p. 411-427. In: The Ecology of Marine Fishes: California and Adjacent Waters. 2006.
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CHAPTER 15

Recruitment

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Introduction: The Ecological Consequences of a Bipartite Life History

The vast majority of demersal[1] marine fishes have a bipartite life history, in which benthic adults produce pelagic offspring capable of dispersing great distances from their parental population (Sale, 1980; Leis, 1991; Booth and Brosnan, 1995; Caley et al., 1996). Consequences of this life history for the population and community ecology of marine fishes are striking. In marked contrast with the life history of terrestrial vertebrates, whose young disperse short distances and contribute directly to the replenishment of their parental populations, the great dispersal potential of many marine fish larvae can decouple the local production and recruitment of young to that adult population (see recent arguments to this widespread perception for coral reef fishes by Cowen et al., 2000; Cowen, 2002; Leis and McCormick, 2002; Planes, 2002; Swearer et al., 2002). Thus, at the scale of local populations, recruitment of young fish from the pelagic larval phase to benthic adult populations is the marine equivalent of births, but can be largely dependent upon the production and dispersal of larvae from parental populations elsewhere (fig. 15-1). By extension, events that influence larval production and dispersal from one population can have strong influences on the dynamics and structure of populations elsewhere. This connectivity among local populations through the dispersal and recruitment of pelagic larvae sets the spatial scale of ecological interactions among fish populations.

Together, spatial and temporal variation in recruitment can have profound effects on the distribution, dynamics and spatial, size, age and genetic structure of reef fish populations. It is not surprising, therefore, that the concept and study of recruitment has long been central to our understanding of demersal fish population and community dynamics and fisheries science. The purpose of this chapter is to explain what fish recruitment is, why it is important, what we know about it for nearshore fishes of California, what we do not know but need to know, and how this information is important with respect to management and conservation.

What Is Recruitment and Why Is It Important?

Recruitment, broadly speaking, is any addition of new individuals to a population. As an ecological concept however, the term has a range of different meanings. For ecologists, interested in the overall structure and dynamics of local populations, recruitment is conceptually equivalent to the addition of new individuals as they enter a local population of demersal juvenile and adult fishes. Recruitment of young to a local population occurs at birth for most viviparous (i.e., live bearing) species such as some sharks, rays and the surfperches (family Embiotocidae), or at the transition from the pelagic to the benthic environment (i.e., settlement) for some primitively viviparous (e.g., rockfishes of the genus *Sebastes*) and most oviparous and ovoviviparous species (fig. 15-2, settlement).

Because of the difficulty of accurately quantifying rates of births and settlement (both of which often occur at night and usually involve very small, transparent organisms), ecologists often define recruitment operationally as the number of individuals recorded at some predefined stage subsequent to birth or settlement, thereby incorporating post-settlement mortality and movement in that estimate (Keough and Downes, 1982; Levin, 1994a). One common application of this measure of recruitment is to describe interannual variation in the number of individuals that have settled and persisted to accumulate at the end of each annual recruitment season (fig. 15-2, Post-settlement). Moreover, the young of many fishes settle from the pelagic habitat to spend time in "nursery" habitats (sensu Beck et al., 2001) such as estuaries and coastal seagrass and kelp beds (Baskin et al., 2003), before migrating to adult populations, thereby recruiting first to nursery habitats, and adult populations several months later (Love et al., 1991; Gillanders et al., 2003). However, because the period soon after settlement to the bottom is typically a time of high mortality, the magnitude of recruitment under this definition is strongly influenced by the time interval between settlement and measurement of recruitment (Booth, 1991; Caley et al., 1996; Hixon and Carr, 1997; Steele and Forrester, 2002). Fisheries

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[1] Demersal refers to fishes that live in close association with the bottom regardless of substratum type. The scope of this chapter is limited to demersal species, excluding the many more highly mobile pelagic species that inhabit the coastal waters of California.

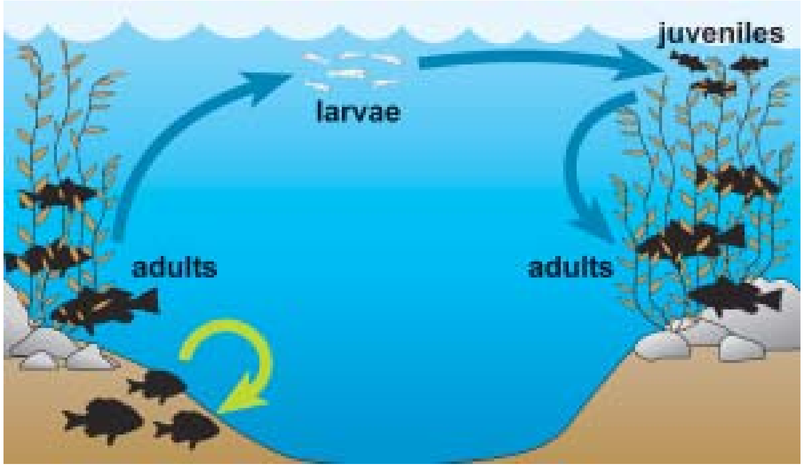

FIGURE 15-1 Consequences of offspring dispersal distances for the spatial structure of demersal fish populations. For species that produce eggs or larvae capable of being transported long distances by ocean currents (e.g., the kelp bass, *Paralabrax clathratus*), replenishment of local populations is determined by the survival, transport, delivery and settlement of young produced elsewhere. Such populations are referred to as open populations. In contrast, for those species that produce young that disperse little and remain within the parental population (e.g., the black perch, *Embiotoca jacksoni*), replenishment is determined by local offspring production. Such populations are referred to as closed populations. The two examples illustrate extremes in the continuum of openness of populations, which is also determined by the spatial scale at which populations are defined. The greater the spatial scale at which a population is defined, and encompasses the scale of larval dispersal, populations become more closed (i.e., self-replenishing). By defining populations (stocks) at these broader spatial scales, fisheries biologists manage large-scale, self-replenishing populations.

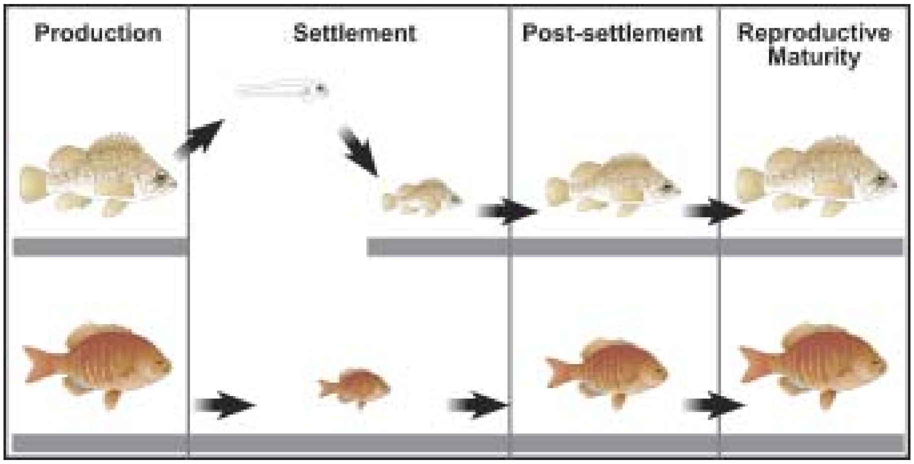

FIGURE 15-2 Recruitment can have a range of definitions. A typical demersal reef fish produces planktonic larvae by releasing eggs into the water column, hatching demersal eggs, or extruding larvae (top panel). Because of the great dispersal potential of planktonic propagules, these offspring often disperse from parental populations to replenish populations elsewhere. The transition from the pelagic existence to a benthic existence often corresponds with metamorphosis of form in a phase known as settlement. Ecologists have generally examined recruitment at some time subsequent to settlement (i.e., when the juveniles can be sampled). Recruitment can also be considered as the stage at which an individual matures and joins the breeding population, whereas fishery biologists typically consider the attainment of harvestable size as recruitment to a fishery. In advanced viviparous live-bearers such as surfperches (lower panel), the young are extruded and immediately commence a demersal existence within the same parental population (depicted by the continuous bar representing benthic habitat). For such species, recruitment is equivalent to the terrestrial ecologists concept of births.

scientists often consider recruitment to be the stage at which a fish reaches a harvestable size, both because their interest is focused on the number of individuals entering a fishery as it relates to forecasting future catch rates and because their estimates are often reliant on fishery-dependent sampling.

In contrast with all of the above, population modelers interested in long-term dynamics might consider recruitment to be the stage at which a fish reaches reproductive age and size and begins to contribute to subsequent generations (fig. 15-2, Reproductive maturity). Thus, recruitment, including births within a population as well as immigration of larvae or older stages, is the addition of individuals to a population and is countered by losses from mortality or emigration. It is critical, therefore, that any discussion of recruitment clarify these definitions.

Local Population Structure, Dynamics and Distribution

At the most basic level, recruitment of larvae or juveniles is important because it is the principal source of population replenishment, and without replenishment any population will ultimately become extinct (excepting immigration at small spatial scales). The importance of this recruitment to the structure and dynamics of fish populations depends on a complex combination of its magnitude and variability, the size and variability of the benthic population, and the extent to which post-recruitment processes dampen or modify recruitment variation. Both the magnitude of and variability in recruitment will have strong effects on adult population size and persistence (see articles cited in reviews by Doherty and Williams, 1988; Doherty, 1991, 2002, Olafsson et al., 1994; Caley et al., 1996; Armsworth, 2002; Forrester et al., 2002; Hixon and Webster, 2002; Osenberg et al., 2002). If low and variable (relative to resource availability), recruitment can limit and determine population size below levels at which resources are limiting (i.e., recruitment limitation, sensu Doherty, 1981; Victor, 1986a). However, if high (relative to resource availability), recruitment can saturate resources and density-dependent post-recruitment processes contribute more to spatial and temporal variability in population size. Thus, to understand the role of recruitment in determining or contributing to the spatial structure and temporal dynamics of fish populations requires a full understanding of recruitment (pre- and post-settlement) and post-recruitment processes. Recognition of this is reflected in the growing number of conceptual and analytical models that explore the relationships among these processes (Armsworth, 2002; Doherty, 2002; Forrester et al., 2002; Hixon and Webster, 2002; Osenberg et al., 2002, and articles cited therein).

The recruitment of demersal fishes fluctuates at many scales of space and time. Within a single breeding season, births, settlement, or recruitment to the reef can occur in a single pulse, a range of pulses or as an apparently chaotic or stochastic process (Pfister, 1996; Dixon et al., 1999; Findlay and Allen, 2002; Davis and Levin, 2002; Steele et al., 2002). Recruitment can also vary between seasons, even when the spawning stock does not vary appreciably. The many examples of interannual and decadal variation in recruitment of California fishes (e.g., Cowen, 1985; Stephens et al., 1986; Schmitt and Holbrook, 1990; Anderson, 1994; Carr, 1994a; Ralston and Howard, 1995; Pfister, 1996; Holbrook et al., 1997; Love et al.,1998a; Hobson et al., 2001), reflect the great temporal variability in recruitment of marine fishes in general (Rothschild, 1986; Houde, 1987; Doherty and Williams, 1988; Sinclair, 1988; Doherty, 1991; see contributions in Chambers and Trippel, 1997). Likewise, the variety of species for which recruitment has been shown to vary markedly over scales of 10s of meters (Larson, 1980a; Ebeling and Laur, 1985; Behrents, 1987; Carr, 1989, 1991; Steele, 1997a,b; Steele and Forrester, 2002; Hartney and Grorud, 2002; Findlay and Allen, 2002) to 100s of meters (Larson, 1980a; Carr, 1994a; Anderson, 1994; Pfister, 1996) are representative of the diverse fish fauna of California. This fine scale variability in combination with larger dispersal scales is likely to decouple local production from the number of juveniles entering a local population. Consequently, stock-recruitment relationships are unlikely to exist or be detectable at scales less than typical larval dispersal distances. These points emphasize the importance of broadening the spatial scale at which ecologists typically study the relationships between recruitment and other demographic processes.

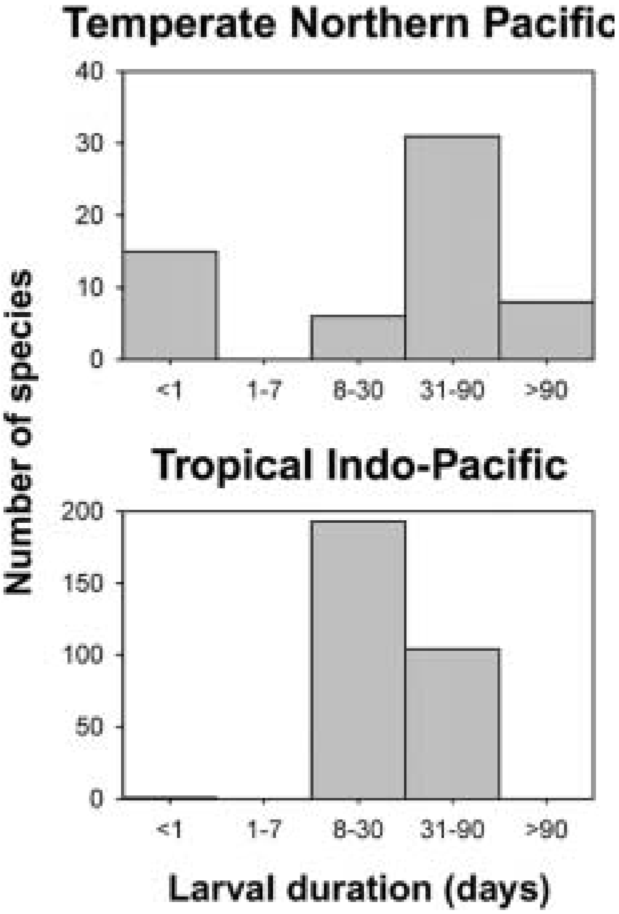

FIGURE 15-3 Larval durations of temperate rocky reef and tropical coral reef fishes from the northeastern Pacific and indo-Pacific, respectively. Differences in sample size reflect differences in larval duration estimates between the two regions. With the exception of the viviparous surfperches, larval duration in temperate fishes is longer, implying greater dispersal potential. Larval duration estimates were compiled from Brothers et al. 1983, Brothers and Thresher 1985, Victor 1986b, Thresher et al. 1989, Wellington and Victor 1989, Cailliet et al. 2000, and Krigsman 2000.

Regional Population Structure, Distribution and Persistence

At larger spatial scales (10s–100s of km), regional populations of benthic juveniles and adults are comprised of multiple local populations, more or less connected with one another by the dispersal and recruitment of larvae. Some evidence suggests that larval dispersal is sufficient to exchange recruits among local populations over a broad regional population. To the extent that larval duration reflects realized dispersal distances, the pronounced larval duration of many California marine fishes suggests substantial connectivity (i.e., dispersal and recruitment between local populations). Existing reviews of larval duration suggest that, as a whole, larval durations for California rocky reef fishes are shifted more toward longer durations than coral reef fishes (fig. 15-3). Three lines of evidence suggest that longer larval duration results in greater dispersal distance. First, there is a general positive relationship between estimates of larval duration and dispersal distance (Shanks et al., 2003). Second, recruitment patterns are often correlated with large-scale oceanographic features that have the potential to transport larvae great distances from source populations. For example, Cowen (1985) found that recruitment to local populations of California sheephead (*Semicossyphus pulcher*) in the northern portion of the Southern California Bight corresponded with El Niño events. He suggested that northerly shifts in currents during these events transported larvae from populations along Mexico to the northern portion of the Bight. Finally, studies of the genetic structure of populations designed specifically to estimate dispersal distances suggest long distance dispersal distances for many species, particularly for fishes (Kinlan and Gaines, 2003; Palumbi, 2003). Nonetheless, a growing number of studies suggest that dispersal distances may be substantially shorter than predicted by larval duration (Swearer et al., 2002) and tools to better estimate the extent of realized dispersal distances are developing rapidly, as are interdisciplinary approaches for determining the physical and behavioral processes that determine dispersal (Thorrold et al., 2002). With the advent of such tools and approaches, the ecology of larval dispersal is clearly one of the most exciting fields in marine fish ecology.

In combination, the heterogeneous spatial structure of regional fish populations and larval connectivity among local populations has important implications for how recruitment and local population dynamics might scale-up to influence the dynamics and persistence of regional populations (Chesson, 1981, 1996, 1998; Armsworth, 2002; Carr et al., 2002; Cowen, 2002; Forrester et al., 2002). This interest in the potential influence of local-scale population processes on regional population dynamics stems from the growing theory on metapopulations and other spatially-structured populations. Much of this theory indicates that the extent to, and manner by, which local population dynamics influences regional population dynamics and regulation[2] is determined by the rates and distribution of larval connectivity among populations, temporal asynchrony in dispersal, recruitment and mortality among populations, and the strength of local density-dependence in larval production and recruitment (Hanski and Gilpin, 1997; Armsworth, 2002). Because larval production and recruitment of at least some California fishes, like many coral reef fishes, are spatially variable and density-dependent (see *Post-settlement Processes* section) and dispersal distances of many species appear to span the spatial scales of regional populations, the persistence of regional fish populations may be strongly influenced by local production, dispersal and recruitment.

Community Structure and Dynamics

The interactions between spatial and temporal variability in larval fish recruitment is central to several models hypothesized to explain the structure, dynamics and persistence of fish communities. Several of these models are direct extensions of models of population dynamics. For example, if population sizes of species constituting a local community are each limited by larval recruitment (and early post-settlement mortality is density-independent), such that their combined abundance remains below that which saturates resources and induces interspecific competition, then their combined and separate population sizes will largely reflect temporal variation in larval recruitment. This competition-free coexistence of a fish assemblage can reflect limited larval supply, primary recruitment limitation (Doherty, 1981), or early and rapid declines in recruit density caused by post-settlement predation, secondary recruitment limitation (Victor, 1986a).

Two related lines of evidence that settlement can be limited by larval supply are provided by studies of the recruitment of kelp bass, *Paralabrax clathratus*, and opaleye, *Girella nigricans*, at the Palos Verdes Peninsula in southern California. In 1987, kelp bass recruitment was strongly and positively correlated with giant kelp density at Santa Catalina Island, but recruitment of kelp bass to kelp beds off Palos Verdes Peninsula was almost nil (Carr, 1994a). Similarly, recruitment of pelagic juvenile opaleye occurred in rocky tidal pools along the coast south of Palos Verdes but was not observed at the Peninsula (Norris, 1963). Norris hypothesized that internal waves transported larval and post-larval opaleye onshore and speculated that recruitment of opaleye at Palos Verdes was preempted by offshore advection and the destruction of internal waves caused by the persistent coastal upwelling characteristic of that area. Not until 20 years later did Shanks (1983, 1988) cleverly examine and support Norris' hypothesis that internal waves transport fish larvae onshore, providing some support for this mechanism of limited recruitment of opaleye at Palos Verdes. In addition, at least one study suggests that population densities of an assemblage of subtidal sculpins in the San Juan Islands exist below levels at which resources (food or space) are limiting (Norton, 1991). However it is unclear if these population densities are limited by larval recruitment or post-settlement mortality.

Recruitment need not be limiting to structure fish assemblages. If recruitment rates are sufficient to saturate free space, but free space is limiting and becomes available unpredictably, and if there is little difference in competitive ability between species, then community structure may appear to be an unpredictable lottery. This lottery hypothesis (Sale, 1991) predicts a cap on total number of individuals in a community, but the relative abundance of species will vary unpredictably over time, and is contingent on recruits being readily available. Few studies have tested both the required assumptions and predictions of this hypothesis for temperate fish assemblages, but those that have looked at the relative effects of variable recruitment, or the resilience or predictability of assemblages have suggested a more deterministic assemblage structure (e.g., Pfister, 1996; Steele, 1997a, 1997b; Steele et al., 1998; see studies reviewed in chapter 17, and Stephens and Zerba, 1981).

The lottery model (vs. lottery hypothesis) and storage effect are extensions of the original lottery hypothesis (Warner and Chesson, 1985). With similar assumptions regarding limiting resources, this model posits that changing environmental conditions favoring recruitment of each species relative to others maintains coexistence despite their competitive equality. The model is similar to Hutchinson's gradual change hypothesis, but focuses on the changing relative strengths of larval recruitment over time to keep each species from becoming competitively excluded. Assuming that favorable recruitment conditions occur sometime during the lifespan of adults and that larvae can be produced to take advantage of favorable

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[2] Regulation refers to the maintenance of a population over time, within limits set by demographic rates such as births and deaths that change in magnitude as a function of population density. This relationship is referred to as density-dependence.

recruitment conditions (i.e., the potential for larval recruitment is stored from one favorable recruitment event to the next over the lifespan of adults), species persist in that assemblage between bouts of larval replenishment. One possible scenario by which this mechanism contributes to coexistence of kelp forest fishes is the ever-changing composition of macroalgal assemblages on rocky reefs (in time and space) and observed differences in recruitment strength of these species in response to different states of these algal assemblages (Carr, 1994a). Some species recruit to dense canopies of giant kelp, others to sparse stands, and others to the algal understory that flourishes in the absence of giant kelp (Carr, 1989; Anderson, 1994). If not excluded by interspecific competition, these species persist between replenishment events associated with changes in algal composition caused by storms and other disturbances.

In contrast with these non-equilibrial hypotheses, in which species composition varies unpredictably over time in response to temporally stochastic recruitment events, are hypotheses that predict stable assemblage structure reflecting predictable relative magnitudes of recruitment. The niche diversification hypothesis assumes that each species is competitively superior in specific niches (particular combinations of environmental conditions and resource states). In the context of recruitment, this hypothesis predicts that recruits of a species will exhibit competitive advantages (or at least differential survival) over recruits of other species under certain environmental conditions, resulting in a partitioning of limited resources (and differences in recruitment) within the assemblage. Tests of this hypothesis are few because of the requirements of demonstrating interspecific competition and resource partitioning (see chapter 17) among recruits. In some cases, where recruitment directly reflects adult distributions (e.g., the young of live bearing surfperches), putative patterns of partitioning may reflect resource partitioning of adults. The depth-related zonation of adult striped seaperch, *Embiotoca lateralis*, and black perch, *E. jacksoni*, where these two species co-occur in sympatry results in similar zonation of their newborn young (S. Holbrook, pers. comm.). In contrast, where the two common gobiids, *Rhinogobiops nicholsii* and *Lythrypnus dalli*, co-occur experimental manipulations indicate no substantive effects on the recruitment of one another (Steele, 1997a). Differences in the timing of recruitment, largely driven by the timing of reproduction, might reflect temporal partitioning of limited nursery resources among species. Year-to-year constancy in the seasonal order of parturition and recruitment of juvenile rockfishes to kelp canopy habitats, in which copper, *Sebastes caurinus*, gopher and black and yellow (*S. carnatus* and *chrysomelas*, respectively), and kelp (*S. atrovirens*) rockfish exhibit lagged peaks in recruitment over the duration of the recruitment season may reflect temporal partitioning of the canopy habitat (Anderson, 1983; Carr, 1991), although such temporal patterns may reflect other ecological processes as well.

Our understanding of the role of recruitment in structuring temperate fish assemblages lags far behind that of coral reef fish ecologists, where the role of recruitment has been a central focus (Sale, 1991, 2002). Further tests of these alternative hypotheses and how their applicability varies across varying environmental conditions in time and space is an enormously fertile direction of study in temperate fish assemblages. Determining the sources of variability in recruitment and how their contributions vary and interact in time and space is fundamental to understanding population persistence and community structure and dynamics.

Processes that Contribute to Spatial and Temporal Variation in Recruitment

Variability in recruitment has been demonstrated to be important in both theoretical and empirical studies. Spatial and temporal variation in the distribution and rate of replenishment of demersal populations will reflect environmental and ecological processes that act prior to the delivery of potential recruits to a population (the pre-settlement phase), during the transition from pelagic to benthic existence (the settlement phase) or at any point subsequent to settlement (the post-settlement phase; Richards and Lindeman, 1987). Moreover, processes occurring in one phase of the recruitment process can interact synergistically with those operating during other phases to generate patterns that might be difficult or impossible to explain by studying each phase in isolation. The difficulty in understanding recruitment dynamics reflects not only the complexity of the life history of demersal fishes, but also the diversity of factors that cause variation in recruitment and the multitude of spatial and temporal scales over which these processes act (fig. 15-4). To understand the absolute and relative effects of the many biotic and abiotic processes that influence larval production, pelagic dispersal and survival, settlement and post-settlement survival requires research programs that examine these processes at spatial scales from meters to 100s of kilometers and temporal scales from hours to centuries.

Pre-settlement Phase: Sources of Variation in the Dispersal and Delivery of Potential Recruits

Prior to settlement to the adult population, processes that contribute to spatial and temporal variability in the distribution and magnitude of recruitment include larval production, dispersal, mortality and condition of eggs and larvae in the pelagic environment (fig. 15-1).

SPATIAL AND TEMPORAL VARIATION IN LARVAL PRODUCTION

As a source of recruitment variation, larval production has received little attention. One reason for this has been the perceived decoupling of local production and recruitment, particularly given the disparate scales of local variation in adult fecundity, and the scale at which the larval pool is thought to replenish local populations. Another reason is that estimated relationships between stock and recruitment in the fisheries literature are frequently weak, suggesting that the high and variable mortality of pelagic eggs and larvae obscure any relationship between production and recruitment. Additionally, the relative magnitude of year-to-year variability in larval production is thought to be much less than that of recruitment, suggesting that other sources of variation are more influential. Recent studies, however, indicate that production might in fact be more important than previously thought.

The perception that variability in local larval production does not scale to or reflect variation in the size of the larval pool from which local recruitment is received, is contingent on the spatial scale of processes that influence larval production and recruitment. If larval production is in fact either autocorrelated or forced by large-scale processes, then estimates of production at the local scale can reflect larger scale variation in production. Although very few studies of temperate fishes have explored this approach, one example of its

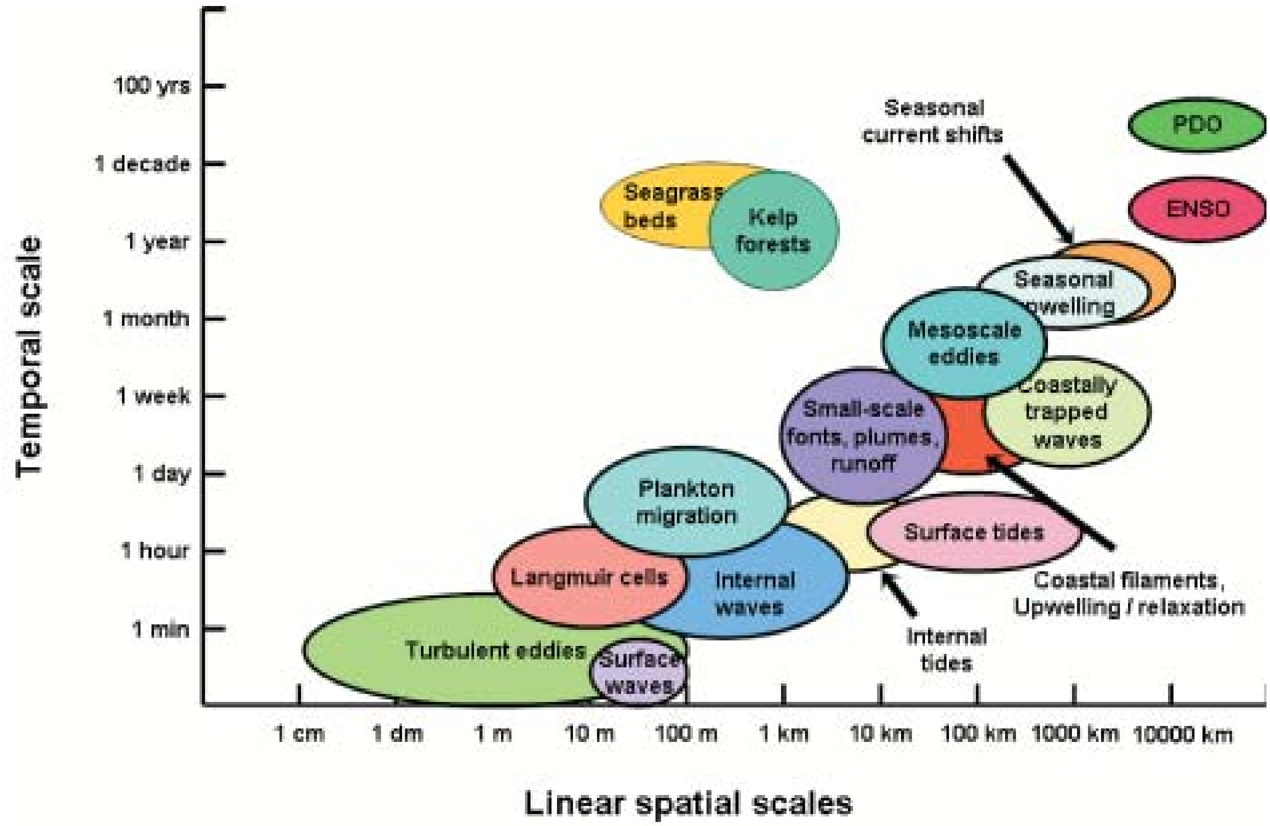

FIGURE 15-4 The multitude of biotic and abiotic processes that influence larval production, pelagic dispersal and survival, settlement and post-settlement survival of demersal fishes act across a daunting array of spatial and temporal scales. Physical oceanographic and geomorphological features, along with species interactions, influence both the productivity and resources available across benthic habitats, which in turn influence larval production and the settlement and post-settlement survival of recruits. Likewise, physical-biological coupling in the pelagic environment causes variation in the transport and survival of eggs, larvae and pelagic-juveniles.

potential merit has been demonstrated for coral reef fishes (Robertson et al., 1988). Evidence that larval production is influenced greatly by regional scale climatic events comes from responses of both local and regional production to episodic and longer-term large-scale environmental variability. For example, during episodes of low productivity corresponding with the El Niño events of 1982–1983 and 1992–1993, both fecundity and recruitment of some rockfishes in central California were greatly depressed (Lenarz and Echeverria, 1986; Lenarz et al., 1995; VenTresca et al., 1995). Likewise, both fecundity and recruitment of an intertidal sculpin, *Clinocottus analis*, in southern California were depressed during the 1997–1998 El Niño (Davis and Levin, 2002). Long-term (one or more decades) effects of climatic change and corresponding responses of both biological productivity and larval production may also explain decade-long periods of poor recruitment. For example, long-term declines (from the late 1970s to the early 1990s) in recruitment of many reef fish species throughout the southern California Bight are thought to reflect negative trend¡s in coastal productivity, resulting in declines in larval production and survival (Holbrook et al., 1997; Love et al., 1998a,b; Brooks et al., 2002).

Concurrent with these environmental sources of decline in larval production were declines in some spawning stocks that have been attributed to fishing (Love et al., 1998b). Because species with more northern distributions (e.g., rockfishes) responded more strongly to these causes of decline than those with more southern distributions, the structure (i.e., relative abundance) of fish assemblages changed over this period. For example, on a rocky reef in the Santa Barbara Channel, recruitment of species with cooler water affinities such as blue rockfish, *Sebastes mystinus*, gradually declined over a period of warming from 1977 through 1982, while recruitment of a warmer water species, the blue chromis, *Chromis punctipinnis*, increased (Ebeling and Hixon, 1991). Similarly, long-term (8-year) patterns of recruitment of two species of rockfish to soft bottom habitats in southern California were inversely related to one another, leading investigators to conclude that years of cooler water temperatures favored recruitment of one species, *Sebastes saxicola*, while warmer years favored recruitment of the other, *S. dalli* (Mearns et al., 1980). Although these large-scale patterns of recruitment confound larval production and dispersal processes, that they may reflect region-wide temporal patterns in larval production is suggested by persistent large-scale (e.g., latitudinal) differences in larval production (Eldridge and Jarvis, 1995), which likely explain persistent regional patterns of larval abundance along the California coast (Moser and Boehlert, 1991).

In contrast with region-wide coherence in environmental conditions and larval production, smaller scale variation in environmental conditions contributing to differences in production and quality of offspring between local populations can be substantial. One example is the strong differences in production of young among local populations of both striped seaperch and black perch along the coast of Santa Cruz Island (Schmitt and Holbrook, 1990). These differences were thought to reflect responses of adult fecundity of each species to variation in local prey availability, related to differences in the local macroalgal assemblages at each site. Similarly, variation in the nutritional components (e.g., protein, lipids, esters) of yellowtail and shortbelly rockfish eggs and larvae at birth varied 2–3 fold between populations inhabiting three submarine canyons off northern California (MacFarlane and Norton, 1999). Thus, while episodic or long-term variation in recruitment at the regional scale may reflect region-wide coherence in responses to changes in productivity and larval production at that scale, differences in environmental conditions and larval productivity between local populations may result in marked differences in their relative contributions to the regional larval pool within and between years. Our understanding of the extent, causes and potential consequences of this variation has been hampered both by the paucity of studies that have examined it, and by the difficulty of decoupling larval production and mortality in the plankton to determine the relative effects of these temporally co-varying processes on the magnitude and variability of recruitment.

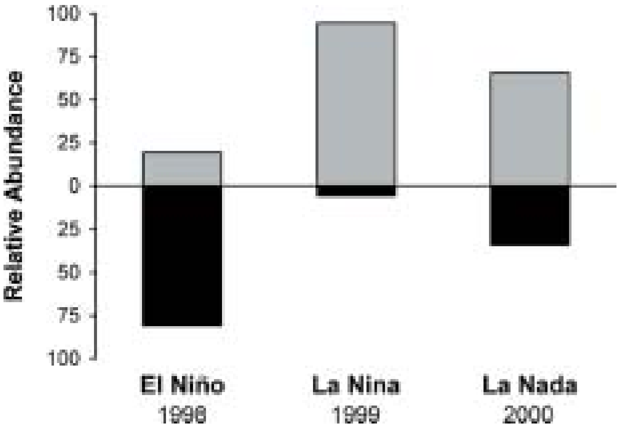

FIGURE 15-5 Relative abundance of midwater complex rockfish recruits (light gray bars above the line) relative to benthic complex rockfish recruits (black bars below line). El Niño conditions favor recruitment of the benthic complex, whereas La Nina favors recruitment of the midwater complex. During normal years, abundances are more equitable.

SPATIAL AND TEMPORAL VARIATION IN LARVAL DISPERSAL, MORTALITY AND CONDITION

Most temperate demersal fishes produce vast numbers of larvae (see chapter 19), and the disparity between this tremendous production of larvae with the few number of young actually delivered to adult populations implies very high pre-settlement mortality (Hjort, 1926; Doherty, 1991; Doherty and Williams, 1988; Leggett and DeBlois, 1994). Small changes in mortality rate over the period that fish larvae spend in the pelagic environment can cause huge changes in the number of young available to replenish local or regional populations (Houde, 1987). Therefore, processes that influence larval loss have been a central focus of fisheries science (Sinclair, 1988; Heath, 1992; and contributions in Chambers and Trippel, 1997). One approach to understanding the importance of variable survival in the plankton is to compare the relationship between successive stages of the recruitment process. For example, Ralston and Howard (1995) compared year-to-year variation in the number of late-stage, pelagic juvenile, rockfish collected in mid-water trawls offshore with that of young recruits observed on shallow rocky reefs along the north coast of California. The strong positive relationship between these two stages suggest that interannual variation in recruitment of young-of-year to populations inhabiting inshore reefs is established early in the larval stage, prior to stages collected by the offshore pelagic juvenile trawls. How this variation in recruitment to reef-associated populations is ultimately manifested in the size and structure of demersal populations and numbers of adults are pressing directions of study (see *Post-settlement processes that can modify or diminish settlement patterns* section).

The dispersal of fish eggs and larvae influences recruitment dynamics in two fundamental ways; as a source of mortality and as a source of spatial and temporal variation in delivery to adult populations. Physical processes that advect larvae far off shore, precluding their return to adult populations, are thought to be a major source of larval mortality. These processes are especially important along coastlines at the western edge of continents, like California, where coastal upwelling can be strong and persistent (Parrish et al., 1981) and where the influences of the California and Davidson Currents and coastal longshore currents shift on and offshore from year-to-year (Hickey, 1979). Large-scale changes in currents coincident with climatic events (e.g., El Niño and La Niña) are also important determinants of larval delivery. For example, Cowen (1985) used otoliths (ear bones) to age and back-calculate the year of larval recruitment of California sheephead (*Semicossyphus pulcher*) at sites throughout northern Baja California and the Southern California Bight. From these recruitment estimates, he ascertained that rates of recruitment shifted among sites in accordance with changes in the California Current. Populations in the northern portion of the species range appear to be replenished during El Niño episodes when northward flowing currents transport larvae produced by parental populations along the coast of Mexico.

Rockfish recruitment along central and northern California is also strongly affected by climatic events, and different responses of species to these events can lead to strong differences in relative rates of species replenishment, and the structure of local assemblages. For example, during the 1992–1993 El Niño event, the relative magnitude of recruitment of two rockfish complexes (genus *Sebastes*) varied markedly (Lenarz et al., 1995). The complex of more solitary benthic species, including kelp, gopher, black and yellow, copper, China, grass and quillback rockfish, are characterized by 1–2 month pelagic durations, whereas the mid-water aggregating complex, including widow, yellowtail, olive, black and blue rockfish have pelagic durations of 3–4 months. Preceding the 1992–1993 El Niño, recruitment was predominated (70–90%) by the mid-water aggregating complex. In sharp contrast, during the 1992–1993 El Niño, the solitary benthic complex recruitment was predominant (60–80%). This pattern was repeated during the more recent 1998 El Niño (fig. 15-5). We monitored recruitment of these two species complexes using diver surveys during the one-year El Niño event, the following La Niña event (1999) and a more typical La Nada condition the following year (2000). As observed during the previous event (1992–1993), the benthic complex dominated recruitment during the El Niño, the mid-water aggregators dominated the La Niña event, and both complexes recruited in more equitable numbers during the more typical La Nada year (fig. 15-5). Knowledge of what life history (e.g., timing of spawning, larval duration) and behavioral attributes (e.g., vertical stratification, thermal preference) contribute to how species respond to differing oceanographic events is key to understanding and predicting recruitment dynamics (e.g., Sakuma and Larson, 1995; Sakuma and Ralston, 1995, 1997; Sakuma et al., 1999; Bjorkstedt et al., 2002).

Smaller scale features (1–10s of kilometers), including wind stress, localized upwelling and relaxation events, offshore jets, eddies, internal waves, tides, tidal bores and others, all may contribute to spatial and temporal variation in larval delivery. Moreover, some of these features (e.g., coastal upwelling, offshore jets, eddies) can be spatially consistent, associated with particular coastal geomorphological features (e.g., angle of the coastline to prevailing wind patterns, headlands, underwater topographic features and bathymetry) and as such, establish persistent spatial patterns of larval delivery (Boehlert and Mundy, 1988; Cowen, 2002). One excellent example of the effect of persistent features is the coast-wide pattern of recruitment of purple sea urchins associated with offshore jets and eddies up current and down current of headlands, respectively along the northern coast of California (Ebert and Russell, 1998). Behavioral (e.g., differential responses to environmental cues) and mechanical (e.g., relative volume and density) responses of pelagic stages and how these responses change with ontogeny influence greatly the relative effects of physical processes on dispersal and onshore transport (Boehlert and Mundy, 1988; Moser and Boehlert, 1991; Larson et al., 1994; Sakuma and Ralston, 1995, 1997; Cowen, 2002). Of particular importance is the vertical stratification of larvae at different stages of development and how position in the water column influences exposure to transport mechanisms (Boehlert and Mundy, 1988; Cowen, 2002; Findlay and Allen, 2002). Moreover, differences in vertical stratification may determine the depth stratification of settlement and recruitment of different species (Love et al., 1991).

Another example of the interaction between behavior and environmental cues is the well-documented association of late-stage pelagic juveniles of several species with biotic structures (e.g., drift macroalgae) associated with physical features (e.g., fronts, slicks, internal waves; Boehlert, 1977; Kingsford, 1993, 1995; Bjorkstedt et al., 2002). Furthermore, behavior independent of environmental features can influence patterns of dispersion (i.e., aggregation) of pre-settlement larvae prior to settlement. Although best documented for a temperate goby in Chesapeake Bay (Breitburg, 1989, 1991), some California reef fishes are known to aggregate prior to settlement to the bottom including gobies (*Lethops connectens*), clinids (*Heterostichus rostratus*, *Gibbonsia* spp.) and sculpins (Marliave, 1986; Carr, 1989, pers. obs.). All of these mechanisms of physical and biological coupling contribute to variation in the delivery of potential recruits to demersal populations.

More recently, efforts to understand both the spatial and temporal patterns of larval supply and the physical processes that determine delivery of potential recruits to a demersal population have focused on sampling delivery at or adjacent to adult populations. An important attribute of this approach is that patterns of delivery of potential recruits to collectors positioned up current of demersal populations and standardized by their size and location sample delivery and settlement independent of benthic habitat features that vary spatially (among reefs) or temporally (among years). In contrast, estimates of delivery and settlement to benthic habitats (e.g., macroalgae), confound patterns of delivery with patterns of habitat quality and availability. An increasingly common approach employed for coral reef fishes has been light traps. These devices exploit the behavioral response of competent pelagic larvae or juveniles for light and entrap individuals attracted to the light. Although this method continues to be explored for sampling temperate reef fishes, it has met with mixed success, presumably because of the lower visibility and ability of larvae to detect the light (Steele et al., 2002). Alternatively, collectors designed to exploit the thigmotaxic (i.e., attraction to physical structure) behavior of fishes has proven to be very useful (Carr, 1991; Ammann, 2001; Findlay and Allen, 2002; Steele et al., 2002). This approach involves suspending structurally complex structures in the water column, and enveloping the structures (and recruits) in fine mesh nets when they are collected for sampling. A third approach has been to construct isolated benthic habitats (typically, these are small artificial structures or reefs constructed of rocky substrate) that are enclosed in cages that exclude predators to prevent post-settlement predation from altering patterns of settlement. All three approaches (light traps, suspended or benthic structures) require frequent sampling both to minimize post-settlement processes from altering settlement patterns and in order to relate patterns of delivery with physical features (e.g., internal waves and tidal flux). Frequent sampling is particularly important for the structural collectors to minimize the possibility of post-settlement emigration of recruits from the structures. Two examples of this approach for determining physical processes that contribute to larval delivery and the importance of delivery in determining patterns of recruitment have been applied to kelp bass, *Paralabrax clathratus*, at Santa Catalina Island off southern California (Findlay and Allen, 2002 and Steele et al., 2002, respectively). Delivery of kelp bass larvae onshore was found to be associated with tidal bores but patterns of larval supply were not reflected in subsequent patterns of recruitment in the reef environment.

In addition to physical forcing, prey availability and predation are thought to be major sources of temporal variability in recruitment (Lasker, 1981; Bailey and Houde, 1989; Sinclair, 1988; Cushing, 1990, 1995; Mullin, 1993). The literature on this subject is too vast to summarize comprehensively here. In addition to determining rates of loss in the plankton, prey availability can affect the size and physiological condition of larvae at settlement, influencing their susceptibility to predation and post-settlement performance and mortality (Searcy and Sponaugle, 2001). Positive interannual relationships between larval mortality and the abundance and distribution of pelagic predators, both invertebrate and fishes, including cannibalism, attest to the potential importance of predation prior to recruitment (e.g., Butler, 1991). These critical biotic interactions are not independent of the many physical processes mentioned in this section and one of the most exciting directions of fisheries ecology is identifying how the spatial and temporal patterns of biotic interactions are coupled with physical features that influence the strength of and variation in these interactions.

Settlement Phase: Transition from the Pelagic to the Demersal Existence

Having survived the vagaries of mortality and dispersal in the pelagic realm, larvae and pelagic juveniles must next survive the transition into an entirely new environment to recruit to nursery or transition habitats or directly to adult populations. Not surprisingly, settlement is one of the least understood phases in the process of recruitment. Because the transition from the pelagic to the demersal existence is brief, often occurs at night and involves small and cryptic individuals, study and knowledge of this process has been extremely limited. Factors likely to influence settlement include 1) hydrodynamic processes, 2) probabilities of encountering suitable habitat or environmental cues 3) behavioral responses to environmental cues, and 4) interactions with resident organisms, including predators.

Small-scale hydrodynamic features (1–10s of m) are likely to influence the distribution of fish settlement. The susceptibility of larvae delivered onshore by hydrodynamic features (e.g., winds, tides, tidal bores) suggests that larvae will continue to be influenced by nearshore hydrodynamic features during settlement. Strong tidal currents capable of pushing entire kelp stands well below the surface could clearly influence the ability of fish to maintain position above the bottom. Strong swell and wave action are also likely to influence the ability of shallow species (especially intertidal fishes) to settle to the bottom. Such small-scale effects are manifested by the accumulation of recently delivered or settled individuals in eddies of physical structures, including rocky outcrops, kelp stands, even individual plants (Breitburg, 1989, 1991).

One of the least explored aspects of settlement is how the spatial distribution of larval delivery and settlement habitat (including cues) influence encounter rates of larvae and their settlement habitat to determine spatial patterns and the overall magnitude of recruitment. Two important aspects of this are the combined effects of patterns of dispersion of larvae and settlement habitat, and temporal variability in availability of settlement habitat. Many of the physical processes described in the *Physical-biological processes that determine dispersal and larval delivery* section create highly aggregated patterns of larval dispersion as they are delivered to the benthic habitat. Varying patch sizes of larval aggregations have been well documented, but how patch size interacts with the number, distribution and size of individual settlement habitats to determine overall settlement rates has been mostly neglected. One example is Levin's (1993, 1994a) experimental assessment of the effect of dispersion patterns (random versus clumped) of algal patches on settlement and recruitment of cunner, *Tautogolabrus adspersus*, an east coast temperate reef fish. Cunner settlement was initially greater in randomly distributed patches, but subsequent recruitment was similar across the two patterns of dispersion. More locally, the presence of giant kelp is known to increase local settlement of several California reef fishes (Carr, 1989, 1991, 1994a,b). This effect is most pronounced for species whose larvae occur in the mid-to-upper portions of the water column, where kelp is a major structure that larvae might encounter as they move along shore.

The shape of a kelp bed and density of plants may have strong effects on whether larvae moving alongshore or onshore encounter a kelp stand or individual plants. Similar conditions exist for species that recruit to any benthic habitat that is distributed non-uniformly. The effects of dispersion of seagrass habitat, as well as other plant characteristics (e.g., plant height and density), have received much attention in temperate estuarine habitats. Several studies provide evidence that attributes of seagrass habitats influence the relative density of recruits within a bed (see references in Valle et al., 1999). However, while these attributes appear to influence the local density of recruits (i.e., for a given level of larval supply), at broader spatial scales patterns of distribution of seagrass beds, such as their proximity to open coast, are better predictors of relative levels of recruitment (Bell and Westoby, 1986; Bell et al., 1987, 1988; Valle et al., 1999).

Similarly, the size, density and species composition of macroalgal assemblages and seagrass beds vary greatly in response to climatic condition, storm disturbance, sediment movement, grazing and disease. For example, the highly dynamic and spatially variable stands of kelps can influence variation in settlement and recruitment within and among reefs, both for species whose larvae settle from the plankton as well as live bearing species whose young are born directly into kelp habitats (Larson and DeMartini, 1984; Ebeling and Laur, 1985; Holbrook et al., 1990a; Bodkin, 1988; Carr, 1989, 1991, 1994a,b; DeMartini and Roberts, 1990; Anderson, 1994; Nelson, 2001). Similar effects have been documented for reef fishes recruiting to non-kelp macroalgal habitats in temperate reefs around the world (Jones, 1984; Choat and Ayling, 1987; Carr, 1989; Levin, 1991, 1993; Levin and Hay, 1996) as well as fishes that recruit to seagrass stands in embayments (Orth and Heck, 1980; Orth et al., 1984; Sogard et al., 1987; Heck et al., 1989; Ferrell and Bell, 1991; Levin et al., 1997; Valle et al., 1999). Those studies that have examined the influence of such settlement habitats both at local (1–100s of meters) and more regional (1–100s of kilometers) spatial scales (Carr, 1994a; Levin et al., 1997; Steele et al., 2002) suggest that large-scale patterns of larval supply become more influential in determining recruitment patterns at larger spatial scales.

Of the many potential environmental cues that have attracted attention of ecologists, two physical cues have been considered; water temperature and physical structure. Using a clever combination of both field surveys and laboratory tests of thermal preference, Norris (1963) demonstrated a positive relationship between density of opaleye, *Girella nigricans*, recruits and increased water temperature in rocky tidepools, and that recently settled opaleye moved to the warmest water temperature available when exposed to a thermal gradient. To determine if settling kelp bass, *Paralabrax clathratus*, preferred particular macroalgae, Carr (1991) conducted both field and laboratory experiments. He suspended replicate clumps of four common species of macroalgae of comparable volume and at similar depths in the water column and recorded the number of recruits that had settled to each algal species. He found significantly greater densities of settlers on the most structurally complex alga (*Sargassum palmeri*), but because the frequency of censuses was at intervals of several days, observed patterns confounded settlement with post-settlement survival. In the laboratory, recently settled kelp bass (9–14 mm TL) were released into large tanks (3 m^3) with discrete clumps of four species of macroalgae and the initial choice and percent of time spent among algal species were recorded. He did not detect preferences (initial choice or percent time) among the different algae, but all four algae were structurally complex, and all individuals associated immediately and consistently with algal structure rather than open portions of the tank. Recruitment of bluebanded gobies (*Lythrypnus dalli*) increased with experimentally manipulated densities of shelter holes (Berhents, 1987; Steele, 1999) and sea urchins (Hartney and Grorud, 2002). Because this relationship existed even when predators were excluded from reefs, Steele suggested that this response might reflect behavioral preferences for shelter at or soon after settlement. The ability of structural collectors and drift macroalgae to accumulate larvae and pelagic juveniles attests to the strong affinity settling fishes have for physical structure (Kingsford, 1993).

The behavioral response of competent (i.e., ready to settle) larvae and pelagic juveniles at settlement, either in the form of attraction to or avoidance of conspecifics, or avoidance of potential competitors and predators, has received increasing attention from coral reef fish ecologists (e.g., Sweatman, 1983; Booth, 1992; Almany, 2002), but tests of this behavior for temperate reef fishes are rare. This is surprising, given the increasing evidence from coral reef systems of both strong positive and negative effects of conspecifics, and the large number of temperate species whose recent settlers form dense aggregations (e.g., *Chromis punctipinnis*, *Heterostichus rostratus*, many species of *Sebastes*). Steele (1997a) found that recruitment of bluebanded gobies (*Lythrypnus dalli*) was greater in the presence of adults compared to similar habitats from which he had removed adults. This difference may reflect settlement facilitated by larvae responding to adult cues. In contrast, similar comparisons of recruitment of blackeye gobies (*Rhinogobiops nicholsii*) were equivocal, and suggested that resident adults were more likely to have a negative effect on recruitment (Steele, 1997a). For both species, no effect of the density of adults on recruitment of the other species was detected. The exclusion of predators also increased the density of *L. dalli* recruits (but not *R. nicholsii*) but because post-settlement mortality occurs quickly and is density-dependent (Steele, 1997b), it is difficult to decouple any of these potential settlement effects from post-settlement losses attributable to predation. Responses to cues provided by prey have not been examined either. Such cues may be directly associated with prey species themselves, or indirectly, associated with habitat attributes that are correlated with prey availability (e.g., water flow for planktivores, macroalgal or other substrate types for epibenthic prey).

Although the effects of predators both as settlement cues (to avoid) and especially as sources of post-settlement mortality have received increasing attention, their role in inflicting mortality during settlement has received less attention. The great potential of planktivorous fishes and some invertebrates (e.g., anemones) to prevent successful settlement is clear from the diversity and abundance of temperate planktivorous fishes (Ebeling and Bray, 1976; Hobson and Chess, 1976, 1986, 2001). The few studies that have compared zooplankton density up current and down current of planktivores (Bray, 1981; Gaines and Roughgarden, 1987; Kingsford and McDiarmid, 1988) suggest that they can strongly alter plankton density. Such studies have mostly examined diurnal planktivores whose effects on larvae that arrive to reefs at night, especially ichthyoplankton, are less clear. Only one study, conducted on coral reefs, has begun to look at rates of predation during settlement at night and concluded that it can be high (Holbrook and Schmitt, 1997). This rapid effect of predators on settlement patterns is suggested by studies documenting very early (i.e., within 24 hr.) post-settlement mortality (Steele and Forester, 2002).

Post-settlement Phase: Benthic Processes that Contribute to Patterns of Recruitment

Ecological processes that occur subsequent to settlement to the benthic environment can act to reinforce, alter, or entirely mask patterns of recruitment created in the pre-settlement and settlement phases. Thus, understanding how and under what conditions post-settlement processes have such effects is critical to understanding the relative importance of each phase of the recruitment process. Three ecological processes that occur subsequent to settlement can have pronounced effects alter patterns of larval settlement—movement, growth and mortality.

POST-SETTLEMENT MOVEMENT

The extent to which fish move subsequent to settling to a benthic habitat varies greatly among species. Extremes vary from those species that appear to establish life-long territories on the order of meters at settlement, to the many species that settle into coastal or estuarine nursery habitats and migrate 10s to 100s of kilometers to adult populations offshore (Love et al., 1991; Gillanders et al., 2003). For example, recruitment (very likely reflecting patterns of settlement) of many rockfishes (genus *Sebastes*) occurs at depths shallower than those typically occupied by their adults (Boehlert, 1977; Love et al., 1991). For those species that move substantial distances between nursery and adult habitats, individuals essentially recruit to populations associated with each habitat type and the duration that individuals inhabit nursery or transition habitats or migrate between habitats varies on the order of days to years (Gillanders et al., 2003). For such species that recruit to a variety of habitats between initial settlement and recruitment to the adult population, understanding the consequences of habitat use and the relative contribution of different juvenile habitats to individual growth and survival are fundamental to understanding the overall structure and dynamics of a population (Beck et al., 2001). For example, although recently settled California halibut, *Paralichthys californicus*, in southern California occur in shallow sand bottom habitats along the open coast, the vast majority appear to occur within estuarine and lagoonal embayments, and those that settle on the open coast migrate to embayments (Plummer et al., 1983; Allen, 1988; Allen and Herbinson, 1990; Kramer, 1991). Although recently settled individuals exhibit little difference in growth rates between the open coast and embayments, mortality from predation appears to be lower for those that recruit to estuarine habitat and older juveniles may grow faster there (Kramer, 1991). The higher productivity and water temperature in embayments may enhance juvenile growth, while vegetation and lower predator densities may enhance survival, both bearing on the eventual contribution to recruitment to offshore adult populations. Temperature related size-specific differences in growth efficiency can explain not only the advantages to smaller fish of inhabiting warmer embayments, but also why older fish move to cooler water as they grow (Boehlert and Yoklavich, 1983).

For species that tend to remain in the habitat to which they settle, the presence of conspecifics and other species may influence post-settlement movement. One example of interspecific effects is the greater rate of post-settlement emigration of recruits of one tide pool sculpin, *Clinocottus embryum*, in the presence of recruits of another, *C. globiceps* (Pfister, 1995). Moreover, for both of these species the per capita rate of emigration from tide pools was related to the density of conspecifics (Pfister, 1996). Although territorial gopher (*Sebastes carnatus*) and black and yellow (*S. chrysomelas*) rockfishes appear to tolerate the presence of recently settled juveniles of either species, with increasing size and competitive interaction recruits eventually emigrate from established territories (Larson, 1980a,b). The greater larval recruitment of painted greenling, *Oxylebius pictus*, in areas where territorial adults were experimental reduced relative to unmanipulated controls may reflect post-settlement movement in response to adults (DeMartini, 1976). For species whose young recruit in greater density in the presence of algal structure, affinity for this structure declines with fish size and is manifested by more equitable densities of older size classes among algal habitats, presumably reflecting post-settlement movement (Ebeling and Laur, 1985; Holbrook and Schmitt, 1984; Holbrook et al., 1990a; Carr, 1989, 1991, 1994a; Anderson, 1994). Thus, local patterns of settlement can be modified by post-settlement emigration in response to a variety of environmental features, including interspecific interactions with competitors and predators.

POST-SETTLEMENT GROWTH

Variation in growth subsequent to settlement is ultimately manifested as an individual's longevity or cohort's rate of mortality and/or future reproductive contribution, including susceptibility to disease. Post-settlement growth rates are influenced directly by such variables as quality (i.e., species composition, size and condition), quantity (i.e. density and abundance) and availability (distribution and susceptibility) of prey, temperature, and water flow (the energetic cost of searching or maintaining position to feed) as well as indirect effects of intra- and interspecific competitors and predators (e.g., interference or risk). Because these variables vary temporally, timing of recruitment can also influence post-settlement growth, survivorship and rate of maturity (Pfister, 1997). Moreover, there is some suggestion that condition of larvae at the time of settlement may influence their post-settlement growth performance. Early juvenile growth can vary markedly and in response to food limitation, even for temperate planktivorous fishes (e.g., Schmitt and Holbrook, 1990; Love et al., 1991; Woodbury and Ralston, 1991; Sogard, 1992; Anderson and Sabado, 1995; Levin, 1994b; Levin et al., 1997). The few studies of temperate fishes that have examined effects of recruit density (Davis and Levin, 2002) and older residents (Steele, 1997a, 1998; Szabo, 2002) on early post-settlement growth or competition for food have found negative effects of conspecific density. Ultimately, these effects on growth can prolong the period that young fish are susceptible to predation and influence the size of a cohort's contribution to the structure and growth of a population (Pfister, 1997; Sogard, 1997; Davis and Levin, 2002).

POST-SETTLEMENT MORTALITY

The importance of post-settlement mortality either as a source of recruitment variation or density-dependent amelioration of such variation, has become a topic of intense interest. Post-settlement modification or dampening of variable larval supply can have strong effects on subsequent population structure and dynamics (Shulman and Ogden, 1987; Sissenwine, 1984; Rothschild, 1986; Holm, 1990; Levin, 1998; Warner and Hughes, 1988; Caley et al., 1996; Forrester et al., 2002; Hixon and Webster, 2002). Post-settlement mortality of temperate fishes can be high and most observational studies documenting this mortality have suggested predation as the cause (Lockwood, 1980; Hallacher and Roberts, 1985; Myers and Cadigan, 1993b; Bailey, 1994; Adams and Howard, 1996; Hobson et al., 2001). Based on a rapid growth in experimental studies over the past decade, there now exists many examples of the substantive causal effects of predators on the survival of early post-settlement juvenile coral reef fishes (reviewed by Hixon and Webster, 2002), as well as a variety of temperate marine species (DeMartini, 1976; Carr, 1991; Steele, 1997a, 1997b; Berhents, 1987; Levin et al., 1997; Steele et al., 1998; Anderson, 2001; Steele and Forrester, 2002; see chapter 16). Environmental disturbance, such as storms and episodes of hypoxia, can also induce substantial post-settlement mortality (Hobson and Howard, 1989; Breitburg, 1992, respectively) and these environmental factors can interact with rates of predation (Breitburg et al., 1994). Because susceptibility is strongly size-dependent, factors that influence growth also influence survivorship, including seasonal variation in settlement (Pfister, 1997).

DENSITY-DEPENDENCE

The extent to which per-capita rates of movement, growth or mortality are dependent on the density of recruits or resident conspecifics can vary substantially in space and time. If such post-settlement or post-recruitment processes are sufficiently strong and density-dependent, much of the effect of variation in larval supply and settlement on population size, growth rate and reproductive potential can be greatly dampened. Because this topic is treated in greater depth by Steele and Anderson (chapter 16), we mention it briefly as it relates to the greater recruitment process. A growing number of studies examining post-settlement mortality provide increasing evidence that the per capita rate of mortality of demersal fishes can be strongly density-dependent (see recent reviews by Hixon and Webster, 2002; Osenberg et al., 2002; Steele and Anderson, chapter 16). Evidence of this density-dependent post-settlement mortality for temperate fishes comes from three sources: 1) observations of strong positive spatial or temporal relationships between the magnitude of recruitment and limiting resources (especially refuge from predation), 2) observational tests of the relationship between the size of recruiting cohorts and their per-capita rate of mortality, and 3) experimental tests of the effect of density on per-capita mortality of recruiting cohorts. One example of the first case is the strong relationship between recruitment of recently settled kelp bass, *Paralabrax clathratus*, and plots of manipulated densities of the giant kelp, *Macrocystis pyrifera* (Carr, 1994a). The positive relationship generated across interspersed replicate kelp density plots suggest that under comparable levels of larval supply, settlers or recruits experienced density-dependent mortality, limiting their eventual numbers to the availability of refuge from predation. Thus, the many examples of positive relationships between recruitment and recruitment habitat such as shelter holes (Berhents, 1987; Steele, 1999) may reflect density-dependent mortality set by the availability of limiting resources. However, as in the case of the kelp bass-giant kelp example, this indirect evidence does not distinguish post-settlement mortality from differential settlement related to encounter rates of larvae with increasing density of plants. Hence, observations of actual rates of per-capita mortality provide stronger evidence for density-dependent mortality.

With few exceptions (Tupper and Boutilier, 1995; Sano, 1997; Pfister, 1996; Davis and Levin, 2002), the majority of observational studies of post-settlement density dependence come from the fisheries literature (e.g., Lockwood, 1980; Myers and Cadigan, 1993b; Adams and Howard, 1996). These studies document the occurrence of early post-settlement density-dependent mortality at broader spatial and temporal scales than can be examined experimentally. Only a handful of these observational studies have been conducted for California fishes. Adams and Howard (1996) detected significant positive inter-annual relationships between the strength of recruitment of blue rockfish, *Sebastes mystinus*, to kelp forests along northern California and rates of cohort mortality. In contrast, a 4-year study of recruitment and population dynamics of an intertidal sculpin along the coast of southern California found that early post-settlement mortality rates were density-independent (Davis and Levin, 2002). Similarly, Pfister (1996) found that early post-settlement survival of three species of intertidal sculpins at sites along the coast of Washington State was largely density-independent, resulting in positive relationships between the total number of recruits in the summer and number of adults the following winter for two of the three species. Recruitment events could be detected in adult populations for short periods of time. Post-recruitment survivorship, however, dampened seasonal recruitment pulses and adult population growth rates were more sensitive to post-recruitment processes.

Such observational studies have motivated experimental assessments of post-settlement density-dependent mortality. In a series of experiments examining the relative contributions of larval supply and post-settlement predation and competition for two species of gobies at Santa Catalina Island, Steele (1997a,b, 1999) Steele et al. (1998), and Steele and Forrester (2002) concluded that variable post-settlement mortality of *Lythrypnus dalli* and *Rhinogobiops nicholsii* caused by predation was very strong and occurred very quickly (e.g., 92% mortality within 24 hr of settlement for *C. nicholsii*) and was sufficiently density-dependent to greatly obscure patterns of larval supply and settlement. However when these effects, detected at spatial scales of tens of meters, were examined at larger spatial scales (100s–1000s of meters) patterns of recruitment were still related to larger-scale variation in larval supply and settlement. This observation underscores the importance of examining the relative roles of pre- and post-settlement processes with a combination of observational studies at broader spatial and temporal scales and experimental tests at smaller spatial scales to elucidate the actual mechanisms and sources of variation in density dependence. Another elegant example of experimental evaluation of density dependence is Anderson's (2001) manipulations of the density of young kelp perch, *Brachyistius frenatus*, in the presence and absence of predators. This work demonstrated that the post-parturition density-dependent mortality experienced by young kelp perch was a result of combined functional and aggregative responses of its primary predator, the kelp bass. To determine if the presence and strength of density-dependence varied as a function of habitat complexity, recruit density was manipulated across a range of habitat complexity. This experiment demonstrated that the direction (positive or negative), presence and magnitude of density dependence are strongly influenced by structural complexity of the habitat (e.g., kelp). Surveys of per-capita mortality of kelp perch occurring at a range of densities across reefs at Santa Catalina Island demonstrated patterns concordant with the density-dependent mortality detected in the experiments. This work demonstrates the broader implications of variation in habitat attributes as they influence post-settlement processes that contribute to density-dependence (e.g., predator and refuge abundance), and more generally as sources of variation in recruitment.

Intra- and interspecific interactions (competition, predation, facilitation) interact with habitat features (e.g., shelter availability) to increase the complexity and variability in how either habitat or species interactions influence recruitment. For example, Behrents (1987) sampled recruitment of bluebanded gobies, *Lythrypnus dalli*, to artificial habitats on which she orthogonally manipulated the presence/absence of conspecific adults and small shelter holes for recruits. In the absence of small shelter holes, the presence of adults reduced larval recruitment, while in the presence of small shelter holes, there was no effect of adults on recruitment. Moreover, this effect of adult conspecifics was opposite to the effect of enhanced recruitment that Steele (1997a,b) detected (see *Settlement phase* section above). The different effects do not seem to be attributable to differences in the presence of predators (Steele, 1997a,b) and exemplify the complexity of these interactions. Another source of complexity is the role of macroalgae and other biogenic sources of habitat structure in moderating species interactions in temperate systems. These sources of habitat structure provide young fish with refuge from predation as well as modify the abundance and availability of their prey. Macroalgal assemblages are highly variable in space and time and these changes create a variable environment within which species interactions take place. Understanding how post-settlement interactions vary in response to these changing conditions is critical to understanding spatial and temporal patterns of recruitment (Holbrook et al, 1990b; Schmitt and Holbrook, 1990; Levin, 1993; Carr, 1994a,b; Anderson, 2001).

Implications of Recruitment for the Management and Conservation of Marine Fishes

Our understanding of the causes and consequences of the variable replenishment of fish populations underpins all past and current approaches to managing and conserving these species as well as the ecosystems that support them. The importance of variable recruitment to the dynamics and management of marine fisheries has been recognized since the dawn of fisheries science. It has been both the Holy Grail that fisheries scientists have endeavored to understand or predict, as well as a bane of their ability to accurately forecast population dynamics. As a fundamental source of uncertainty, it has often impeded traditional management approaches based upon stock-recruitment relationships. While this uncertainty has compelled scientists and managers to consider additional approaches to complement traditional management (e.g., hatcheries, marine reserves), recruitment remains a critical consideration for the potential contribution and uncertainty of these schemes as well.

The temporally variable, often episodic, recruitment of marine fishes influences the frequency at which populations are replenished. The availability of adults to produce potential recruits during such windows of favorable recruitment conditions is critical to the persistence of a population. This storage effect (sensu Warner and Chesson, 1985) implies that reducing the longevity of adults to durations less than intervals between successful recruitment events can jeopardize the persistence of a population. Similarly, if some level of larval production and recruitment is necessary to maintain populations through periods detrimental to their maintenance (e.g., detrimental climatic regimes), additional fishing mortality during such periods may incapacitate buffers in population size critical to larval production. Thus, identifying the temporal patterns of recruitment and the environmental processes that explain those patterns is critical to understanding and predicting the temporally variable effects of reducing the age and number of adults incurred from fishing mortality. Temporal patterns of recruitment also inform mangers of the relative consequences of fishing mortality during periods of differing rates of replenishment. Reducing rates of fishing mortality during prolonged periods of reduced rates of recruitment may be necessary to maintain stocks at levels capable of rebounding with the return of environmental conditions favorable for recruitment.

The spatial scale of larval dispersal and recruitment sets the scale of influence of a population and, by extension, can determine the spatial scope of human impacts. Local extirpation of adults can act both to preempt recruitment to populations elsewhere, and, to the extent that local recruitment is influenced by the presence of adults, prevent replenishment of that local population where adult density has been altered (Raimondi and Reed, 1996). Similarly, localized human activities that alter the dispersal patterns or survival of fish larvae as they encounter altered environments can have regional impacts well down current of such activities (Kingsford and Gray, 1996; Nisbet et al., 1996). Examples include the potential entrainment of larvae by power plants, or discharge plumes of altered salinity, temperature, turbidity, or toxicants. Thus, knowledge of the processes that determine dispersal and the relationships between larval production, survival and recruitment are critical to understanding and predicting the scale and magnitude of human impacts on these three processes.

The spatial scale of dispersal and recruitment also sets the spatial scale at which populations interact with one another. As such, dispersal and recruitment are fundamental to the purpose, design and evaluation of spatially explicit management approaches such as marine reserves. Several studies have discussed the implications of larval dispersal for the potential role of marine reserves as sources of replenishment of exploited populations and the importance of dispersal distance for the design (size, spacing and location) of reserve networks (Plan Development Team, 1990; Carr and Reed, 1993; Roberts, 1997; Planes et al., 2000; NRC, 2001, contributions in volume S13 of Ecological Applications, 2003). The extent to which larval retention enhances local recruitment determines the extent to which populations within reserves are self-replenishing. Alternatively, the apparent reliance of local populations on larval transmission among populations (i.e., connectivity) is the basis for the necessity of reserve networks. With better understanding of dispersal processes, we are more likely to design true networks of reserves whose replenishment and sustainability are independent of less protected populations outside reserves. Spatial patterns of larval production, dispersal and population connectivity also determine the relative contribution of local populations to the replenishment and persistence of broader regional populations that constitute metapopulations or exploited stocks. Knowledge of such contributions, measured as per-capita survival, larval production, dispersal and realized recruitment to the regional population, identifies potential source and sink populations. Identification of such populations can be useful for targeting populations for protection in reserves or for predicting or assessing the potential or realized benefit of artificial reefs for augmenting regional fish populations or mitigating for habitat loss (Carr and Hixon, 1997; Grossman et al., 1997; Holbrook et al., 2000).

The degree to which density-dependent post-settlement processes (e.g., competition, predation) and resource limitation determine recruitment to a fishery or an adult population will greatly influence the potential value of propagation (e.g., hatcheries) and habitat enhancement (e.g., restoration and artificial reefs) for augmenting populations. Thus, knowledge of the relative contributions (and constraints) of each phase of the recruitment process (production, pelagic survival and dispersal, settlement and post-settlement performance), will inform decisions of alternative or complementary management approaches.

Future Directions

Four future research areas, each essentially complementary to the others, emerge from this review of our understanding of fish recruitment and population ecology. First is the growing recognition of the necessity to conduct comprehensive studies that examine the entire recruitment process from larval production, supply, through the post-settlement phase to recruitment to the adult population. To date, there are many well-studied pieces of the puzzle, but they provide an incomplete understanding of the overall recruitment process. Without a more complete picture for a subset of model species representative of key life history traits (e.g., reproductive mode, fecundity, larval duration), our understanding of the relative importance of each phase of the recruitment process and how this varies among oceanographic and other environmental conditions, will continue to impair our ability to predict both recruitment dynamics and its consequence to the structure and dynamics of demersal fish populations and the communities they constitute.

Second is the shift from the current focus on single, local populations to multiple regional-scale populations. Included with this broader perspective are explorations of larval dispersal and connectivity among populations. Only through a greater understanding of the spatial scale of dispersal and population interaction and how this varies among species and oceanographic conditions can our science begin to understand how processes acting at the scale of local populations scale-up to regional, metapopulation, scales. Only with this larger scale understanding will we understand processes that contribute to the persistence of both local and regional populations and develop the capacity to inform spatially explicit management and conservation efforts.

In order to do this effectively will require the third direction of research; a more interdisciplinary effort that brings to bear the tools and insights of genetic, physiological, oceanographic and other disciplines to address these complex questions. Genetic and chemical signatures and analytical approaches will be required to determine patterns of dispersal and these are being developed rapidly. Concomitant oceanographic studies will be required to interpret dispersal and recruitment patterns generated from the use of such signatures. Multidisciplinary efforts examining processes of dispersal and recruitment in coastal oceans are critical to our understanding of how larger scale processes (e.g., the California Current) interact with coastal processes (e.g., tidal bores, upwelling and its relaxation) to influence recruitment dynamics and population connectivity along the west coast of North America and upwelling-dominated ecosystems throughout the world.

Finally, there is a need to formally integrate these different levels of inquiry into explanatory and predictive frameworks that relate local scale processes, such as post-settlement density dependence, to regional scale dynamics such as metapopulation structure and persistence. These frameworks need to provide a means by which scientists can both understand the dynamics of fish populations and communities, and provide resource managers with predictions and forecasts about outcome of conservation and management actions. The tremendous research capacity along the West Coast has long been poised to provide models for this type of effort, and recent assessments of fish populations indicate that the need for these kinds of programs is greater now than ever. These are very exciting and important times to pursue such endeavors.

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Literature Cited

Adams, P.B., and D.F. Howard. 1996. Natural mortality of the rockfish, *Sebastes mystinus*, during their first year in nearshore benthic habitats. U.S. Fish. Bull 94:156–162.

Allen, L.G. 1988. Recruitment, distribution, and feeding habits of young-of-the-year California halibut, (*Paralichthys californicus*) in the vicinity of Alamitos Bay Long Beach Harbor, California, 1983–1985. Bull. So. Cal. Acad. Sci. 87:19–30.

Allen, M.J., and K.T. Herbinson. 1990. Settlement of juvenile California halibut, *Paralichthys californicus,* along the coasts of Los Angeles, Orange, and San Diego counties in 1989. California Cooperative Oceanic Fisheries Investigations Report. 31:84–96.

Almany, G.R. 2002. Priority effects in coral-reef fish communities. Ecology 84:1920–1935.

Ammann, A.J. 2001. SMURFs: standard monitoring unit for the recruitment of temperate reef fishes. J. Exp. Mar. Biol. Ecol. 299:135–154.

Anderson, T.W. 1983. Identification and development of nearshore juvenile rockfishes (genus *Sebastes*) in central California kelp forests, pp. 216. California State University, Fresno.

________. 1994. Role of macroalgal structure in the distribution and abundance of a temperate reef fish. Mar. Ecol. Prog. Ser 113:279–290.

________. 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. Ecology. 82:245–257.

Anderson, T.W., and B.D. Sabado. 1995. Correspondence between food availability and growth of a planktivorous temperate reef fish. J. Exp. Mar. Biol. Ecol. 189:65–76.

Armsworth, P.R. 2002. Recruitment limitation, population regulation, and larval connectivity in reef fish metapopulations. Ecology. 83: 1092–1104.

Bailey, K.M. 1994. Predation on juvenile flatfish and recruitment variability. Netherlands J. Sea Res. 32:175–189.

Bailey, K.M., and E.D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. Mar. Biol. 25:1–83.

Baskin, Y., M.W. Beck, K.L. Heck, K.W. Able, D.L. Childers, D.B. Eggleston, B.M. Gillanders, B.S. Halpern, C.G. Hays, K. Hoshino, T.J. Minello, R.J. Orth, P.F. Sheridan, and P.M. Weinstein. 2003. The role of nearshore ecosystems as fish and shellfish nurseries. Issues Ecology. 11:1–12.

Beck, M.W., K.L. Heck, K.W. Able, D.L. Childers, D.B. Eggleston, B.M. Gillanders, B. Halpern, et al. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Biosci. 51:633–641.

Behrents, K.C. 1987. The influence of shelter availability on recruitment and early juvenile survivorship of *Lythrypnus dalli* Gilbert (Pisces: Gobiidae). J. Exp. Mar. Biol. Ecol 107:45–60.

Bell, J.D., A.S. Steffe, and M. Westoby. 1988. Location of seagrass beds in estuaries: effects on associated fish and decapods. J. Exp. Mar. Biol. Ecol 122:127–146.

Bell, J.D., and M. Westoby. 1986. Variation in seagrass height and density over a wide spatial scale: effects on common fish and decapods. J. Exp. Mar. Biol. Ecol 104:275–295.

Bell, J.D., M. Westoby, and A.S. Steffe. 1987. Fish larvae settling in seagrass: do they discriminate between beds of different leaf density? J. Exp. Mar. Biol. Ecol 111:133–144.

Bjorkstedt, E.P., B. Grantham, Y. Shkedy, L. Rosenfeld, and J. Roughgarden. 2002. Distribution of larval rockfishes *Sebastes* spp. across nearshore fronts in a coastal upwelling region. Mar. Ecol. Prog. Ser 242:215–228.

Bodkin, J.L. 1988. Effects of kelp forest removal on associated fish assemblages in central California [USA]. J. Exp. Mar. Biol. Ecol 117:227–238.

Boehlert, G.W. 1977. Timing of surface-to-benthic migration in juvenile rockfish, *Sebastes diploproa*, off southern California. U.S. Fish. Bull. 75:887–890.

Boehlert, G.W., and B.C. Mundy. 1988. Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. Am. Fish. Soc. Symp. 3:51–67.

Boehlert, G.W., and M.M. Yoklavich. 1983. Effects of temperature, ration, and fish size on growth of juvenile black rockfish, *Sebastes melanops*. Environ. Biol. Fish. 8:17–28.

Booth, D.J. 1991. The effects of sampling frequency on estimates of recruitment of the domino damselfish *Dascyllus albisella* Gill. J. Exp. Mar. Biol. Ecol 145:149–160.

________. 1992. Larval settlement patterns and preferences by domino damselfish *Dascyllus albisella* Gill. J. Exp. Mar. Biol. Ecol 155:85–104.

Booth, D.J., and D.M. Brosnan. 1995. The Role of Recruitment Dynamics in Rocky Shore and Coral Reef Fish Communities. Adv. Ecol. Res. 26:309–385.

Bray, R.N. 1981. Influence of water currents and zooplankton densities on daily foraging movements of blacksmith, *Chromis puntipinnis*, a planktivorous reef fish. Fish. Bull 78:829–841.

Breitburg, D.L. 1989. Demersal schooling prior to settlement by larvae of the naked goby. Env. Biol. Fish 26:97–103.

________. 1991. Settlement patterns and pre-settlement behavior of the naked goby, *Gobiosoma bosci*, a temperate oyster reef fish. Mar. Biol. 109:213–221.

________. 1992. Episodic hypoxia in Chesapeake Bay interacting effects of recruitment behavior and physical disturbance. Ecol. Monogr. 62: 525–546.

Breitburg, D.L., N. Steinberg, S. Dubeau, C. Cooksey, and E.D. Houde. 1994. Effects of low dissolved oxygen on predation on estuarine fish larvae. Mar. Ecol. Prog. Ser 104:235–246.

Brooks, A.J., R.J. Schmitt, and S.J. Holbrook. 2002. Declines in regional fish populations: Have species responded similarly to environmental change? Mar. Fresh. Res. 53:189–198.

Brothers, E.B., and R.E. Thresher. 1985. Pelagic duration, dispersal, and the distribution of Indo-Pacific coral reef fishes, p. 53–69. In*:* The Ecology of Coral Reefs, NOAA Symp. Ser. Undersea Res. Vol. 3. M. L. Reaka (ed.). NOAA, Rockville, Maryland.

Brothers, E.B., D.M. Williams, and P.F. Sale. 1983. Length of larval life in twelve families of fishes at "One Tree Lagoon," Great Barrier Reef, Australia. Mar. Biol. 76:319–324.

Butler, J.L. 1991. Mortality and recruitment of Pacific sardine, *Sardinops sagax caerulea*, larvae in the California Current, [Pacific Ocean]. Can. J. Fish. Aqua. Sci. 48:1713–1723.

Cailliet, G.M., R.J. Larson, D.A. Ventresca, R.N. Lea, and E. Knaggs. 2000. Biological characteristics of nearshore fishes of California: a review of existing knowledge and proposed additional studies. Pacific States Marine Fisheries Commission.

Caley, M.J., M.H. Carr, M.A. Hixon, T.P. Hughes, G.P. Jones, and B.A. Menge. 1996. Recruitment and the local dynamics of open marine populations. Ann. Rev. Ecol. Sys. 27:477–500.

Carr, M.H. 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. J. Exp. Mar. Biol. Ecol 126:59–76.

________. 1991. Habitat selection and recruitment of an assemblage of temperate zone reef fishes. J. Exp. Mar. Biol. Ecol 146:113–137.

________. 1994a. Effects of macroalgal dynamics on recruitment of a temperate reef fish. Ecology (Tempe). 75:1320–1333.

________. 1994b. Predicting recruitment of temperate reef fishes in response to changes in macrophyte density caused by disturbance, p. 255–269. In*:* Theory and application in fish feeding ecology. D.J. Stouder, K.L. Fresh, and R.J. Feller (eds.). University. South Carolina Press, Columbia, South Carolina.

Carr, M.H., T.W. Anderson, and M.A. Hixon. 2002. Biodiversity, population regulation, and the stability of coral-reef fish communities. Proc. Nat. Acad. Sci. U.S.A. 99:11241–11245.

Carr, M.H., and M.A. Hixon. 1997. Artificial reefs: the importance of comparisons with natural reefs. Fish. Oceanog. 22:28–33.

Carr, M.H., and D.C. Reed. 1993. Conceptual issues relevant to marine harvest refuges: Examples from temperature reef fishes. Can. J. Fish. Aqua. Sci. 50:2019–2028.

Chambers, R.C., and E.A. Trippel. 1997. Early life history and recruitment in fish populations. Chapman and Hall, London, UK.

Chesson, P. 1996. Matters of scale in the dynamics of populations and communities, p. 353–368. In*:* Frontiers of Population Ecology. R. B. Floyd, A. W. Sheppard and P.J. De Barro (eds.). CSIRO Publishing, Melbourne.

________. 1998. Recruitment limitation: A theoretical perspective. Austr. J. Ecol. 23:234–240.

________. 1998. Spatial scales in the study of reef fishes: A theoretical perspective. Austr. J. Ecol. 23:209–215.

Chesson, P.L., and R.R. Warner. 1981. Environmental Variability Promotes Coexistence in Lottery Competitive Systems. Am. Nat. 117:923–943.

Choat, J.H., and A.M. Ayling. 1987. The Relationship Between Habitat Structure and Fish Faunas on New Zealand Reefs. J. Exp. Mar. Biol. Ecol 110:257–284.

Cowen, R.K. 1985. Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: Causes and implications. J. Mar. Res. 43: 719–742.

________. 2002. Larval dispersal and retention and consequences for population connectivity, p. 149–170. In*:* Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. P. F. Sale (ed.). Academic Press, San Diego, California.

Cowen, R.K., K.M.M. Lwiza, S. Sponaugle, C.B. Paris, and D.B. Olson. 2000. Connectivity of marine populations: Open or closed? Science. 287:857–859.

Cushing, D.H. 1990. Plankton production and year class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. 26:249–293.

________. 1995. Population production and regulation in the sea: a fisheries perspective. Cambridge University Press, Cambridge.

Davis, J.L.D., and L.A. Levin. 2002. Importance of pre-recruitment life-history stages to population dynamics of the woolly sculpin *Clinocottus analis*. Mar. Ecol. Prog. Ser 234:229–246.

DeMartini, E.E. 1976. The adaptive significance of territoriality and egg cannibalism in the painted greenling, *Oxylebius pictus* Gill, a northeastern Pacific marine fish. Ph.D. Dissertation, University of Washington.

DeMartini, E.E., and D.A. Roberts. 1990. Effects of giant kelp (*Macrocystis*) on the density and abundance of fishes in a cobble-bottom kelp forest. Bull. Mar. Sci. 46:287–300.

Dixon, P.A., M.J. Milicich, and G. Sugihara. 1999. Episodic fluctuations in larval supply. Science. 283:1528–1530.

Doherty, P.J. 1981. Coral reef fishes: recruitment-limited assemblages? Proc. Fourth Internat. Coral Reef Symp. 2:465–470.

________. 1991. Spatial and temporal patterns in recruitment.

________. 2002. Variable replenishment and the dynamics of reef fish populations, p. 327-355. In: Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. P. F. Sale (ed.). Academic Press, San Diego, California.

Doherty, P.J., and D.M. Williams. 1988. The replenishment of coral-reef fish populations. Oceanogr. Mar. Biol. 26:487–551.

Ebeling, A.W., and R.N. Bray. 1976. Day versus night activity of reef fishes in a kelp forest off Santa Barbara, California. U.S. Fish. Bull 74:703–717.

Ebeling, A.W., and M.A. Hixon. 1991. Tropical and temperate reef fishes comparison of community structures. *In:* The Ecology of Fishes on Coral Reefs. P. F. Sale (ed.). Academic Press, San Diego, California.

Ebeling, A.W., and D.R. Laur. 1985. The influence of plant cover on surfperch abundance at an offshore temperate reef. Env. Biol. Fish 12: 169–180.

Ebert, T.A., and M.P. Russell. 1998. Latitudinal variation in size structure of the west coast purple sea urchin: A correlation with headlands. Limn. Oceanogr. 33:286–294.

Eldridge, M.B., and B.M. Jarvis. 1995. Temporal and spatial variation in fecundity of yellowtail rockfish. Trans. Am. Fish. Soc. 124: 16–25.

Ferrell, D. J., and J.D. Bell. 1991. Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. Mar. Ecol. Prog. Ser 72:15–24.

Findlay, A.M., and L.G. Allen. 2002. Temporal patterns of settlement in the temperate reef fish *Paralabrax clathratus*. Mar. Ecol. Prog. Ser 238:237–248.

Forrester, G., R.R. Vance, and M.A. Steele. 2002. Simulating large-scale population dynamics using small-scale data, p. 275–301. In*:* Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. P. F. Sale (ed.). Academic Press, San Diego, California.

Gaines, S.D., and J. Roughgarden. 1987. Fish in offshore kelp forest affect recruitment to intertidal barnacle populations. Science. 235: 479–481.

Gillanders, B.M., K.W. Able, J.A. Brown, D.B. Eggleston, and P.F. Sheridan. 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Mar. Ecol. Prog. Ser 247:281–295

Grossman, G.D., G.P. Jones, and D.M. Williams. 1997. Do artificial reefs increase regional fish production? A review of existing data. Fisheries. 22:17–23.

Hallacher, L.E., and D.A. Roberts. 1985. Differential utilization of space and food by the inshore rockfishes (Scorpaenidae: *Sebastes*) of Carmel Bay, California [USA]. Env. Biol. Fish 12:91–110.

Hanski, I.A., and M.E. Gilpin. 1997. Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego.

Hartney, K.B., and K.A. Grorud. 2002. The effect of sea urchins as biogenic structures on the local abundance of a temperate reef fish. Oecologia. 131:506–513.

Heath, M.R. 1992. Field investigations of the early life history of marine fish. Adv. Mar. Biol. 28:1–174.

Heck, K.L., Jr., K.W. Able, M.P. Fahay, and C.T. Roman. 1989. Fishes and decapod crustaceans of Cape Cod eelgrass meadows: species composition, seasonal abundance patterns and comparison with unvegetated substrates. Estuar. 12:56–65.

Hickey, B.M. 1979. The California current system—hypothesis and facts. Progr. Oceanogr.:191–279.

Hixon, M.A., and M.H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. Science. 277:946–949.

Hixon, M.A., and M.S. Webster. 2002. Density dependence in reef fish populations, p. 303–325. *In:* Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. P. F. Sale (ed.). Academic Press, San Diego, California.

Hjort, J. 1926. Fluctuations in the year classes of important food fishes. Journal du Conseil. 1:1–38.

Hobson, E.S. 1986. Relationships among fishes and their prey in a nearshore sand community off southern California. Env. Biol. Fish 17:201–226.

Hobson, E.S. 2001. Influence of trophic relations on form and behavior among fishes and benthic invertebrates in some California marine communities. Env. Biol. Fish 60:411–457.

Hobson, E.S., and J.R. Chess. 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. U.S. Fish. Bull 74:567–598.

Hobson, E.S., J.R. Chess, and D.F. Howard. 2001. Interannual variation in predation on first-year *Sebastes* spp. by three northern California predators. U.S. Fish. Bull. 99:292–302.

Hobson, E.S., and D.F. Howard. 1989. Mass strandings of juvenile shortbelly rockfish and pacific hake along the coast of northern California USA. Calif. Fish Game. 75:169–172.

Holbrook, S.J., R.F. Ambrose, L. Botsford, M.H. Carr, P.T. Raimondi, and M.J. Tegner 2000. Ecological issues related to decommissioning of California's offshore production platforms. Report to University of California Marine Council by the Select Scientific Advisory Committee on Decommissioning.

Holbrook, S.J., M.H. Carr, R.J. Schmitt, and J.A. Coyer. 1990a. Effect of giant kelp on local abundance of reef fishes the importance of ontogenetic resource requirements. Bull. Mar. Sci. 47:104–114.

Holbrook, S.J., and R.J. Schmitt. 1984. Experimental analyses of patch selection by foraging black surfperch (*Embiotoca jacksoni* Agazzi). J. Exp. Mar. Biol. Ecol 79:39–64.

________. 1997. Settlement patterns and process in a coral reef damselfish: in situ nocturnal observations using infrared video, p. 1143–1148. In*:* Proceedings of the 8th International Coral Reef Symposium. Vol. 2.

Holbrook, S.J., R.J. Schmitt, and R.F. Ambrose. 1990b. Biogenic habitat structure and characteristics of temperature reef fish assemblages. Austr. J. Ecol. 15:489–504.

Holbrook, S.J., R.J. Schmitt, and J.S. Stephens. 1997. Changes in an assemblage of temperate reef fishes associated with a climate shift. Ecol. Appl. 7:1299–1310.

Holm, E.R. 1990. Effects of density-dependent mortality on the relationship between recruitment and larval settlement. Mar. Ecol. Prog. Ser 60:141–146.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symposium. 2:17–29.

Jones, G.P. 1984. Population ecology of the temperate reef fish *Pseudolabrus celidotus* Bloch and Schnieder (Pisces: Labridae). I. Factors Influencing recruitment. J. Exp. Mar. Biol. Ecol 75:257–276.

Keough, M.J., and B.J. Downes. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia. 54:348–352.

Kingsford, M.J. 1993. Biotic and abiotic structure in the pelagic environment: Importance to small fishes. Bull. Mar. Sci. 53:393–415.

________. 1995. Drift algae: A contribution to near-shore habitat complexity in the pelagic environment and an attractant for fish. Mar. Ecol. Prog. Ser 116:297–301.

Kingsford, M.J., and C.A. Gray. 1996. Influence of pollutants and oceanography on abundance and deformities of wild fish larvae, p. 235–252. In: Detecting ecological impacts: concepts and applications in coastal habitats. R. J. Schmitt and C. W. Osenberg (eds.). Academic Press, San Diego.

Kingsford, M.J., and A.B. MacDiarmid. 1988. Interrelations between planktivorous reef fish and zooplankton in temperate waters. Mar. Ecol. Prog. Ser 48:103–117.

Kinlan, B.P., and S.D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: A community perspective. Ecology. 84: 2007–2020.

Kramer, S.H. 1991. Growth, mortality, and movements of juvenile California halibut *Paralicthys californicus* in shallow coastal and bay habitats of San Diego County, California. U.S. Fish. Bull 89:195–207.

Krigsman, L.M. 2000. A review of larval duration for Pacific coast temperate reef fishes, including kelp rockfish, *Sebastes atrovirens*, 32 pp. In: Biology. University of California Santa Cruz, Santa Cruz.

Larson, R. J. 1980a. Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. Ecol. Monogr. 50: 221–239.

________. 1980b. Influence of territoriality on adult density in two rockfishes of the genus *Sebastes*. Mar. Biol. 58:123–132.

Larson, R.J., and E.E. DeMartini. 1984. Abundance and vertical distribution of fishes in a cobble-bottom kelp forest off San Onofre, California. U.S. Fish. Bull 82:37–53.

Larson, R.J., W.H. Lenarz, and S. Ralston. 1994. The distribution of pelagic juvenile rockfish of the genus *sebastes* in the upwelling region off central California. CalCOFI Rep. 35:175–221.

Lasker, R. 1981. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: contrasting years, 1975 through 1978. Conseil international pour l' Exploration de la Mer 178:375–388.

Leggett, W.C., and E. Deblois. 1994. Recruitment in marine fishes: Is it regulated by starvation and predation in the egg and larval stages? Netherlands J. Sea Res. 32:119–134.

Leis, J.M. 1991. The pelagic stage of reef fishes: the larval biology of coral reef fishes, p. 183–230. In: The Ecology of Fishes on Coral Reefs. P. F. Sale (ed.). Academic Press, San Diego, California.

Leis, J.M., and M.I. McCormick. 2002. The biology, behavior and ecology of the pelagic, larval stage of coral reef fishes, p. 171–199. In: Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. P. F. Sale (ed.). Academic Press, San Diego, California.

Lenarz, W.H., and T.W. Echeverria. 1986. Comparison of visceral fat and gonadal fat volumes of yellowtail rockfish, *Sebastes flavidus,* during a normal year and a year of El Niño conditions. U.S. Fish. Bull 84:743–745.

Lenarz, W.H., D.A. Ventresca, W.M. Graham, F.B. Schwing, and F. Chavez. 1995. Explorations of El Niño events and associated biological population dynamics off central California. CalCOFI Rep. 36:106–119.

Levin, L.A., R. Petrik, and J.C. Malone. 1997. Interactive effects of habitat selection, food supply and predation on recruitment of an estuarine fish. Oecologia. 112:55–63.

Levin, P.S. 1991. Effects of microhabitat on recruitment variation in a gulf of Maine reef fish. Mar. Ecol. Progr. Ser. 75:183–189.

________. 1993. Habitat structure, conspecific presence and spatial variation in the recruitment of a temperate reef fish. Oecologia. 94: 176–185.

________. 1994a. Fine-scale temporal variation in recruitment of a temperate demersal fish—the importance of settlement versus postsettlement loss. Oecologia. 97:124–133.

________. 1994b. Small-scale recruitment variation in a temperate fish—the roles of macrophytes and food-supply. Env. Biol. Fish 40: 271–281.

________. 1998. The significance of variable and density-independent post-recruitment mortality in local populations of reef fishes. Austr. J. Ecol. 23:246–251.

Levin, P.S., W. Chiasson, and J.M. Green. 1997. Geographic differences in recruitment and population structure of a temperate reef fish. Mar. Ecol. Progr. Ser. 161:23–35.

Levin, P.S., and M.E. Hay. 1996. Responses of temperate reef fishes to alterations in algal structure and species composition. Mar. Ecol. Progr. Ser. 134:37–47.

Lockwood, S.J. 1980. Density-dependent mortality in O-group plaice (*Pleuronectes platessa* L.) populations. J. Cons. Int. Explor. Mer. 39: 148–153.

Love, M.S., M.H. Carr, and L.J. Haldorson. 1991. The ecology of substrate-associated juveniles of the genus *Sebastes*. Env. Biol. Fish 30:225–244.

Love, M.S., J.E. Caselle, and K. Herbinson. 1998a. Declines in nearshore rockfish recruitment and populations in the southern California Bight as measured by impingement rates in a coastal electrical power generating stations. U.S. Fish. Bull. 96:492–501.

Love, M.S., J.E. Caselle, and W. Van Buskirk. 1998b. A severe decline in the commercial passenger fishing vessel rockfish (*Sebastes spp.*) catch in the Southern California Bight, 1980–1996. CalCOFI Rep. 39:180–195.

MacFarlane, R.B., and E.C. Norton. 1999. Nutritional dynamics during embryonic development in the viviparous genus *Sebastes* and their application to the assessment of reproductive success. U.S. Fish. Bull. 97:273–281.

Marliave, J.B. 1986. Lack of planktonic dispersal of rocky intertidal fish larvae. Trans. Am. Fish. Soc. 115:149–154.

Mearns, A.J., M.J. Allen, M.D. Moore, and M.J. Sherwood. 1980. Distribution, abundance, and recruitment of soft-bottom rockfishes (Scorpaenidae: *Sebastes*) on the southern California mainland shelf. CalCOFI Rep. 21:180–190.

Moser, H.G., and G.W. Boehlert. 1991. Ecology of pelagic larvae and juveniles of the genus *Sebastes*. Env. Biol. Fish 30:203–224.

Mullin, M.M. 1993. Webs and scales: physical and ecological processes in marine fish recruitment. University of Washington Press, Seattle.

Myers, R.A., and N.G. Cadigan. 1993b. Density-dependent juvenile mortality in marine demersal fish. Can. J. Fish. Aqua. Sci. 50:1576–1590.

National Research Council. 2001. Marine protected areas: tools for sustaining ocean ecosystems. National Academy Press, Washington, D.C.

Nelson, P.A. 2001. Behavioral ecology of young-of-the-year kelp rockfish, *Sebastes atrovirens* Jordan and Gilbert (Pisces: Scorpaenidae). J. Exp. Mar. Biol. Ecol 256:33–50.

Nisbet, R.M., W.W. Murdoch, and A. Stewart-Oaten. 1996. Consequences for adult fish stocks of human-induced mortality on immatures, p. 257–275. In: Detecting ecological impacts: concepts and applications in coastal habitats. R.J. Schmitt and C.W. Osenberg (eds.). Academic Press, San Diego.

Norris, K.S. 1963. The functions of temperature in the ecology of the percoid fish *Girella nigricans* (Ayres). Ecol. Monogr. 33:23–62.

Norton, S.F. 1991. Habitat use and community structure in an assemblage of cottid fishes. Ecology. 72:2181–2192.

Olafsson, E.B., C.H. Peterson, and W.G. Ambrose. 1994. Does recruitment limitation structure populations and communities of macroinvertebrates in marine soft sediments: the relative significance or pre- and post-settlement processes. Ann. Rev. Oceanogr. Mar. Biol. 32:65–109.

Orth, R.J., and K.L. Heck, Jr. 1980. Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay-fishes. Estuaries. 3:278–288.

Orth, R.J., K.L. Heck, Jr., and J.V. Van Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predatory-prey relationships. Estuaries. 7:339–350.

Osenberg, C.W., C.M. St. Mary, R.J. Schmitt, S.J. Holbrook, P.L. Chesson, and B.A. Byrne. 2002. Rethinking ecological inference: density dependence in reef fishes. Ecology Letters. 5:715–721.

Palumbi, S.R. 2003. Population genetics, demographic connectivity and the design of marine reserves. Ecological Applications. 13:S146–S1158.

Parrish, R.H., C.S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biological Oceanography. 1:175–203.

Pfister, C.A. 1995. Estimating competition coefficients from census data: A test with field manipulations of tidepool fishes. Am. Nat. 146:271–291.

________. 1996. The role and importance of recruitment variability to a guild of tide pool fishes. Ecology 77:1928–1941.

________. 1997. Demographic consequences of within-year variation in recruitment. Mar. Ecol. Prog. Ser. 153:229–238.

Plan Development Team. 1990. The potential of marine fishery reserves for reef fish management in the U.S. southern Atlantic. NOAA Tech. Mem, NMFS-SEFC-261. U.S. Dept. of Comm. Washington, D.C.

Planes, S. 2002. Biogeography and larval dispersal inferred from population genetic analysis, p. 221–238. In*:* Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. P. F. Sale (ed.). Academic Press, San Diego, California.

Planes, S., R. Galzin, A. Garcia Rubies, R. Goñi, J.-G. Harmelin, L. Le Diréach, P. Lenfant, and A. Quetglas. 2000. Effects of marine protected areas on recruitment processes with special reference to Mediterranean littoral ecosystems. Environmental Conservation 27:126–143.

Plummer, K.M., E.E. DeMartini, and D.A. Roberts. 1983. The feeding habits and distribution of juvenile-small adult California halibut, (*Paralichthys californicus*) in coastal waters off northern San Diego County. CalCOFI Rep. 24:194–201.

Raimondi, P.T., and D.C. Reed. 1996. Determining the spatial extent of ecological impacts caused by local anthropogenic disturbances in coastal marine habitats, p. 179–196. In*:* Detecting ecological impacts: coastal applications in coastal habitats. R.J. Schmitt and C.W. Osenberg (eds.). Academic Press, San Diego, CA.

Ralston, S., and D.F. Howard. 1995. On the development of year-class strength and cohort variability in two northern California rockfishes. U.S. Fish. Bull 93:710–720.

Richards, W.J., and K.C. Lindeman. 1987. Recruitment dynamics of reef fishes planktonic processes settlement and demersal ecologies and fishery analysis. Bull. Mar. Sci. 41:392–410.

Roberts, C.M. 1997. Connectivity and management of Caribbean coral reefs. Science 278:1454–1457.

Robertson, D.R., D.G. Green, and B.C. Victor. 1988. Temporal coupling of production and recruitment of larvae of a Caribbean reef fish. Ecology. 69:370–381.

Rothschild, B.J. 1986. Dynamics of marine fish populations. Harvard University Press, Cambridge, Massachusetts.

Sakuma, K.M., and R.J. Larson. 1995. Distribution of pelagic metamorphic-stage sanddabs *Citharichthys sordidus* and *C. stigmaeus* within areas of upwelling off central California. U.S Fish. Bull. 93:516–529.

Sakuma, K.M., and S. Ralston. 1995. Distributional patterns of late larval groundfish off central California in relation to hydrographic features during 1992 and 1993. CalCOFI Rep. 36:179–192.

________. 1997. Vertical and horizontal distribution of juvenile Pacific whiting (*Merluccius productus*) in relation to hydrography off California. Reports of California Cooperative Oceanic Fisheries Investigations [Calcofi Rep.]. 38:137–146.

Sakuma, K.M., S. Ralston, and D.A. Roberts. 1999. Diel vertical distribution of postflexion larval *Citharichthys* spp. and *Sebastes* spp. off central California. Fish. Oceanogr. 8:68–76.

Sale, P.F. 1980. The ecology of fishes on coral reefs. Oceanogr. Mar. Biol. 18:367–421.

________. 1991. Reef fish communities open nonequilibrial systems, p. 564–596. In*:* The ecology of coral reef fishes. P. F. Sale (ed.). Academic Press, San Diego.

________. 2002. Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, California.

Sano, M. 1997. Temporal variation in density dependence: Recruitment and postrecruitment demography of a temperate zone sand goby. J. Exp. Mar. Biol. Ecol 214:67–84.

Schmitt, R.J., and S. J. Holbrook. 1990. Contrasting effects of giant kelp on dynamics of surfperch populations. Oecologia. 84:419–429.

Searcy, S.P., and S. Sponaugle. 2001. Selective mortality during the larval-juvenile transition in two coral reef fishes. Ecology 82:2452–2470.

Shanks, A.L. 1983. surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Progr. Ser. 13:311–315.

________. 1988. Further support for the hypothesis that internal waves can cause shoreward transport of larval invertebrates and fish. U.S. Fish. Bull 86:703–714.

Shanks, A.L., A.B. Grantham, and M.H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecol. Appl. 13:S159–S169.

Shulman, M.J., and J.C. Ogden. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. Mar. Ecol. Prog. Ser 39:233–242.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. University Washington Press. Seattle, Washington.

Sissenwine, M.P. 1984. Why do fish populations vary?, p. 59–94. In*:* Exploitation of Marine Communties. R.M. May (ed.). Springer-Verlag, Berlin.

Sogard, S.M.1992. Variability in growth rates of juvenile fishes in different estuarine habitats. Mar. Ecol. Prog. Ser 85:35–53.

________. 1997. Size-selective mortality in the juvenile stage of teleost fishes: A review. Bull. Mar. Sci. 60:1129–1157.

Sogard, S.M., G.V.N. Powell, and J.G. Holmquist. 1987. Epibenthic fish communities on Florida Bay banks: relations with physical parameters and seagrass cover. Mar. Ecol. Prog. Ser 40:25–39.

Steele, M.A. 1997a. The relative importance of processes affecting recruitment of two temperate reef fishes. Ecology. 78:129–145.

________. 1997b. Population regulation by post-settlement mortality in two temperate reef fishes. Oecologia 112:64–74.

________. 1998. The relative importance of predation and competition in two reef fishes. Oecologia. 115:222–232.

________. 1999. Effects of shelter and predators on reef fishes. J. Exp. Mar. Biol. Ecol 233:65–79.

Steele, M.A., and G.E. Forrester. 2002. Early post-settlement predation on three reef fishes: effects on spatial patterns of recruitment. Ecology 83:1076–1091.

Steele, M.A., G.E. Forrester, and G.R. Almany. 1998. Influences of predators and conspecifics on recruitment of a tropical and a temperate reef fish. Mar. Ecol. Prog. Ser 172:115–125.

Steele, M.A., J.C. Malone, A.M. Findlay, M. Carr, and G. Forrester. 2002. A simple method for estimating larval supply in reef fishes and a preliminary test of population limitation by larval delivery in the kelp bass *Paralabrax clathratus*. Mar. Ecol. Prog. Ser 235:195–203.

Stephens, J.S., Jr., G.A. Jordan, P.A. Morris, M.M. Singer, and G. McGowen. 1986. can we relate larval fish abundance to recruitment or population stability? A preliminary analysis of recruitment to a temperate rocky reef. CalCOFI Rep. 27:65–83.

Stephens, J.S., Jr., and K.E. Zerba. 1981. Factors affecting fish diversity on a temperate reef. Env. Biol. Fish 6:111–121.

Swearer, S.E., J.S. Shima, M.E. Hellberg, S.R. Thorrold, G.P. Jones, D.R. Robertson, S.G. Morgan, K.A. Selkoe, G.M. Ruiz, and R.R. Warner. 2002. Evidence of self-recruitment in demersal marine populations. Bull. Mar. Sci. 70:251–271.

Sweatman, H.P.A. 1983. Influence of conspecifics on choice of settlement sites by larvae of two pomacentrid fishes (*Dascyllus aruanus* and *D. reticulatus*) on coral reefs. Mar. Biol. 75:225–229.

Szabo, A.R. 2002. Experimental tests of intercohort competition for food and cover in the tidepool sculpin (*Oligocottus maculosus* Girard). Can. J. Zool. 80:137–144.

Thorrold, S.R, G.P. Jones, M.E. Hellberg, R.S. Burton, S.E. Swearer, J.E. Neigel, S.G. Morgan, R.R. Warner 2002. Quantifying larval retention and connectivity in marine populations with artificial and natural markers. Bull. Mar. Sci. 70:291–308.

Thresher, R.E., P.L. Colin, and L.J. Bell. 1989. Planktonic duration, distribution and population structure of Western and Central Pacific damselfishes (Pomacentridae). Copeia. 2:420–434.

Tupper, M., and R.G. Boutilier. 1995. Effects of conspecific density on settlement, growth and postsettlement survival of a temperate reef fish. J. Exp. Mar. Biol. Ecol. 191:209–222.

Valle, C.F., J.W. O'Brien, and K.B. Wiese. 1999. Differential habitat use by California halibut, *Paralicthys californicus*, barred sand bass, *Paralabrax nebulifer*, and other juvenile fishes in Alamitos Bay, California. U.S. Fish. Bull 97:646–660.

Ventresca, D.A., R.H. Parrish, J.L. Houk, M.L. Gingras, S.D. Short, and N.L. Crane. 1995. El Niño effects on the somatic and reproductive condition of blue rockfish, *Sebastes mystinus*. CalCOFI Rep. 36:167–174.

Victor, B.C. 1986a. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecol. Monogr. 56:145–160.

________. 1986b. Duration of the planktonic larval stage of one hundred species of Pacific Atlantic wrasses (family Labridae). Mar. Biol. 90:317–326.

Warner, R.R., and P.L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: A field guide to the storage effect. Am. Nat. 125:769–787.

Warner, R.R., and T.P. Hughes. 1988. The population dynamics of reef fishes, p. 149–155. In*:* Proc. 6th Intern. Coral Reef Symposium. Vol. 1, Townsville.

Wellington, G.M., and B.C. Victor. 1989. Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Mar. Biol. 101:557–567.

Woodbury, D., and S. Ralston. 1991. Interannual variation in growth-rates and back-calculated birth-date distributions of pelagic juvenile rockfishes (Sebastes spp.) off the central California coast. Fishery Bulletin 89:523–533.