a mechanism to retain larvae near their natal site.

Larvae also may be able to reduce dispersal by remaining in the benthic boundary layer (BBL) where flow is reduced to very low levels (Nowell and Jumars, 1984; Butman, 1987; Denny, 1988). Among fishes, post-flexion or late-stage larvae of several temperate and tropical families have been found in or near the benthic boundary layer (Barnett et al., 1984; Jahn and Lavenburg, 1986; Leis, 1986; Lindeman, 1986; Steffe, 1990; Breitburg, 1991; Kaufman et al., 1992). For the larvae of several fishes (Barnett et al., 1984; Jahn and Lavenburg, 1986), copepods, barnacles (Barnett and Jahn, 1987) and other larval invertebrates (reviewed by Young and Chia, 1987), this behavior probably decreases offshore dispersal. Shanks et al. (in press) found that for a number of taxa with larvae that remain in the BBL, dispersal distance is less than that predicted based on PLD.

Early attempts to model larval dispersal often had the simplifying assumption that vertical position in the water column makes no difference to horizontal movements of larvae (e.g., Williams et al., 1984; Tegner and Butler, 1985; Roberts, 1997). Recently, more

realistic three-dimensional models take vertical position of larvae into account (Black et al., 1991; Werner et al., 1993; Tremblay et al., 1994; Manuel and O'Dor, 1997; Wolanski et al., 1997; Armsworth, 2000), and are, therefore, more likely to predict accurately the dispersal of larvae. Overall, active vertical positioning by larvae enables greater control over horizontal transport and should enhance self-recruitment.

HORIZONTAL SWIMMING ABILITY OF LARVAE

Until recently, the literature supported the view that larvae were relatively ineffectual swimmers, with reported values for sustained swimming of less than 3 cm s^{-1} for invertebrate larvae (Chia et al., 1984) and less than 5 cm s^{-1} for fish larvae (Blaxter, 1986). However, a growing body of evidence suggests that some late-stage larvae of fishes and decapods are capable of directed onshore swimming. Larvae that can swim faster than surrounding currents (i.e., 'effective' swimmers sensu Leis and Stobutzki, 1999), should be better able to control their trajectory during the pelagic period than larvae with little or no swimming ability. Hence, retention could be achieved behaviorally and would not depend entirely on hydrographic 'retention cells'.

Lobster and crab postlarvae may have directed shoreward swimming (Cobb et al., 1989) for 40–60 km at velocities reaching 30 cm s^{-1} (Phillips and Sastry, 1980). Data supporting this contention include the observation that crab postlarvae orient into flow and swim in straight lines at moderate flow velocities (Mackay, 1943; Luckenbach and Orth, 1990; Fernandez et al., 1994; Shanks, 1995) and toward dissolved chemical cues emanating from estuaries (Wolcott and DeVries, 1994). Late-stage larvae of coral-reef fishes also swim at high speeds (averaging ca 20 cm s^{-1} ; some species up to 65 cm s^{-1}) that can be maintained for substantial periods (up to 194 h, covering 94 km; Stobutzki and Bellwood, 1997; Leis and Carson-Ewart, 1997; Leis and Stobutzki, 1999). Such swimming capabilities clearly counter the prevailing view (e.g., Roberts, 1997) that larvae are passive.

Self-recruitment in some reef fishes and crustaceans may be a two-step process. As swimming is not well developed at hatching for many species (Leis and Carson-Ewart, 1997; Fisher et al., 2000), young, poorly developed larval stages are likely retained by depth regulation or entrainment in hydrographic features until they become 'effective' swimmers that can control their trajectories and recruit onshore by directed swimming. This transition from ineffective to effective swimmers can occur within a few days to weeks of hatching in some species (Fisher et al., 2000), but may occur later in others. Such a scenario was proposed for bluefish along the east coast of the U.S. (Hare and Cowen, 1993, 1996). Similarly, Chiswell and Booth (1999) concluded that shoreward swimming of $4\text{--}10 \text{ cm s}^{-1}$ by rock lobster post larvae (*Jasus edwardsii*) off New Zealand was required to match observed larval distributions, whereas passive drift best described the distributions of mid-stage larvae. In sum, the capacity for horizontal swimming may enable larvae to exhibit some independence from ocean currents (Armsworth, 2000), reducing (or eliminating) passive dispersal and enhancing self-recruitment.

SENSORY CAPABILITIES OF LARVAE AND ENVIRONMENTAL CUE STRENGTH

Successful settlement into coastal or isolated environments may depend on the presence and strength of habitat-specific cues to which larvae respond. If larvae have pelagic larval durations of days to months then the probability of returning to a natal area is likely to be low if there is no information on the direction of suitable habitat. Furthermore, the ability of larvae to detect such habitat cues and orient toward those cues should signifi-

cantly influence their horizontal positioning and the degree to which they can return to a natal site.

Many physical and biological cues could be used by organisms in the marine environment and their concentrations, frequencies and intensities can vary in ways that can be useful for orientation (see reviews by Myrberg and Fuiman, *in press* and Kingsford et al., this issue). Chemical stimuli, with directional information, may be found in estuarine and reefal plumes (Crossland et al., 1980; Wolanski and Hamner, 1988; Grimes and Kingsford, 1996), from sandy beaches (Kalmun, 1982) and perhaps algae (Walters and DiFiori, 1996). Variation in ambient noise and vibration is considerable and biological (e.g., snapping shrimps, fishes) and physical (waves) sound sources may be relatively predictable in space and time (Rogers and Cox, 1988; Janssen et al., 1990; Cato, 1992). Visual cues including celestial bodies and related polarized light may also provide cues (Waterman, 1989). Local variation in magnetic fields due to magnetic anomalies preserved in volcanic rocks is considerable and potentially more useful for navigation (e.g., salmonids, Quinn and Dittman, 1990), as is the highly predictable magnetic field of the earth itself.

Many invertebrates and fishes can sense variation in water chemistry, sound and vibrations, hydrography, celestial bodies, magnetism, visibility and electrical fields (Phillips and MacMillan, 1987; Blaxter, 1988; Kalman, 1982; Hara, 1994; Kingsford et al., this issue). Salmonid fishes (Quinn and Tolson, 1986), turtles (Grassman et al., 1984) and some invertebrates (Atema and Cowan, 1986) are known to respond to small variations in water chemistry. Tripterygiid fish larvae were recently shown to use sound to navigate (Tolimieri et al., 2000). Larval fishes and invertebrates are influenced by environmental cues close to settlement (Sweatman, 1983, 1985; Seki and Taniguchi, 1996; Welch et al., 1997) and have the necessary sensory morphology for broader scale detection of suitable settlement sites (e.g., Lara, 1999). However, our knowledge of how these senses are used by larval forms for orientation and choice in the pelagic environment is largely speculative. Although much work remains to be done in this area (see Kingsford et al., this issue), the prediction is that the stronger the cues and the better able a larva is to detect and respond to such cues, the greater the likelihood is of self-recruitment.

PHYSICAL PROCESSES

GEOGRAPHICAL SITE ISOLATION

The more isolated a site is, the more likely it is that the population there is maintained entirely by self-recruitment simply because it is unlikely that an isolated population could be maintained from a distant source. This view is supported by the analysis of Cowen et al. (2000), who show that diffusion and mortality during the pelagic phase should result in extremely low numbers of larvae ever reaching a location from a distant source. For more closely spaced or continuously distributed populations, the exchange of larvae from nearby sources should result in a reduction in the proportion of new recruitment that is locally-derived, and this may occur without a decrease in the absolute number of self-recruits. That is, the recruitment subsidy from nearby locations may increase while the absolute amount of self-recruitment may remain unchanged.

Relevant studies to evaluate these ideas are rare. The case of endemic species is an obvious one, though reflective of longer (evolutionary) time scales. The degree of endemism is greatest (and often the overall diversity is lowest) at the most physically isolated locations (Robertson 2001; see Swearer et al., this issue). At intermediate levels of isola-

tion, some long-distance exchange may maintain gene flow thereby reducing the level of endemism, but the occurrence of such long-distance dispersal events may be too infrequent to be of ecological significance (Schultz and Cowen, 1994).

Examples of isolation are most common for oceanic islands and seamounts, though some estuarine environments are also highly spatially isolated. Depending on the scale of the population (including relative mobility and PLD), a rocky reef in the middle of a long sandy stretch could be considered an isolated habitat. Isolation of neighboring areas also may occur as a result of particular oceanographic conditions (e.g., both sides of major promontories may isolate populations due to topographically-steered currents; see below).

Where sites are largely contiguous, the degree to which self-recruitment is important is largely unknown. Recent studies suggest that levels of self recruitment may be in the range of 30–60%, even where nearby sources are as little as a few km away (Jones et al., 1999) to 100 km (Swearer et al., 1999). However, because neither the actual sources of the exogenous larvae nor the processes leading to such input were identified, the generality of these results remains uncertain.

In summary, isolated sites with large and sometimes endemic faunas demonstrate that self-recruitment mechanisms exist, but this provides no insight as to how important such mechanisms are to typically less isolated populations. Less isolated populations may have similar absolute rates of self-recruitment, although dilution by subsidy from neighboring populations may reduce the overall proportion of self-recruitment. The linkage between site proximity and the relative importance of self-recruitment warrants further study.

COASTAL COMPLEXITY

As current flows along a shoreline, it will interact with the topographic relief to generate a complex flow field across a range of length scales characterized by eddies, fronts, upwelling, jets, and convergences (Bakun, 1986; Wolanski and Hamner, 1988; Nittrouer and Wright, 1994). Closely tied to the length scale of these interactions is the time scale of the resulting flow feature. Thus, there is a non-linear interaction between coastal complexity (in terms of both topographic complexity and basin size) and the persistence or residence time of various circulation features. Although clearly subject to interactions, each component (topographic complexity, basin size and residence time) is considered separately as potentially convenient correlates of larval retention.

Topographic Complexity.—At a small scale (1 to 10 km), topographically influenced circulation has been most actively studied in areas with strong tidal currents. Tidally driven flow variability is evident around topographically complex coral islands (e.g., in the Great Barrier Reef, Wolanski, 1994; Black, 1994) and in the vicinity of headlands (Signell and Geyer, 1991). These conditions serve as mechanisms directly enhancing retention by increasing local water residence time (e.g., short-lived, largely passive larvae of corals and Crown of Thorns starfish, Black et al. 1991; Black, 1994; Sammarco, 1994). For larvae with short pelagic periods or short passive portions of the PLD (i.e., < several days), tidally generated secondary circulation may play an important role in limiting or directing dispersal (Wolanski, 1994). These features are likely less important for organisms with longer larval durations because secondary circulation such as small scale fronts and eddies often break down when the tides reverse (Hamner and Hauri, 1977; Wolanski et al., 1984; Black and Gay, 1987). However, these features can create signals

that may serve as guideposts for recruiting animals that extend some distances from the island or topographic feature (Kingsford et al., 1991; Reynolds and Sponaugle, 1999).

At mesoscales (10–100 km), coastal complexity may have a large influence on the degree of self-recruitment. Flow along the western coast of North America provides a clear example of the interaction between coastal complexity and flow (Largier et al., 1993) and its potential influence on recruitment. The coastline is composed of a series of headlands that divert the flow offshore, creating eddies in the lee of the headlands (Ebert and Russell, 1988). These eddies serve as retention-favorable areas for a variety of larvae (Wing et al., 1995a,b, 1998). Upwelling ‘shadows’ along a coast (Graham et al., 1992) may play a similar role. In the northwestern Atlantic, cod population structure has been found to occur on mesoscales reflecting the bathymetric complexity of the coast (Bentzen et al., 1996; Ruzzante et al., 1998). This structure is likely the result of local retention due to larval interactions with the resulting oceanography (Ruzzante et al., 1999). Modeling has supported this contention for scallops, cod and haddock, and similar examples exist for herring populations in the Pacific (O’Connell et al., 1998) and Atlantic (Iles and Sinclair, 1982; Shaw et al., 1999). Topographically-steered flow also may play a role in retaining larvae on isolated islands such as Barbados, West Indies (Cowen and Castro, 1994; see Cowen, in press). Although detailed genetic and/or larval and oceanographic data are rare for many other species and systems, mesoscale circulations associated with coastal bathymetry are likely to be a potent source of larval retention.

At larger scales, great distances between headlands result in relatively large reaches of coastline with potential for uninterrupted flow. Currents along these coastlines may run long distances relatively unimpeded, leading to the potential for greater dispersal of larvae and thereby diminishing the likelihood of self-recruitment. Where a cape or headland protrudes (e.g., Cape Hatteras or Pt. Conception), major currents often meet and large-scale gyres may ensue (Csanady and Hamilton, 1988). Such gyres may serve to close entire populations of organisms, such as the Slope Sea in the western North Atlantic for squid (Trites, 1983) and mesopelagic fishes (Backus et al., 1977; Olson and Backus, 1985), but at scales considerably larger than the local scale of 10s–100 km.

In summary, topographically-influenced flow likely has a key role in the distribution and retention of larvae, but the greatest effect is probably at intermediate spatial scales. Thus, increasing coastal complexity should contribute to greater opportunities for self-recruitment up to a point, then the effect of increased complexity (i.e., at small scales) will diminish the likelihood of self-recruitment except for the shortest lived larval stages.

Embayment or Basin Size.—As noted above, one means of classifying coastal complexity is by the relative size (or scale) of embayments, or basins. The relationship between embayments and self-recruitment depends on the size and openness of the basins. In the case of open basins, the relationship between degree of self-recruitment and basin scale is not linear. Small basins such as small open coves may have a low probability of larval return (i.e., larvae are readily flushed away and the probability of returning to a small point is low), intermediate sized basins may have a high probability of larval return (i.e., larvae do not leave the basin), and very large basins may have little probability of larval return (i.e., larvae are swept far away from the natal source). In the case of enclosed or semi-enclosed basins (e.g., coastal and atoll lagoons and estuaries), larval return to natal sites in small basins would be more likely than in large basins.

Atoll Lagoons.—Available evidence supports the hypothesis of increased self-recruitment in small semi-enclosed basins. For example, in the atoll lagoons of the western

Pacific, a variety of coral-reef fish species are self-recruiting based on distribution and size structure of the larvae (Leis, 1994; Leis et al., 1998) and genetic data (Planes et al., 1998). Likely retention mechanisms are reasonably straightforward: Lagoon circulation consists of inflow through deep channels and across the reef flat by wave pumping and tidal currents balanced by outflow through deep channels or across the leeward reef flat. Water exchange is limited to depths less than the outflow sill depth and vertical stratification may reinforce this limited exchange of water. However, because of wind and boundary mixing and a lack of significant freshwater inflow, lagoon waters are frequently well mixed. Wind generated surface currents cause upwelling on the windward side of the lagoon and water is fed into the upwelling zone from a deep counter-current. Strong wave pumping may, however, prevent upwelling or the deep return flow. These vertical differences in flow may assist in the retention of larvae, particularly for larvae remaining at depths greater than the outflow sill depth. Lagoon size and the number of fish species completing their pelagic phase in the lagoon are weakly related (Leis et al., submitted). However, even in a large lagoon such as Rangiroa Atoll, Tuamotu Islands (161,000 ha), probably <10% of the fish species complete their pelagic phase in the lagoon (Leis, unpubl.). Despite the seeming advantage of larval development within a lagoon, few fish species complete their larval development there.

Estuaries.—Larval transport in estuaries has been well studied. Many estuarine populations of crabs, barnacles, oysters, and fish are largely self-recruiting (Bousfield, 1955; Wood and Hargis, 1971; Cronin, 1982; Weinstein et al., 1980; DiBacco and Levin, 2000), though in these studies no direct measure was made of the spatial scale of the estuary versus the degree of self-recruitment. At least three physical processes may affect the transport of larvae within an estuarine: (1) residual two-layer circulation, (2) tides, and (3) fronts.

Deep estuaries with high river runoff and strong tides often display two-layer circulation; river runoff flows seaward at the surface, seawater flows landward along the bottom, and the residual flow is zero at the interface between these currents. Larvae capable of regulating their depth may exploit these currents to control their dispersal and increase the probability of self-recruitment. For example, during ontogenetic vertical migrations, early larval stages occur in surface currents where they are transported downstream from adult habitats, and older larval stages are transported back upstream by sinking into bottom currents. Larvae capitalizing on these flow patterns can complete their development in estuaries.

Tidal currents often mix the water column disrupting stratification. Larvae can be retained in a mixed estuary by remaining near the bottom throughout the tidal cycle or migrating higher in the water column during flood than during ebb tides. Tidally timed vertical migrations or tidal stream transport has been observed in a number of taxa. For example, post-larvae of the pink shrimp *Penaeus duorarum* enter nearshore estuarine nursery habitats by ascending into the water column for several hours in response to an increase in salinity and are thus taken shoreward in a series of tidal 'hops' with each flood tide (Hughes, 1969).

Larvae of some estuarine dependent organisms develop on the continental shelf and return to estuaries as post-larvae. Within an estuary, larval retention and export can occur concurrently indicating that passive physical processes alone are insufficient to explain this differential transport; the larvae must exhibit active behavior. Species that develop on the shelf can recruit as reliably as do species that develop entirely within estuaries,

suggesting that reliable biophysical transport mechanisms also exist in the water of the continental shelf. Coastal gyres may be associated with river discharge plumes, which may act to transport larvae away from the plumes and return them to the shore within days to weeks thus promoting self recruitment (e.g., Cochrane and Kelly, 1986; Epifanio and Garvine, 2001; see also Grimes, 2001). Evidence for self-recruitment of estuarine species that develop in coastal waters, however, remains inferential.

Large Basins.—There is almost no evidence for the scale of self-recruitment in large basins. Coastal species often are tied to some sort of habitat or circulation feature that may restrict the scale of larval exchange within large basins. For example, many cod and herring populations in the North Atlantic exist at scales much smaller than the scale of the North Atlantic basin (Sinclair, 1988; Ruzzante et al., 1998; Shaw et al., 1999; Pogson et al., 2001). Similarly, the system of eddies in the Gulf of California (Badan-Dangon et al., 1985) may enhance self-recruitment of the Gulf sardine (Hammann et al., 1988) at scales smaller than the basin itself.

The utility of the hypothesis that self-recruitment is related to the size or scale of the basin is compromised by limited evidence and the complex interactions of other factors. Thus, although the prediction is that self-recruitment would peak at intermediate basin sizes, there is no evidence of a clear relationship between basin size and degree of self-recruitment, *sensu stricto*, and more work is needed to refine and test this hypothesis.

Water Residence Time.—Residence time of the water is a factor that is related to the size of a basin as well as to other topographic or oceanographic features. However, because the relationship between basin size or topographic feature and water residence time is not necessarily linear, the variables are treated separately. If the likelihood of self-recruitment is inversely related to the rate at which larvae flux away from the natal population, the residence time of the water should play a role in retention. The probability of larval return to their natal sites should decrease in sites where water residence times are short. For example, Gaines and Bertness (1992) explained reduced barnacle settlement in Narragansett estuary in years of lower residence times due to higher freshwater flow rates.

In the open ocean, water residence time can play an important role. Loder et al. characterized the oceanography at four large banks with anticyclonic gyres. Only Georges Bank had water residence times equal to or greater than the recirculation time of the gyre suggesting that larvae might be consistently passively retained. A similar situation occurs at open ocean seamounts and islands, which interact with currents to create complex flows that may retain larvae (Boehlert and Mundy, 1993; Genin et al., 1989; Cowen, in press). At timescales relevant to larval retention (weeks to months), Taylor columns or caps (anticyclonic vortices above topographic obstacles) may be the most likely retention mechanism (Owens and Hogg, 1980; Genin and Boehlert, 1985; Tremblay et al., 1994; Barton et al., 1998). Other flow complexities, including tidal currents and eddies, upwelling along the flanks of the seamount and associated radial inflow, internal wave reflection, topographically-steered flow (Cowen and Castro, 1994), trapped waves (Brink, 1989), and eddies that remain attached to the seamount or island may also contribute to larval retention.

Residence time may vary vertically in the water column (e.g., benthic boundary layer versus surface, wind-driven layer) and spatially along a coast. Black et al. (1990) modeled the likely residence time of neutrally-buoyant material around a coral reef at scales of 100's of m, including tidal and frictional forces, and found that water may be resident

for days on portions of the reef. Although there are other physical studies of water residence times (particularly in bays and estuaries), these rarely have been directly linked to biological studies. The relative effect of the flow field on larval dispersal will depend on the longevity of the flow relative to the duration of the pelagic larval phase: the greater the longevity of the flow field, the greater its role may be in generating self-recruitment. Furthermore, the interaction of biological factors, particularly larval behavior, may upset simple physical relationships by enhancing or decreasing probability of expulsion (Morgan, 1995b; DiBacco and Levin, 2000).

In summary, it is plausible that self-recruitment is positively related to water residence time, but there is limited direct evidence to test this theory other than those studies stated above. Examining residence time for neutrally-buoyant particles seldom may be relevant because nearly all larvae are capable of vertical movements and other behaviors in the water column. Calculations of residence time with consideration of such behavioral capabilities will likely lend support to this general hypothesis, though scaling issues will continue to confound the relationship.

FLOW VARIABILITY (VERTICAL, HORIZONTAL) AND WATER COLUMN STRATIFICATION

As a medium of larval transport, water motion can be broken into advective (or flow) and diffusive (or mixing) components. Under strictly non-turbulent conditions, advective properties predominate, and these serve to advect (or carry) larvae away (i.e. unidirectionally). Such flow conditions express limited variability and would result in low larval retention. Under highly turbulent (~ chaotic) conditions, unidirectional advective properties of the flow may be reduced, and the mixing or diffusive properties can be large. Under these conditions, larvae may be highly dispersed, again not favoring retention. However, if the turbulent flow is more coherent and/or convergent, thereby reducing some of the diffusive properties, while reversing some of the advective properties (e.g., tidal reversal, eddies), the resulting transport and dispersal of larvae may be greatly reduced. It is under these conditions of variable flow that larval retention is facilitated.

Flow varies in both horizontal and vertical planes. The processes contributing to this variability also range over wide spatial and temporal scales. The flow environment of most coastal oceans is typified by tidal, wind, seasonal and/or episodic (e.g., storm generated) variability which exists in both horizontal and vertical planes. Such variability provides a variety of mechanisms by which larvae may either be retained within a certain geographical area or to which larvae may actively respond to enhance local retention. However, without the interaction of some sort of behavioral response by the larvae with the flow variability, some highly variable flow conditions might actually enhance diffusion of larvae away from natal sources by mixing. Flow on shelf systems is complex, especially in areas of high topographic complexity like coral reefs. This complexity is often not understood by biologists, and yet it offers many opportunities for both physical and biophysical retention of larvae, leading to self-recruitment.

In addition to variability in the horizontal plane, most flows exhibit vertical flow variability related to factors such as the source of forcing, rotational effects, bottom friction, geostrophic adjustment, and horizontal and vertical gradients in stratification. In conditions where the water column exhibits a two-layer stratification, the upper and bottom layers may move in opposite directions. In these situations, common in coastal oceans, the strongest component of the two-way flow is often in the cross-shore direction (Winant and Olson, 1976). These flows often are associated with the internal tide, and reverse at

diurnal, semidiurnal, or double-semidiurnal periods (Baines, 1986). By reducing mixing, such water column stratification should reduce the diffusion of passive propagules, thereby enhancing self-recruitment. If larval behavior is factored in, even greater self-recruitment may be accomplished.

Given the inherent importance of flow variability to larval transport and retention, we follow with a discussion of many of the processes that contribute to variable flow. The intent is to describe the processes and forcing mechanisms in light of examples relating to larval retention (or at least transport). Where behavior interactions can be invoked, the biophysical implications are also discussed. For simplicity, we have categorized by process and not forcing mechanism.

Upwelling/Downwelling.—Through Ekman transport, winds blowing along a coastline generate upwelling or downwelling. For example, along the West Coast of North America, north winds push the surface waters (depths $< \sim 50$ m) offshore drawing deeper waters to the surface. These denser, upwelled waters converge with the lower density surface waters offshore, creating the upwelling front. South winds, in contrast, push the lower density surface waters shoreward causing downwelling flow adjacent to the coast (Winant, 1980; Wing et al., 1995a,b, 1998). With reversals in wind direction, the flow regime quickly changes from one state to the other. During a reversal, the water adjacent to the shore is exchanged with offshore water. The traditional upwelling zones (e.g., Peru-Chile, California, Benguela and Canary Current Systems) have been most actively studied and are the most energetic, with less energetic upwelling occurring along other coasts.

Upwelling and downwelling affect both the cross and along-shore dispersal of larvae. Larvae associated with a water mass will remain adjacent to the shore as long as that water mass remains adjacent to the shore. However, upwelling, downwelling, and the transition between states are characterized by vertical currents. Although few larvae can swim against typical horizontal currents, most can swim more rapidly than vertical currents (Franks, 1992), and have behaviors that could be used to maintain a preferred depth and thus limit their cross-shore dispersal. For example, during upwelling, larvae in surface waters will be swept offshore to the upwelling front. Upwelled waters converge and sink at the front and larvae swimming upward against this sinking water will be trapped at the convergence. When the winds reverse, these larvae may be transported shoreward; the upwelling front becomes a moving convergence (see below) and may 'collide' with the shore, resulting in a recruitment pulse for coastal species. Alternatively, near the coast, larvae may be carried away from the surface by downwelling. Larvae swimming upward against this current again will be trapped in a convergence, but in this case, adjacent to shore.

Alongshore flows in upwelling/downwelling systems are typically on the order of 10s of cm s^{-1} . Larvae spawned into an upwelling event could be transported 10s of km alongshore. However, upon a reversal in the winds and the onset of downwelling, these larvae could be transported back toward the site from which they were spawned. The oscillation from upwelling to downwelling may limit the net alongshore dispersal of larvae and increase the chances that larvae settle back into their natal population.

Evidence for the adaptive exploitation of these currents generated by upwelling and downwelling is sparse. Parrish et al. (1981) suggest that many fishes associated with the California Current system spawn in winter to avoid offshore transport of larvae by coastal upwelling in summer. In the Oregon upwelling zone, ontogenetic vertical migrations maintain copepod populations close to shore. Similarly, adaptive vertical migrations have been

suggested for mero- and holoplankters. During upwelling, pelagic juvenile rockfish are distributed deeper in the water column, presumably avoiding the offshore flow and retarding their offshore transport.

Fronts.—Fronts represent the boundary between water masses and as such, are often characterized by strong horizontal gradients in biological and physical properties as well as strong vertical motions and convergent flow. Larvae or other plankton that are positively buoyant or swim upwards in response to the downwelling at the frontal convergence zone will collect and remain at the front (see review by Le Fèvre, 1986). Therefore, fronts may act as a barrier to the dispersal of larvae, but because they are often ephemeral, their formation and persistence varies with the season, tides, and the weather, and their effectiveness as a retention mechanism depends on the timing of reproduction and larval duration. To be effective, larvae must be released when a front is present and the front should persist during a major portion of the PLD for passive taxa or of the passive portion of the PLD for active taxa.

Fronts at the mouth of estuaries (estuarine plume fronts) usually form during ebb tides when lower density estuarine water flows out into the ocean; a front forms between these estuarine waters and the higher density seawater (Grimes and Finucane, 1991; Govonni and Grimes, 1992; Largier, 1993; O'Donnell, 1993). Because estuarine plume fronts dissipate and reform with the changing tides (e.g., Kingsford and Suthers, 1994), evidence that they act as a barrier to dispersal from estuaries is limited and mixed. Perhaps the best evidence that estuarine fronts can limit passive dispersal is the finding by Tyler et al. (1982) that the distribution of red-tide dinoflagellates was sharply limited by a frontal boundary that kept them within the estuary during summertime bloom conditions. In addition to serving as a barrier, fronts also may funnel surface-dwelling post-larvae into estuaries from adjacent coastal waters (Kingsford and Suthers, 1994; Eggleston et al., 1998). At the mouth of estuaries during flood tides, axial fronts form parallel to shore. Post-larvae may be advected along these fronts and into the estuaries thereby facilitating recruitment to adult populations.

Fronts parallel to shore found over the continental shelf (e.g., shelf break fronts, upwelling fronts, and shallow sea mixing fronts) may limit the extent of the offshore dispersal of larvae, but because they do not limit the alongshore dispersal of larvae, these fronts may be relatively unimportant in promoting the self-recruitment of populations. Topographically generated fronts, if they persist long enough, may constrain both the along and cross-shore dispersal of larvae and, hence, may play an important role in self-recruitment. For example, if 'upwelling shadow' fronts (fronts that form on the lee side of points in upwelling systems) act as a barrier to larval dispersal, they could trap larvae in the waters immediately adjacent to the lee side of a point.

Moving Convergences.—Moving convergences can transport larvae shoreward. The most ubiquitous type of moving convergence is that caused by tidally generated internal waves. The tide ebbing off the shelf or flowing across a bank or reef generates a lee wave. With the reversal in the tide, the lee wave is 'released' and propagates shoreward or across the reef as a soliton or non-linear internal wave. As the wave propagates, the original lee wave evolves into a set of solitons. Flow over the top of the waves generates a convergence zone that travels along with the propagating waves. If the tidal currents are large enough, the leading wave of the set can break, forming an internal bore. Internal bores can transport a mass of water shoreward causing a form of upwelling. Although larvae in near bottom waters may be caught up in the bore and carried shoreward, larval

transport by internal bores has received little attention. These large tidally generated internal waves and bores are common in all oceans (e.g., Leichter et al., 1998).

To be transported by a moving convergence an organism must behaviorally remain in the convergence despite the vertical currents present there. A large diversity of organisms are concentrated in moving convergences and transported by them. Most of these organisms are late-stage larvae or post-larvae that can remain in the convergence through buoyancy or by vertical swimming (Le Fèvre, 1986; Larson, 1992; Franks, 1992), and be carried shoreward along with the moving convergence.

Moving convergences alone may have little affect on self-recruitment. However, where hydrography limits alongshore larval dispersal, moving convergences may play an important role in transporting larvae back to the coast where they may recruit into their natal population. Because internal waves are refracted by the bottom topography, a greater number of larvae may be transported shoreward along stretches of coastline where waves are focused. Local retention of larvae by the offshore hydrography coupled with differential transport by internal waves may lead to alongshore differences in the amount of self-recruitment.

Ocean Eddies.—Eddies frequently have been proposed to enhance larval retention along continental shelf systems and near islands. Based on extensive physical oceanographic measurements, Lee et al. (1994) and Lee and Williams (1999) hypothesized that the cyclonic circulation of the Tortugas gyre in combination with surface Ekman transports and coastal counter-currents promotes retention of locally-spawned larvae along the Florida Keys. Spin-off eddies of the Florida Current may help retain and transport reef fish larvae to inshore settlement (Limouzy-Paris et al., 1997). As with other oceanographic processes, for retention to occur, the temporal scales of the eddy must correspond to the length of larval life or at least the pre-effectiveswimming phase. Larvae must be transported into the eddy, remain there for their larval period, and then be transported back to suitable juvenile habitat by the end of the larval period.

Island wake eddies have received much attention as potential retention mechanisms (Sale, 1970; Lobel and Robinson, 1988; Boehlert et al., 1992; Barton, 1998). Flow in the lee of islands can take the form of an eddy or be broadly unorganized (e.g. Pingree and Maddock, 1980; Heywood et al., 1990; Graham et al., 1992; Wolanski, 1994). Either flow regime may enhance localized retention of larvae (sensu Hamner and Hauri, 1981; Wing et al., 1995a,b). Some island wakes clearly have enhanced primary production and abundances of larval fishes, and feeding of the larvae and their condition is enhanced in these areas (e.g., Emery, 1972; Boehlert et al., 1992; Barton et al., 1998; Rissik and Suthers, 2000). This suggests that the wakes are not only sites of larval retention, but also sites of increased growth and survival of larvae, and this should lead to enhanced self-recruitment. However, other eddies contain very few larval fishes (see Lobel and Robinson, 1988). The degree to which eddies truly retain larvae and contribute to self-recruitment is unknown.

Counter-Currents.—Current systems are often bordered by shear-driven counter-currents (e.g., the equatorial and subtropical counter currents). Nearshore current systems such as the California Current have both nearshore (e.g., the Davidson current) and deep counter-currents. Such counter currents play a role in maintaining oceanic zooplankton communities (McGowan, 1972) and also may influence larval retention (Parrish et al., 1981). For example, counter-currents may retain lobster larvae inshore of both the East Cape Current off New Zealand and the Kuroshio Current off Japan.

Although not considered in the literature, without variability in alongshore flow, many larvae would tend to be advected unidirectionally away from the natal source. For example, larvae that make extensive vertical migrations may migrate between counter currents, limiting their alongshore transport. Pelagic juvenile splitnose rockfish, *Sebastes diploproa*, spend up to a year in the California Current, where they generally are transported southward. Prior to recruitment, they migrate to midwater depths, where they are transported northward and shoreward by the deep undercurrent. It is clear that unidirectional flows are not an accurate depiction of ocean circulation. Rather, the inherent flow variability that exists in the ocean may lead to considerable capacity for restricted larval dispersal. At the extreme, however, highly variable flows will be totally chaotic (e.g., storm conditions), sharply increasing the loss of propagules and reducing the likelihood of self-recruitment.

SUMMARY: BIOPHYSICAL LARVAL RETENTION

The degree to which marine populations are 'open' is dependent upon a complex blend of biological and physical factors. The interplay between behavior and physics results in larval distributions that are non-random and often occur as species-specific patterns at varying distances from the source population. The analysis of such larval assemblages (Boehlert and Mundy, 1993; Leis et al., 1998) in light of physical correlates often provides the strongest inferential evidence of retention, because the specific processes creating the assemblages are difficult to observe and have only recently been studied in detail (e.g., Werner et al., 1993; Paris and Cowen, in prep.).

Although many of the above correlates a priori (or empirically) predict self-recruitment, some probably are more important than others and none can be considered in isolation. Furthermore, some of the correlates are inter-dependent (e.g., water residence time and basin size; fecundity and parental investment). Adult characteristics that most influence larval position in the water column are temporal and spatial patterns of spawning, both of which likely contribute to self-recruitment. There is little doubt that larval behavior, including vertical positioning and horizontal swimming ability, is critical to estimates of self-recruitment. Pelagic larval duration clearly influences larval transport and the chance of retention, but as a correlate, it may be primarily useful for organisms with very short larval durations. Physical processes such as flow variability will significantly influence larval retention, while water residence time is probably only applicable for species with very short larval periods or those living in enclosed basins or estuaries, and site isolation is only useful for highly isolated habitats. Biophysical retention is achieved through the interaction of multiple biological traits with multiple physical processes thus many of these variables will have little predictive value when considered in isolation. The interaction of these variables may be additive or synergistic.

Physical factors that result in departure from unidirectional, depth-uniform water flow provide the opportunity for retention of larvae, and therefore self-recruitment. These physical factors are very common in the ocean and vary in intensity among locations and times. Some enable retention of passive larvae (physical retention), whereas others lead to retention only with active behavioral input by the larvae (biophysical retention). Larval behavior that can contribute to or result in retention or return to natal sites ranges from simple vertical orientation that is within the capabilities of the larvae of most taxa to complex sensory abilities and strong swimming that are known to occur in larvae of

relatively few taxa, particularly decapod crustaceans and fishes. For all taxa, both the pelagic larval duration and the time to behavioral competency will have a strong influence on likelihood of self-recruitment.

Recent work shows that larvae of some taxa have behavioral capabilities that were unexpected a few years ago. Increasing evidence indicates that at least fish and crab larvae are very flexible in their behavior. For example, larvae of coral reef fishes alter their swimming depths in different environments (lagoon vs ocean or on different sides of the same island) and swim faster in open water than adjacent to reef settlement sites, or swim faster in some directions than in others (see review in Leis and McCormick, in press). Behavior also is flexible across a species' range. The timing of larval release and vertical swimming by crabs changes seasonally and across tidal regimes in response to changes in the phasing of tidal and light-dark cycles (Morgan, 1994, 1996a,b; Schell, 1996; Anastasia, 1999). The ability to adjust behavior to different situations in time and space should greatly enhance survival, retention and self-recruitment.

Until the direct estimates of self-recruitment in marine populations becomes widely feasible (see Thorrold et al., this issue), it often will be necessary to gather indirect evidence of self-recruitment and attempt predictions, such as those described above. On the other hand, estimates alone will not reveal the biophysical mechanisms by which self-recruitment occurs, and without knowledge of these mechanisms, generalizations will be impossible. Further study into the role of these various processes will help to focus our attention on mechanisms that are the most important contributors to controlling the scale of population connectivity in marine populations. The predictions outlined here are meant to serve as a point of departure—primarily for gathering data to test such relationships but also for estimating the potential for self-recruitment. Knowledge in this area necessitates both progress in direct estimates of self-recruitment and an understanding of the mechanisms by which it occurs. Understanding the relative importance of self-recruitment to local marine populations is a precursor to addressing fundamental ecological and evolutionary questions (see also Strathmann et al., this issue), as well as issues critical to the successful management and conservation of marine populations.

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