

Chapter 6

Mechanisms Affecting Recruitment Patterns of Fish and Decapods in Tropical Marine Ecosystems

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Abstract

The early benthic life history of fishes and decapods in tropical coastal ecosystem can be partitioned into three main stages – settlement, post-settlement transition, post-settlement stage – which culminate in recruitment. Although most species go through these early life history stages, not all species follow the same strategy. Life history strategies occur in three general categories: Habitat Specialists, Habitat Generalists, and Ontogenetic Shifters. Despite this variation in life history strategy, common processes affect the early life history stages of tropical marine fishes and decapods. The life history transition from planktonic larva to benthic post-larva connects oceanic and coastal habitats. However, benthic features and benthic processes affect early life history stages so that settlement and post-settlement distributions are not perfect reflections of larval supply patterns. The abundances and distributions of settlement and post-settlement life history stages result from complex interactions of larval supply, larval behavior, and the interactions of early settlers with the benthic environment. Since much of the very high mortality that occurs during settlement and early post-settlement appears to be due to predation, the direct effects of predators may be the most important factors acting on these early life history stages. Habitat selection, priority effects, predator avoidance, inter- and intra-specific competition, and aggression during and after settlement are also important influences on abundances and distributions of settlement and post-settlement fishes and decapods. The connection between nursery habitat availability and adult population abundances has been demonstrated, so it is likely that these other interactions of early life history stages with the benthic environment have demographic implications that are not yet understood.

Keywords: habitat selection, mortality, post-settlement, priority effects, settlement

Introduction

Some three decades ago, tropical marine ecologists were struck with the fact that profound ignorance of recruitment mechanisms hampered understanding of population dynamics and community ecology in tropical ecosystems. Knowledge of the processes affecting larval-through-juvenile life stages still lags well behind knowledge of adults, but much has been learned. Through a review of this knowledge, we can begin to discern some of the patterns of recruitment, surmise some underlying processes, and think of how the focus of future research might be sharpened on critical recruitment issues.

The transition from larval to benthic life history phase connects oceanic and coastal habitats. The distribution of settlers in benthic habitats depends on the distribution of larvae in oceanic habitats, but benthic distributions are not a simple reflection of oceanic distributions. Distributions of settlers reflect a complex interaction of larval supply, larval behavior and the interactions of early settlers with benthic features. In addition, the condition of settling larvae during the planktonic phase influences post-settlement growth and survival, further connecting oceanic and benthic processes. Oceanic and early benthic processes have demographic consequences because unsuccessful individuals will not join adult populations. Finally, different benthic habitats are often connected as early life history stages undergo ontogenetic habitat shifts. Thus, recruitment-associated ontogenetic processes connect the habitat mosaic of nearshore tropical systems, with habitat-associated features of coastal tropical systems have a powerful influence on recruitment.

Section 6.1 Defining Recruitment

Since definitions of early life history stages of fish and decapods have been ambiguous in the peer-reviewed literature, some of the conflicting results among studies may be simply semantic. Here we provide a distinct definition of the early life history stages that culminate in recruitment. Recruitment occurs at the end of the post-settlement stage, and incorporates effects of larval, settlement, and post-settlement processes. Recruitment is characterized by entrance into a period of lower mortality, and marks the first record of an individual in the juvenile stage. Thus, it is the early juvenile stage when many recruitment surveys occur (references for and definitions of pre-recruitment stages are in Table 6.1).

Most tropical marine fishes and invertebrates have a two-phase life cycle that decouples local reproduction from recruitment into the local population. For these species, larvae are planktonic, and juveniles and adults are demersal. As a general rule, fertilization for these species is external and eggs are buoyant. Duration of the planktonic period varies among species, and also depends on environmental conditions. At the end of the planktonic phase, larvae search for appropriate settlement habitats and enter the demersal portion of their life history, many undergoing metamorphosis as they settle out of the water column. The processes affecting the transition from larva to juvenile, and the early period of the juvenile stage have important demographic implications that could be critical to population regulation.

Knowledge of the early life history of a species is critical to understanding the mechanisms affecting recruitment. To some extent, the comparative importance of these mechanisms remains unclear because the literature often doesn't sufficiently partition the early life history stages of fishes and invertebrates. In many cases, for example, the term 'juvenile' is used to refer to all life stages after larval settlement and before maturity (e.g., St. John 1999), even though recent research has shown that the relative importance of different mechanisms

influencing early life histories changes as individuals grow (Jones 1991). Predation is typically most important within 48 hours of settlement (Almany 2004b, Almany and Webster 2004), whereas competition may be more important in later stages (Risk 1998).

Research would benefit from a clearly delineated nomenclature describing early life history of fishes and decapods. Common use of terms will clarify discussion, promote testing of findings and formulation of predictions, and provide a framework for applying these results on a larger scale. Moreover, a common delineation of early life history stages will help bring about a common structure to future discussion and research. It is the overall structure proposed here, rather than the early life history delineations themselves, that is new. Heretofore, each definition of an early life history stage has, for the most part, stood alone, independent of the context of other early stages. For our discussion on recruitment, we follow a structure assembled from four definitions proposed by Adams et al. (2006), since it provides a clear and convenient breakdown of the life history stages that contribute to fish and decapod recruitment in tropical ecosystems (Table 6.1).

Section 6.2 Defining Early Life History Strategies

Within the general and ubiquitous life history strategy of planktonic larvae and demersal juveniles and adults are three categories based on the patterns of habitat use by the demersal juvenile and adult life stages (Table 6.2). In Strategy I, *habitat specialists*, planktonic larvae settle into the same location they will remain throughout their demersal life stages. In Strategy II, *habitat generalists*, larvae can stay, or move among, numerous habitats, and are not site attached. In Strategy III, *ontogenetic shifters*, larvae tend to settle in habitats and locations different from those used by adults, and undergo ontogenetic transitions to the adult life stage.

This categorization of early life history strategies underscores the limitations of applying species-specific research findings at the community level. For example, much early research on the implications of early life history processes focused on the lottery hypothesis (Sale 1977, 1978), which emphasized the chanciness of larval settlement, and postulated that natural selection must produce habitat generalists to maximize the probability of finding appropriate settlement sites. To a great extent, the lottery hypothesis was based upon the prevalence of research on site-attached species, such as territorial pomacentrids (e.g., Doherty 1983). Since that time, research has shown extreme variation among species in habitat use during early life stages (reviewed in Adams et al. 2006), plasticity in early life stage habitat use within species (reviewed in Adams et al. 2006), and previously undetected changes in habitat use by pre-recruitment fishes (e.g., Kaufman et al. 1992). In addition, habitat variability greatly modifies species interactions such as competition and predation (e.g., Anderson 2001, Almany 2004a).

Given the categorization of life history strategies, and the need to find general patterns that apply within these categories, it is useful to first determine which species fall into which categories. Unfortunately, the strategy used does not appear to be phylogenetically constrained, in that life history category can vary within the family, and even the genus level, so species-specific data are needed. Among eight species of labrids studied by Green (1996), two exhibited ontogenetic shifter patterns, whereas six species were habitat generalists. Similarly, McGehee (1995) found that three species (*Stegastes planifrons*, *S. variabilis*, and *S. partitus*) of pomacentrids exhibited high site fidelity (habitat specialists), while the fourth species (*S. leucostictus*) showed poor site fidelity (habitat generalist). One method that may be useful in predicting life history strategy is to use patterns of larval metamorphosis as predictors (McCormick and Makey 1997), which can be done via larval collection and lab observations.

At the community level, Gratwicke et al. (2006) determined that 47% of species surveyed in a study of non-estuarine lagoons and adjacent reefs in the Caribbean exhibited habitat use patterns indicative of ontogenetic habitat shifts. Similarly, Nagelkerken et al. (2002) found evidence for ontogenetic shifter strategy for 21 of the 50 (42%) most common reef species. In a survey of juvenile and adult densities of 17 species of nocturnal reef fishes at Moorea Island, Lecchini (2006) found that 47% showed ontogenetic habitat shifts. In contrast, when Adams and Ebersole (2002), working in the Caribbean, examined all fishes within lagoon and backreef habitats, they found clear ontogenetic lagoon (juvenile) – reef (adult) division for only 22 of 96 (23%) species. Differences in these estimates were due largely to the suite of species surveyed, but also to assignment of different size classes to ontogenetic stages.

Characterizing the life history stages of a species can be difficult. For many species the early life history stages are not clearly defined (but see Shulman and Ogden 1987 for a clear depiction of ontogeny by size class for *Haemulon flavolineatum*). When ontogeny is inadequately represented by defining life history stages only by size or characterizing all immature fishes as juveniles, the inference that a given habitat is a nursery for some species may be incorrect. More research elucidating early life history is needed to better evaluate factors affecting recruitment.

The following sections review the growing knowledge base of fish and decapod recruitment, set in a framework that follows the definitions set forth above. We hope that this review will contribute to a synthesis of research already completed and help focus the design of future research.

Section 6.3 Larval Settlement (departure from the pelagic environment and entrance into benthic habitats)

Oceanographic processes influence settlement of coral reef fishes and decapods by transporting and influencing the survival of larvae (Choat et al. 1988, Acosta and Butler 1999). That larval settlement patterns can be temporally consistent across space at multiple scales (e.g., Fowler et al. 1992, Caselle and Warner 1996, Acosta and Butler 1997, Tolimieri et al. 1998, Vigliola et al. 1998, Schmitt and Holbrook 1999b) demonstrates the important impact of oceanographic processes on larval supply. In Barbados, the occurrence of late stage larvae in light traps corresponded with the first appearance of juveniles of these species on reefs, suggesting that larval supply was a good indicator of settlement (Sponaugle and Cowen 1996). Moreover, larvae of some fishes (e.g., *Stegastes partitus* and *Acanthurus bahianus*) were consistently associated spatially and temporally, suggesting these species were influenced similarly by oceanographic processes such as prevailing currents, tidal currents, wind-induced water flow, and large-scale externally forced events. Similarly, appearance of postlarval spiny lobsters in the Florida Keys is strongly related to tides, and less strongly related to favorable winds (Acosta and Butler 1997, Eggleston et al. 1998). Postlarvae of brachyuran crabs in Barbados also responded to tidal influences, generally producing the greatest supply of post-larvae at third-quarter moons with minimal tidal amplitude (Reyns and Sponaugle 1999).

6.3.1 Modification of Larval Supply

However, the patterns of larval supply established by oceanographic processes can not be expected to persist through settlement. Butler and Herrnkind (1992) found that spatial patterns of benthic settlement for spiny lobster (*Panulirus argus*), for example, differed from abundance patterns of planktonic larvae at local scales in Florida Bay and in the Florida Keys (though the patterns sometimes agreed at regional scales). Settling larvae begin to interact with the bottom

well before they actually reach it (Choat et al. 1988). Attacks of benthic-dwelling predators provide but one example of how benthic-associated processes may directly influence the abundance of settling larvae (Choat et al. 1988, Fowler et al. 1992, Booth and Beretta 1994, Gibson 1994, Booth and Brosnan 1995, Tolimieri 1998a, Tolimieri et al. 1998). Behavioral responses to such features by settlement-phase fishes and decapods also serve to modify the pattern of larval supply (for fishes, see Sweatman 1988, Booth and Beretta 1994, Fernandez et al. 1994, Elliot et al. 1995, Shanks 1995, Leis and Carson-Ewart 1999, Almany 2003, Garpe and Ohman 2007; for decapods, see Forward 1974, 1976, Knowlton, 1974, Forward and Hettler 1992, Welch et al. 1997, Gimenez et al. 2004, Gimenez 2006). Overall, complex interactions of larval supply, larval behavior, and benthic features ultimately determine patterns of settlement. Furthermore, consistency in spatial patterns of larval settlement is usually not the case for fishes or decapods (e.g., Fowler et al. 1992, Green 1998, Tolimieri et al. 1998, Vigliola et al. 1998, Montgomery and Craig 2005) because the relative importance of oceanographic vs. benthic processes varies among species, among locations, and over time.

Habitat dispersion interacts with larval behavior to influence the distribution of settlers. Larvae are not passive particles. Fish (e.g., Stobutzki and Bellwood 1997, Stobutzki 1998, Leis and Carson-Ewart 1999) and decapod (e.g., Fernandez et al. 1994, Shanks 1995) larvae are capable of active swimming for considerable distances. Swimming ability, however, differs among species (e.g., Stobutzki and Bellwood 1997, Stobutzki 1998), and their behavior influences timing and location of settlement. Furthermore, competent larvae are capable of active searching for appropriate settlement habitats based on a variety of criteria (for fishes, see Sweatman 1988, Booth and Beretta 1994, Elliot et al. 1995, Leis et al. 2002, Almany 2003, Leis and Lockett 2005, Garpe and Ohman 2007; for decapods, see Knowlton, 1974, Welch et al.

1997, Gimenez et al. 2004, Gimenez 2006). The combination of larval supply, larval behavior, and availability of settlement habitats determines patterns of settlement.

Recent research has shown that settlement-stage larvae of many species use a variety of cues to find reefs and appropriate settlement habitats. Sound is important for finding reefs (e.g., Tolimieri et al. 2000, reviewed in Montgomery et al. 2001, Leis and Lockett 2005, Arvedlund and Kavanagh this book), whereas olfactory senses are important for settlement site selection (e.g., Sweatman 1988, Butler and Herrnkind 1991, Elliot et al. 1995, Harvey 1996, reviewed in Montgomery et al. 2001, Atema et al. 2002, Horner et al. 2006). Settlement cues are discussed in detail in Chapter 6.

6.3.2 Behavior of Settlement-Stage Larvae

Regardless of the mechanisms used by larvae to find suitable settlement habitats, larval behavior during the settlement process modifies patterns of settlement so that they differ from patterns of offshore larval distribution (e.g., Sponaugle and Cowen 1996, Cruz et al. 2007). Settlement patterns can be used to make strong inferences about settlement behavior. For example, working in French Polynesia, Schmitt and Holbrook (1999b) found consistent patterns of settlement by three species of *Dascyllus* (all habitat specialists): at the island scale, one species settled primarily on the north end of the island, whereas the other two species tended to settle toward the south end of the island. At the lagoon scale, they found that *D. trimaculatus* settled throughout the lagoon, whereas *D. aruanus* settled on habitats in the nearshore, and *D. flavicaudus* in the offshore, portions of the lagoon. Since they used standardized, initially empty, settlement habitats specific to each species, habitat availability was not a factor. The implications are clear: for *D. trimaculatus*, finding suitable settlement habitats was highly likely because of

the widespread pattern of settlement. However, for the other two species, larval behavior and habitat availability likely limit the extent to which settlement would be successful – if suitable habitats are not present in nearshore (*D. aruanus*) or offshore (*D. flavicaudus*) areas, these species will be absent regardless of larval supply. Working in Hawaii, Kobayashi (1989) also found species-specific differences in larval behavior. Larvae of two gobiid species used visual cues to remain near reef settlement habitats, whereas larvae of *Foa brachygramma* (Apogonidae - Cardinalfishes) and *Encrasicholina purpurea* (Engraulidae - Anchovies) were most abundant at off-reef sample stations. Similar effects of larval behavior are evident at the community level, where, overall, more species settle on offshore than nearshore areas (Planes et al. 1993, Hamilton et al. 2006).

Although cues used at settlement by ontogenetic shifters and habitat generalists have not been examined as closely as in habitat-specialist damselfishes, consistent settlement patterns suggest active settlement site selection. In the Caribbean, for example, larvae of many reef fishes (*Acanthurus* spp. Adams and Ebersole 2002, 2004; *Epinephelus striatus*, Eggleston 1995, Dahlgren and Eggleston 2000; *Haemulon flavolineatum*, McFarland 1980, Shulman 1985a) and decapod crustaceans (e.g., Panuliridae – Spiny Lobsters, Acosta and Butler 1999) pass over reef habitats to reach lagoon habitats, which suggests that these larvae are using some cue to find these habitats, and olfactory differentiation of lagoonal versus oceanic water has been shown for some fishes (Atema et al. 2002, Huijbers et al. 2008).

Active habitat selection also implies that non-reef habitats provide advantages toward successful recruitment that compensate for the fitness costs of additional energy expenditure and predation risk experienced by the incoming larvae, and by the juveniles that must later move again to adult habitats on the reef. Moreover, it is likely that many species use the rather large

target of non-reef benthic habitats as settlement habitat, and then move to more suitable post-settlement micro-habitats within the lagoon (e.g., Herrnkind 1980, McFarland 1980, Marx and Herrnkind 1985a, 1985b, Herrnkind and Butler 1986, Robertson 1988, reviewed in Parrish 1989, Adams and Ebersole 2004). Gratwicke et al. (2006) found that 67% of the fishes of reefs and non-estuarine lagoons in the British Virgin Islands exhibited patterns of ontogenetic habitat partitioning between lagoon and reef habitats, so such a strategy may be widespread.

6.3.3 Mortality and Larval Condition

Mortality is extremely high during larval settlement (and post-settlement transition – see below). For example, Doherty et al. (2004) estimated that 61% of the nocturnally settling fish larvae entering their study area in Moorea Island (French Polynesia) were lost by morning. Similarly high rates of predation on settling and recently settled spiny lobsters have been found by Acosta and Butler (1999) in the Florida Keys. Although the high mortality rate continues for days (or longer, depending on species), mortality during settlement makes a significant contribution to overall mortality of the recruitment phase.

Since mortality is extremely high during the settlement and post-settlement process (Almany 2004a, Almany and Webster 2004, Doherty et al. 2004), any advantage provided by good condition has survival implications. For example, in a laboratory experiment, McCormick and Molony (1992) found that reef fish larvae at their study site near Lizard Island, Great Barrier Reef, Australia, receiving more food were larger and in better condition, so were able to settle faster than were low condition fish. They conjectured that these advantages would provide greater flexibility in the timing of settlement and hence increased opportunity to select habitat at settlement. Lower condition larvae were able to recover rapidly, feeding at rates similar to those

in the high feed treatment and settling soon after -- but it is unclear whether this compensatory ability would offset advantages of reduced exposure to predation in the water column and larger size at settlement that the well-fed larvae experienced.

Does high lipid content translate directly to high larval fitness (Sponaugle and Grorud-Colvert 2006)? Settlement-stage larvae with greater lipid stores are able to swim greater distances (Stobutzki 1998), enabling them to search more widely for suitable settlement habitat. Positive connections between nutritional condition, larval growth, and juvenile survival have also been established for decapod crustaceans (Knowlton, 1974, Gimenez et al. 2004, Gimenez 2006). Larvae entering the recruitment process in poor condition are more likely to be preyed upon (Hoey and McCormick 2004, McCormick and Hoey 2004), though this is not always the case: in some cases increased aggression (Jones 1987) or size-selective predation (Sogard 1997) is focused on the largest individuals. Even small-scale variation in larval growth and condition can be important (McCormick 1994).

The degree to which larval size and condition are environmentally versus genetically controlled is unclear. In the Caribbean – western Atlantic Sponaugle and Grorud-Colvert (2006) and Sponaugle et al. (2006) used growth as a proxy for condition (condition traditionally measured by physiological metrics such as the amount of lipid stores), and found that environmental variability affected growth (and thus implied condition) of bluehead wrasse (*Thalassoma bifasciatum*) larvae, and that these larval characteristics influenced survival. In the Florida Keys, Sponaugle et al. (2006) examined otoliths of post-settlement bluehead wrasse to examine the effect of water temperature on larval growth, pelagic larval duration, and other factors, and the effect of these factors on size-at-settlement. Size-at-settlement, a function of larval growth and pelagic larval duration, was greatest at intermediate temperatures. They

concluded that larvae grow fastest at metabolically optimal temperatures. Perhaps most important, larval growth was positively correlated with early juvenile growth (Fig. 6.1) (also in Vigliola and Meekan 2002, Nemeth 2005), and mortality was lower for fish with good larval condition and high early juvenile growth (Sponaugle and Grorud-Colvert 2006), which likely increased survival.

Although they worked on post-settlement stages, Vigliola et al's (2007) results from western Australia are also applicable here. They suggest that some of the variation in traits exhibited by settlement-stage larvae may be inherited. They found size selective post-settlement mortality, with smaller, slower-growing individuals suffering highest mortalities in all cohorts they examined. This size-selective mortality was so severe, in fact, that it affected the genetic composition of juvenile populations as measured by mtDNA haplotypes. To the extent that these traits were linked to the condition and size of settling larvae, their results have both demographic and population-level genetic effects because of the apparent links between larval condition at settlement and subsequent juvenile survival. To the extent that larval growth rate is a heritable trait, these factors are especially important to examining effects of settlement-stage larval condition on juvenile survival because coral reef fishes invest in rapid growth as an opportunistic bet hedging strategy to achieve a selective advantage in the highly competitive and structurally complex coral reef environments (Fonseca and Cabral 2007).

Larval size at settlement is not always a good indicator of condition. McCormick and Molony (1993) found a poor correlation between condition and fish length for a tropical goatfish (*Upeneus tragula*) in Australia, and age at settlement was not correlated with standard measures of condition (carbohydrate content, lipid content, burst swimming speed). Their results indicate that a multi-faceted analysis of settlement-stage larval condition is necessary to make predictions

on post-settlement survival and recruitment. In addition, in some cases increased aggression (Jones 1987) or size-selective predation (Sogard 1997) can be focused on the largest individual. So bigger is not always better, which underscores the need to examine species individually.

Section 6.4 Post-Settlement Transition (A distinct behavioral phase during which individuals are associated with the benthos but are not yet functioning as juveniles.)

6.4.1 Delayed Metamorphosis

During the post-settlement transition, larvae of many species are able to re-enter the pelagic phase to search for better habitat (Kaufman et al. 1992). Reviewing observations of larval settlement behaviors by others, Kaufman et al. (1992) estimated that the post-settlement transition phase applied to 68 species of coral reef fishes in the US Virgin Islands, showing the phenomenon to be widespread. Transitional individuals often have specialized behavioral and morphological characteristics particular to this phase. The post-settlement transitional phase may last hours to weeks (McCormick and Makey 1997), depending on the species, and metamorphosis may occur before, during, or after the post-settlement transition (Kaufman et al. 1992). In general, transition individuals differ in appearance from larval and juvenile conspecifics.

The ability to delay or accelerate metamorphosis associated with settlement appears to be common in fishes and decapods, and this may influence post-settlement processes. For example, Butler and Herrnkind (1991) have shown that pueruli larvae of spiny lobster (*Panulirus argus*) of the Caribbean and western Atlantic accelerate metamorphosis slightly when exposed to the red alga that is the preferred settlement habitat. In a laboratory study of three Florida hermit crabs

(*Pagurus maclaughlinae*, *Paguristes tortugae*, and *Clibanarius guttatus*), Harvey (1996) found that exposure to water previously inhabited by conspecific adults inhabiting shells accelerated metamorphosis in two species, and all three species delayed metamorphosis in the absence of empty shells. Kaufman et al. (1992) observed a four-fold difference in size of post-settlement *Acanthurus* larvae in the Caribbean, which they attributed to the species' ability to delay metamorphosis. The largest individual initially settled, but then re-entered the water column, presumably to continue searching for a settlement site. Using cages to place settlement-stage *Acanthurus triostegus* larvae on the benthos or suspended in the upper water column in French Polynesia, McCormick (1999) showed that many of the pelagic-caged larvae were able to delay metamorphosis, whereas all of the benthic-caged fish completed metamorphosis within five days. However, the individuals that delayed metamorphosis still deposited a settlement mark on their otoliths, indicating competency to settle. It is unclear whether this settlement mark is deposited for other species that delay settlement, and the extent to which this might influence estimates of post-settlement growth rates. Leis and Carson-Ewart (1999) captured settlement stage larvae of the coral trout (*Plectropomus leopardus*) at night, and observed their swimming behavior during daylight hours. Many of the released larvae (26 to 32%) exhibited their ability to delay metamorphosis and swam toward open water away from the reef, presumably to attempt settlement the next night. Other larvae searched for settlement locations on the reef.

6.4.2 Habitat Selection

A post-settlement transitional phase implies that selective settlement is occurring, but does it occur in many species? Though spiny lobster pueruli tend to stick with the *Laurencia* algae clump where they first settled if that clump is isolated, they rapidly emigrate from the

clump when other clumps form a more continuous mat – and are especially likely to leave when food is scarce on the first clump (Marx and Herrnkind 1985b). Sancho et al (1997) observed transitional surgeonfish (acanthurid) larvae (*Ctenochaetus strigosus*) swimming upcurrent in search of suitable settlement habitat. When the habitats explored were not suitable or already occupied, the transitional larvae resumed swimming upcurrent. During their observations of coral trout larvae (*Plectropomus leopardus*, Serranidae – Sea Basses) at Lizard Island, Great Barrier Reef, Leis and Carson-Ewart (1999) noted active swimming to search for settlement sites – with avoidance of areas with predators, but no selection of specific settlement habitats.

Given that finding appropriate settlement habitat is challenging, species with less restrictive settlement habitat requirements may have an initial advantage. For example, Robertson (1988) and Parrish (1989) suggested that lagoon seagrass, algal plain, and other common non-reef habitats provide large target areas for larval settlement, with subsequent movement to nearby suitable recruit and juvenile habitats such as rubble, patch reef, mangroves, or back-reef. This settlement-and-movement strategy would allow post-settlement fishes to respond to benthic processes such as priority effects, competition, and predation. Priority effects refer to the process by which the presence of one species in a habitat decreases the probability of colonization by another. One species can reduce recruitment of another via interference competition (adult and subadult residents or settling juveniles can interfere with larval settlement), or preemption of resources, or predation (predatory adult and subadult residents can decrease local settlement directly by preying on settlers or indirectly by inducing settlers to choose sites without predators (Shulman et al. 1983). Adams and Ebersole (2004) conjectured that observed juvenile abundance patterns in St. Croix, United States Virgin Islands for the surgeonfish *Acanthurus chirurgus* and grunts (*Haemulon* spp.) may have resulted from this

settlement strategy. Use of this 'settle and move' strategy is also suggested by the patterns of habitat use by the early juveniles of spiny lobsters (*Panulirus argus*, reviewed in Lipcius and Eggleston 2000) and Nassau groupers (*Epinephelus striatus*, Eggleston 1995).

A likely reason for use of non-reef habitats by juveniles of species with reef-associated adults is reduced inter-specific interactions – especially reduced predation. In tethering experiments, Acosta and Butler (1999) found much higher predation on recently settled transparent larvae and pigmented postlarvae of Caribbean spiny lobsters on coral reefs than on inshore vegetated habitats (Fig. 6.2). And the plant stems inhabited by post-larval brown shrimp (*Penaeus aztecus*) protect them from predators (Minello and Zimmerman 1983a,b; Zimmerman and Minello, 1984; Zimmerman et al., 1984; Minello and Zimmerman 1985)

Predation on juvenile French grunts (*Haemulon flavolineatum*) in the US Virgin Islands in seagrass beds decreased with distance from the backreef (Shulman 1985a). Similarly, predator encounter rates for juvenile surgeonfish (*Acanthurus chirurgus*) in seagrass beds in the Caribbean decreased with distance from patch reefs, as did aggression from territorial herbivores (Sweatman and Robertson 1994). Moreover, effects of predators, and the suite of predators that impact recruits, change with degree of patch reef isolation (Overholtzer-McCleod 2006). Marx and Herrnkind (1985b) concluded that recently settled spiny lobsters in Florida choose to live in clumps of *Laurencia* algae because this habitat provides both food and protection from predators, and the predation experienced by newly settled Caribbean lobsters in the mangrove proproots they choose is less than they would encounter with coral shelter (Acosta and Butler (1997); microhabitat (shelter size) and habitat location continue to be important to survival of juvenile spiny lobsters (Eggleston and Lipcius 1992, Mintz et al. 1994).

Searches for suitable habitats by post-settlement transition individuals may be influenced by saturation of habitats (Shulman et al. 1983, Forrester 1995, 1999, Schmitt & Holbrook 1999b). In comparisons of juvenile abundance on lagoon and back-reef habitats of the US Virgin Islands, Adams and Ebersole (2002) suggested that suitable juvenile habitats on the back-reef became saturated early during the summer (high settlement season), so that later-arriving fishes settle on lagoon habitats that are not yet saturated. In this scenario, lagoon habitats attracted more settlers in summer because resources (food, shelter, and space) were more available than on the back-reef, which is crowded with fish of all ages competing for these resources. In winter, when the density of fishes is lowest, incoming larvae may settle on the first appropriate habitat they encounter—which is the back-reef. These findings were similar to those of Munro et al. (1973) and Shulman (1985a). In this scenario, post-settlement transition individuals seek out alternative habitats where fish densities are lower, evening out the per capita use of resources among habitats.

Much of the habitat selection by settlement-stage larvae likely takes place during the post-settlement transition. During this period, larvae are associated with the benthos, but have not yet taken on full occupancy of benthic habitats or juvenile behaviors, so individuals may be able to make additional assessments of potential settlement sites. The post-settlement transition is also when most priority effects (e.g., Shulman et al. 1983, Almany 2003, 2004b) take place. Post-settlement often involves competitive and aggressive interactions, (Booth and Brosnan 1995), but how these interactions act to modify patterns established at settlement varies among species (Almany 2003, 2004a). For example, Caribbean post-larval spiny lobsters in the “algal” phase (so-named because clumps of red *Laurencia* are a preferred habitat at this stage) are solitary and fiercely agonistic toward conspecifics (Andree 1981, Marx 1983, Marx and

Herrnkind 1986). Sancho et al. (1997) observed that transitional individuals of the Pacific surgeonfish *Ctenochaetus strigosus* were rebuffed by conspecifics as they explored potential settlement sites at Johnston Atoll, Central Pacific. Moreover, this competitive/aggressive priority effect likely had an indirect effect on survival, since predation on schools of transitional *C. strigosus* searching for settlement sites was also observed. Territorial damselfishes (pomacentrids) are particularly prone to using aggression to inhibit settlement of hetero- and con-specifics (e.g., Shulman et al. 1983, Sweatman 1985, Risk 1998). For example, in an experiment that manipulated the presence of adults on experimental reefs in the Caribbean, Almany (2003) found that adult beaugregory (*Stegastes leucostictus*) reduced conspecific recruitment. Settlement and post-settlement persistence of surgeonfishes (*Acanthurus* spp.) was reduced by the presence of the beaugregory damselfish (*S. leucostictus*) (Shulman et al. 1983; Risk 1998). Priority effects such as these may be strictly hierarchical, as in the consistent exclusion of post-settlement *Acanthurus* surgeonfishes by beaugregory damselfishes (Shulman et al. 1983) or the consistent effects imposed by interspecific competition among *Dascyllus* damselfishes found by Schmitt and Holbrook (1999b). In contrast, Munday (2004a) found no competitive hierarchy between two coral-dwelling gobies in the Pacific.

6.4.3 Predation

Predation is often a strong influence on recruitment, especially during the first 48 hours of settlement (Webster 2002, Almany 2004b, Almany and Webster 2004), which is well within the post-settlement transition window for many species (e.g., *Acanthurus triostegus* post-settlement metamorphosis takes up to five days (McCormick 1999)). Almany (2003) manipulated the presence of resident piscivores, and found that piscivores reduced settlement of

the beaugregory damselfish (*Stegastes leucostictus*). However, on reefs where adults of other damselfish species were also present, the piscivores had no effect on recruitment, suggesting that interspecific aggression was indirectly influencing settlement. The effects of resident piscivores on recruitment on another pomacentrid (*S. partitus*) were similar, but were not significant because of overall low larval supply. In the same study, Almany (2003) found that resident piscivores also reduced recruitment of the surgeonfish (*A. coeruleus*).

Almany's (2003) study is especially pertinent because he surveyed his experimental reefs on a daily basis, so he was able to observe post-settlement transitional individuals. Although Almany concluded that his results could be explained by post-settlement mortality, with much of this mortality occurring within hours of settlement (often before his daily visual censuses), his visual censuses included new settlers and post-settlement individuals – and so mixed settlement (site selection by larvae) and post-settlement effects. Shulman et al (1983) and Tupper and Juanes (1999) found that settlement of Caribbean grunts (*Haemulon* spp.) was lower where juveniles of predatory fishes such as snappers (lutjanids) had already settled, suggesting that some species select settlement sites to avoid potential future predation.. Webster (2002) and Almany (2004b) found similar results on the Great Barrier Reef, where presence of resident piscivores reduced recruitment of most fishes, with losses occurring mostly during the first 48 hours after settlement. However, as with Almany's (2003) findings in the Caribbean, the relative effects of resident piscivores on recruitment varied among fish species. Some species (e.g., the damselfish *Pomacentrus amboinensis*) experienced density-dependent mortality, whereas others (e.g., the damselfish *Neopomacentrus cyanomos*) experienced density-independent mortality. Density-independent mortality resulted in recruitment that reflected larval supply, but density-dependent mortality modified patterns of larval supply.

The examples listed above on differences in settlement site selection suggest that caution must be used when applying findings across species and families of fishes and decapods. The community-level effects of differential predation on post-settlement fishes are underscored in a study by Almany and Webster (2004). They censused post-settlement fishes of 20 species on the Great Barrier Reef, and 15 species in The Bahamas, on reefs with and without predators. The predators were serranids (sea basses) and pseudochromids (dottybacks) in Australia, and serranids and muraenids (morays) in the Bahamas. The species they surveyed for recruitment represented Acanthuridae (surgeonfishes), Chaetodontidae (butterflyfishes), Labridae (wrasses), Pomacentridae (damselfishes), Pomacanthidae (angelfishes), and Siganidae (rabbitfishes). Using rarefaction analysis to examine whether predator effects on recruitment directionally changed fish community composition, they found that recruitment species richness was higher on reefs without piscivores, predators had a greater effect on relatively rare species, and some species were present only on reefs without predators. Although they acknowledged that their study did not discriminate between settler avoidance of reefs with piscivores versus predation of post-settlers, they cited previous research (Almany 2003) which used caged piscivores to demonstrate that piscivore presence did not effect settlement (i.e., effects were due to post-settlement predation). Although they measured effects over a period of 44 to 50 days, most settlement modification via predation occurred within the 48 hours of settlement that generally includes the post-settlement transition.

Section 6.5 Post-Settlement Stage (Time period directly after metamorphosis, and one of total benthic association. A period of high benthic mortality.)

The post-settlement transition merges into the post-settlement stage, with the rate of progress varying among species. Post-settlement stage fishes and decapods are entirely benthic-

oriented, yet remain within the high mortality period extending from settlement. As stated in previous sections, the first days of association with benthic habitats are a period of extreme mortality (e.g., Acosta and Butler 1999, Minello et al. 1989, Webster 2002, Almany 2004a, Almany and Webster 2004, McCormick and Hoey 2004, Doherty et al. 2004).

6.5.1 Mortality

Predation is a primary cause of mortality for post-settlement fishes and decapods, but effects vary among species. Following cohorts of post-larval and juvenile brown shrimp (*Penaeus aztecus*) inside and outside predator-exclusion cages allowed Minello et al. (1989) to determine that high mortality in these stages in coastal Texas is due almost entirely to predation – with declines in mortality as the shrimp grow older and larger.

Doherty et al. (2004) followed cohorts of settling unicornfish (*Naso unicornis*) to determine mortality rates over time on coral reefs of Moorea. Initial mortality rates of approximately 61% during the first night of settlement were density-independent, and the density-dependent loss of post-settlement fishes on the first day after settlement ranged from only 9% to 20%, depending on post-settler abundance. Since fish were censused on all available habitats throughout the entire lagoon, all the mortality could be attributed to predation, rather than emigration or re-settlement away from the study area.

Webster (2002) also manipulated resident predators to examine effects of predation on post-settlement mortality of seven species and three family groups at Lizard Island, Great Barrier Reef. In predator-absent treatments, mortality was density-independent. Resident predators negatively affected survival of all species, primarily within two days of settlement -- and, in contrast with predator-absent treatments, mortality was density-dependent for most species (Fig.

6.3). Although the intensity of predator impacts varied among species, mortality rates ranged from 1.1 to 3.7 times higher than in treatments without predators, with predators causing complete recruitment failure for some rarer species (Chaetodontidae - Butterflyfishes).

The influence of post-settlement density-dependent mortality (presumably due to predation) may even vary among cohorts of a single species in a single reef system. Schmitt and Holbrook (1999c) found that the majority of mortality occurred very soon after settlement, but density-dependent mortality was not evident in all cohorts in French Polynesia. Rather, earlier-arriving cohorts experienced density-independent mortality, but their presence induced density-dependent mortality in later-arriving cohorts. These results demonstrate the need to incorporate time and space into studies of post-settlement processes to include inherent variability both within (e.g., Schmitt and Holbrook 1999c) and among (Webster 2002) species.

Density-dependent mortality probably has its greatest impact during the post-settlement stage (Hixon and Webster 2002), although density-dependence may not be apparent (Osenberg et al. 2002). Although their research occurred over a longer time period than recruitment, Hixon and Jones (2005), building upon previous experimentation, showed that competition and predation interacted to cause density-dependent mortality of fishes at Lizard Island, Great Barrier Reef. Although competition generally did not appear to cause mortality directly, the eventual result of competitive exploitation and aggression was predation (Fig. 6.4).

6.5.2 Competition

Competition leading to slower growth rates may be a particular problem for late arriving settlers, since small size is likely to place them lower in competitive hierarchies than earlier-arriving conspecifics. High densities of post-settlement individuals also creates competition for

resources, and may decrease growth rates (Jones 1991). Such competition may result in predation since slower growth rates often result in higher mortality (Jones 1991), but this is not always the case. For example, Forrester (1990) found that although growth rates were lower at high densities because food was less available, this did not influence survival. Moreover, since some predation is selective toward a particular size (Sogard 1997), rapid growth rates resulting in larger individuals may not be a universally positive trait.

The importance of competition probably increases greatly in the post-settlement stage. During settlement, selecting structurally suitable microhabitat is generally more important than avoiding competition (Jones 1991). During the post-settlement transition, and continuing into the post-settlement phase, competition for space – either among settlers or between settlers and occupants – becomes important. The change in relative importance of competition with progressing life phases is exemplified by the tropical Atlantic surgeonfish *Acanthurus bahianus*. Initial settlement of *A. bahianus* is higher in the presence of conspecifics, but post-settlement individuals later compete for limited nocturnal shelter (Risk 1998).

Fishes and decapods fare better when they use shelter appropriate to their body size. Beets (1997) and Hixon and Beets (1993), for example, found that survival of post-settlement Caribbean fishes was lower on artificial reefs with shelter holes large enough for predators, and that survival increase on reefs with shelter holes sized appropriately for post-settlement fishes. Similarly, Nemeth (1998) found that survival of juvenile bi-colored damselfish (*Stegastes partitus*) was higher in habitats with more and smaller crevices they could use as shelter. Since the main source of mortality was encounters with predators, appropriate-size shelters were probably a limiting resource.

Competition for appropriate-sized shelter likely leads to increased mortality, mainly due to predation (Hixon and Menge 1991, Eggleston and Lipcius 1992, Friedlander and Parrish 1998). Competition for suitable shelter is important in shaping post-settlement abundances. Settlement of two *Dascyllus* damselfishes in French Polynesia, for example, was suppressed 80% to 90% by insufficient supply of suitable microhabitats (Schmitt and Holbrook 2000), and post-settlement intra- and inter-specific competition for shelter strongly influenced juvenile abundance (Schmitt and Holbrook 1999b). Aggressive interactions between adult and juvenile damselfishes can make the juveniles more susceptible to predation (Holbrook and Schmitt 2002, Almany 2003). In numerous site-attached species, ontogenetic partitioning of habitat reduces competition between life stages, and enables settlement. For example, juvenile three-spot damselfish (*Stegastes planifrons*) escaped competition for space from territorial adults by settling in dead coral heads (primarily *Agaricia tenuifolia*) – and avoiding the adults that were mostly in live *Agaricia tenuifolia* (Lirman 1994). Similarly, *Pomacentrus sulfurous* appeared to undergo ontogenetic microhabitat shifts (Bergman et al. 2000). Juveniles were associated with branching corals, and were mostly associated with the benthos. In contrast, adult abundance was negatively related to substrate diversity, indicating more general habitat requirements. In addition, adults spent most of their time in the water column.

The appropriate shelter size changes with body size. In the Bahamas, habitat complexity was not a factor in mortality of the damselfish *Stegastes leucostictus* during and immediately after settlement: resident predators (Serranidae – sea basses, Muraenidae - morays) and competitors (territorial adult damselfishes *S. leucostictus* and *S. partitus*) negatively affected survival on both high and low habitat complexity reefs (Almany 2004a). This was attributed to

the ability of competitors and small predators to access the shelter holes available to post-settlers. Over time, as post-settlers grew, survival became higher on reefs with higher complexity.

6.5.3 Movement among Habitats

Type of predator and habitat dispersion can interact to influence the effects of predation. Overholtzer-McLeod (2006) experimentally examined the effect of habitat dispersion on interactions between predators and juveniles on the damselfish *Stegastes leucostictus* and the wrasse *Halichoeres garnoti* in The Bahamas. Both species experienced density-dependent mortality on spatially-dispersed patch reefs (separated by 50m), and density-independent mortality on aggregated patch reefs (separated by 5m). She attributed high (nearly 100%) mortality on aggregated reefs to visits by transient predators that occurred independent of prey densities. In contrast, most of the predation on spatially-dispersed reefs was caused by resident predators (primarily the small grouper *Cephalopholis fulva*). Although the resident predators were also present on the aggregated reefs, their impact on mortality was swamped by the transient predators that generally ate all juveniles present.

Unfortunately, Overholtzer-McCleod's (2006) discounted movement among reefs by *Stegastes leucostictus* as an effect on mortality estimates – and this damselfish shows relatively low site fidelity (McGehee 1995) and the ability to colonize apparently isolated habitats during all benthic life phases (Adams and Ebersole 2002) – but her results reflect an emerging view that the interaction between species vagility and habitat contiguity has community-level effects (Ault & Johnson 1998). The importance of contiguous habitats to community-level processes was emphasized by Ault and Johnson (1998). They found that vagile fishes are able to move among isolated habitats in response to resource availability, whereas more sedentary species seem to

require contiguous habitats for larger scale movement. Habitat contiguity, in conjunction with predator behavior, may also facilitate an aggregative response by predators (e.g., Anderson 2001), with subsequent increases in post-settlement mortality.

Section 6.6 Recruitment (Occurs at the end of the post-settlement stage, and incorporates effects of larval and post-settlement processes.)

The recruitment phase of early life history of fishes and decapods, when individuals can properly be called juveniles, is generally when most surveys occur or begin, so much of the information we have on recruitment has been gathered during this stage. Depending on the species and locations, it has been argued that post-recruitment surveys may provide accurate assessments of larval supply (reviewed in Jones 1991). As seen in previous sections, however, more recent evidence points to very strong modification of abundances from initial larval supply due to settlement through post-settlement processes, which would negate the use of post-recruitment surveys as assessments of larval supply. Although recruitment is characterized by entry into a period of lower mortality compared to that of the settlement through post-settlement stages, some of the same factors influencing those earlier stages – predation, competition for shelter and food resources, and aggression – are also influential for juveniles in the recruitment phase.

Habitat quality and individual condition may interact to influence recruit condition and growth rates of recruits -- and subsequently affect density-dependent mortality. In other words, processes observed in recruits are connected backward to the larval settlement stage. A series of studies on recruitment of *Thalassoma hardwicke* in French Polynesia suggested that individual traits (as measured by growth and lipid content) and habitat quality have synergistic effects on

survival. Condition (as measured by lipid content) and growth rates of individuals were rapid at high quality habitats, and these habitats also had more strongly density-dependent mortality (Shima et al. 2006). The combination of higher settlement and condition at higher quality sites and density-dependent synergy of habitat quality produce extra high recruitment, which may be augmented further by the reduced predation associated with good condition (Booth and Hixon 1999). The overall recruitment patterns that result are complex, however, and the extent to which habitat quality and individual intrinsic traits contribute to differences in density-dependent mortality and survival remains unclear.

6.6.1 Growth and Shelter Size

Survival also depends on growth, especially during the recruitment phase. In a study of the planktivorous damselfish *Neopomacentrus filamentosus* in Western Australia from settlement to three months after settlement, faster growing recruits had higher survival, with size-selective mortality (presumably due to predation) causing the loss of the smallest and slowest growing recruits (Vigliola et al. 2007). Moreover, the intensity of this size-selective mortality was higher in the more numerous of two sequential cohorts, indicating density-dependent mortality. This intense natural selection for large size is indicated by the genetic differences between settlers and recruits that resulted from the intense size-selective mortality. Genetic differences were less evident for a second, less numerous cohort (20% the size of the first cohort), suggesting that natural selection was reduced at the lower density. Alternatively, size-selective mortality in the second, less numerous cohort may have been hard to detect because the mortality rates were so low (Sogard 1997). In any event, the ultimate effect of such size-selective mortality on evolutionary trajectories is unclear.

Changes in habitat requirements with recruit size underscore the importance of appropriately sized shelter. Small crevices that were suitable for post-settlement individuals become too small to provide shelter as the individuals grow. The need for size-specific shelter means that several different life stages may be forced through population bottlenecks. By providing more shelters, Shervette et al. (2004) identified such a bottleneck for juvenile stone crabs (*Menippe adina*) of coastal Mississippi. In bays of coastal Florida, Beck (1995) found that larger stone crabs (*M. mercenaria*) grew slowly, molted infrequently, and were slow to produce eggs when appropriately sized shelter holes were not available.

Post-settlement Caribbean spiny lobster (*Panulirus argus*) use structurally complex microhabitats, such as macro-algae, and move as juveniles to larger, less complex crevice habitats in sponges, soft corals, coralline algae, seagrass, and rock-rubble habitats as they grow too large for the shelter provided by the macro-algae (reviewed in Lipcius et al. 1998). Aggregation becomes part of the anti-predator defense of crevice-dwelling juveniles, since detection of predators and repulsion by antenna-lashing are more effectively accomplished by groups (Eggleston and Lipcius 1992), and juveniles use olfactory cues to find crevices with conspecifics (Nevitt et al. 2000). This association of body size with crevice size continues in later stages, as older juveniles and adults utilize ever-larger crevice-type habitats for shelter. Within the context of this early life history ontogeny, Lipcius et al. (1998) tethered juvenile lobsters of two size classes in experimental plots of varying algal biomass (their proxy for habitat structure) in seagrass beds, and derived a habitat-survival function (HSF) to describe the effect of habitat structure and size on juvenile lobster survival. There was a large increase in survival of both large and small juvenile lobster associated with moderate increases in algal biomass, until an asymptote was attained as algal biomass increased further. Notably, survival of small

juveniles was significantly better than survival of large juveniles. The authors conjectured that this inverted size effect resulted from habitat-body size scaling, such that the algal habitat did not provide appropriate refuge for large juveniles – and the functional habitat area diminishes as individuals grow larger.

Changes in habitat requirements with body size were also evident in an examination of tradeoffs between growth and predation for juvenile Nassau grouper (*Epinephelus striatus*) in the Caribbean. Eggleston and colleagues (Eggleston 1995, Eggleston et al. 1998, Grover et al. 1998, Dahlgren and Eggleston 2001) documented ontogenetic habitat and diet shifts for Nassau grouper from post-settlement to late juvenile stages. In a study that compared habitats in shallow, protected areas that received grouper larvae, Eggleston (1995) identified previously undocumented juvenile habitats: grouper settled exclusively in clumps of macroalgae and not in seagrass or on sand; post-settlement fish (25 - 35 mm TL) resided within the algae clumps; early juveniles (60 - 150 mm TL) resided adjacent to the algae; and juveniles larger than 150mm TL colonized natural and artificial patch reefs in areas apparently removed from the post-settlement and early juvenile habitat. Adult Nassau groupers are associated with deeper, high-relief reefs (Sluka et al. 1998).

With ontogenetic habitat and diet shifts as a foundation, Dahlgren and Eggleston (2000) used caging and tethering to examine the tradeoffs between growth and predation that might underlie the observed habitat use patterns. They found a dynamic trade-off between predation risk and growth, where the relative costs and benefits changed over time; overall, minimal predation risk with maximal growth was achieved through ontogenetic shifting of habitat. Although their research focused on ontogenetic shifts of later-stage juveniles, their findings

should be generally applicable to examining habitat-growth interactions for earlier life stages and other species (Fig. 6.5).

6.6.2 Competition

Interspecific competition may become more important as individuals reach the recruit phase. Shervette et al. (2004) found that stone crabs in the Mississippi Sound faced competition from mud crabs (*Eurypanopeus depressus* and *Panopeus simpsoni*) for available shelter. The intensity of competitive relationships may change with competitor size. For example, the aggression elicited by intruders from the territorial damselfish *Stegastes leucostictus* is directly related to their potential to consume algal food resources, so that larger intruders tend to elicit a stronger aggressive reaction (Ebersole 1977). In a more focused study, Risk (1998) found that aggression from *S. leucostictus* toward intruding juvenile *Acanthurus bahianus* was greatest for the largest intruders, and this aggression was sufficient to decrease the persistence of juvenile *A. bahianus* in *S. leucostictus* territories. Territorial pomacentrids have similar negative effects on recruits of many herbivorous species (Almany 2003).

Overholtzer and Motta (1999) observed inter- and intra-specific aggressive behavior in mixed-species aggregations of juvenile parrotfishes (Scaridae) in the Caribbean, focusing on *Scarus iserti*, *Sparisoma aurofrenatum*, and *Sparisoma viride*. Inter-specific aggression occurred among the focal species and between the focal species and damselfishes (Pomacentridae), grunts (Haemulidae), and wrasses (Labridae). They concluded that the aggressive interactions would likely have implications for later life stages because these interactions would act as precursors to territoriality as adults. This is an example of the potential demographic implications of

mechanisms occurring during recruitment (i.e., connectivity between recruitment and adult populations).

The effects of interspecific interactions on the abundance and distribution of juveniles may not be reciprocal. Manipulating presence/absence of congeneric planktivorous damselfishes to examine effects of competition on abundance of recruits, Schmitt and Holbrook (1999b) found that groups of *Dascyllus aruanus* that would show a 50% increase in numbers over three months in the absence of *D. flavicaudus* experienced a 55% decline when the congeneric competitor was present. However, this strong negative impact of *D. flavicauda* on *D. aruanus* recruits was entirely one-sided; the presence of *D. aruanus* had no discernible effect on the population growth rates of *D. flavicaudus* groups (Fig. 6.6). Accordingly, the modification of larval settlement pattern to recruitment pattern in abundance and distribution were greater for *D. aruanus* than *D. flavicaudus*.

Section 6.7 Use of reef and non-reef areas as recruitment habitats.

As summarized in preceding sections of this chapter, individual fish and decapod larvae, post-settlers, and recruits are capable of selecting habitat and moving among habitats. Ontogenetic shifters, especially, undergo directional habitat selections and movements, using multiple habitats to maximize survival to adulthood. Until recently, few researchers had examined use of multiple lagoon and reef habitats, despite the observed presence of juvenile fishes and decapods in multiple habitats. Such studies are needed to determine the importance of reef and non-reef habitats as essential nursery habitats (Beck et al. 2001) or effective juvenile habitats (Dahlgren et al. 2006).

6.7.1 Habitat Mosaics

Dispersion of habitat types within coastal tropical ecosystems is an important habitat component, affecting habitat selection as well as survival and growth of early life stages. Habitat dispersion is the spatial distribution of habitat types within a defined area, and includes the entire habitat mosaic to which recruits may be exposed. An important feature of this definition is the differentiation of habitat types from habitats: habitat type describes a distinct feature in some general way (e.g., mangrove, seagrass, algal plain, reef); habitat elaborates on the description of a habitat type by including its location in the overall habitat mosaic, thereby taking into account the contiguity or isolation of habitat types (e.g., continuous reef versus small patch reefs in a seagrass matrix.).

Although the typical definition of essential nursery habitat (e.g., Beck et al. 2001) implies that some early life stage of a species depends upon a single habitat type, recent research has shown that recruits of many species depend upon a mosaic of contiguous habitat types. For example, although conventional sampling indicates that recruits of Caribbean-western Atlantic snappers (Lutjanidae) and grunts (Haemulidae) use mangroves as shelter during the day, stable isotope and gut content analyses show that these fishes feed in adjacent seagrass beds at night (Harrigan et al. 1989, Serafy et al. 2003, Kieckbush et al. 2004, Nagelkerken & van der Velde 2004). Risk (1998) saw low persistence for post-settlement surgeonfish (*A. bahianus*) that suffered aggression from territorial damselfish (*S. leucostictus*), but attributed their eventual absence to movement to other locations rather than (immediate) mortality. Whether post-settlement fishes risk such early life history movement to escape site-specific problems (e.g., aggression or competition for resources) is an open question.

Habitat mosaics are important to the early life history stages of non-reef-associated individuals as well. Laegdsgaard and Johnson (2001) conducted experiments in Australia to examine factors affecting use of mangrove habitats by juvenile fishes, and found that use of complex mangrove prop-root habitats and less complex adjacent habitats changed with growth. Artificial mangrove prop-root structure plus fouling algae attracted juvenile fishes of more species and more total individuals than bare structure. In lab experiments, the use of artificial mangrove prop-root shelters by small juveniles increased in the presence of predators, but this effect was not evident for larger individuals. Small juveniles also fed most effectively within mangrove habitat, whereas their larger counterparts fed at higher rates on adjacent mud flats. Thus, habitat use can change as juveniles grow and develop even when habitat associations are unchanged. Community-level sampling of mangrove and seagrass habitats in tropical Australia corroborates these experiments, with significantly more juvenile fish and crustaceans captured in mangroves than seagrass habitats (Robertson and Duke 1987), indicating the importance of mangrove roots as shelter for small fishes.

The 'settle-and-move' strategy of ontogenetic shifting species (Robertson 1988, reviewed in Parrish 1989, Sweatman and Robertson 1994, Adams and Ebersole 2004), whereby larvae settle into an extensive habitat (e.g., mangrove prop roots, seagrass, algal beds) and move later to microhabitats (e.g., patch reef, rubble) within the settlement habitat, exemplifies the importance of habitat as a mix of habitat types in close proximity (i.e., a habitat mosaic). These species may briefly settle in habitats different from post-settlement habitats, and then move quickly to habitats that provide better resources. For example, Caribbean *Haemulon* spp. settle to algal plain and sparse seagrass, but later, as they grow, move to structure located near seagrass such as rubble patches, patch reefs, or back-reefs located near seagrass --where many researchers first

note their presence (McFarland 1980, Shulman and Ogden 1987, Adams and Ebersole 2004). The common Caribbean French grunt, *Haemulon flavolineatum*, provides a detailed example of the importance of habitat mosaics to early life history, since it has a well-described ontogenetic pattern of habitat use. Larvae settle in seagrass, algal plain, or soft-bottom habitats and then move (via numerous ontogenetic shifts) to adult habitats on reefs (Shulman and Ogden 1987, Adams and Ebersole 2002). Through most of their benthic existence (excluding the early post-settlement stage) French grunts feed on benthic invertebrates living in soft-bottom. They feed primarily at night, and spend the day in close association with hard-bottom structure (rubble, patch reef, larger coral reef, mangrove). Juvenile French grunts appear to use structure within their settlement habitats (e.g., tiny patch reefs or queen conch shells in seagrass beds) before moving to adult habitats on larger reefs. Using benthic maps developed from GIS and high-resolution aerial photos and in situ, day-time censuses of fish to examine influence of habitat distribution on juvenile French grunt abundance, Kendall et al. (2003) found that the abundance of juveniles (post-recruits) on hard-bottom was inversely related to the distance from soft-bottom feeding areas, and that when refuge and feeding habitats were in close proximity, refuges near larger feeding areas had more juveniles (Fig. 6.7). The extent the habitat mosaic also influenced post-settlers and recruits is unclear. Similarly, a mixture of seagrass or algae (settlement habitats) and patch reefs (juvenile habitat) increases movement and enhances survival of juvenile spiny lobsters (*Panulirus argus*) (Acosta and Butler 1999).

Pollux et al. (2007) and Adams and Ebersole (2002) each used a comparative approach in the Caribbean to demonstrate that the importance of non-reef habitat dispersion varies among species. Pollux et al. (2007) conducted post-settlement censuses of *Acanthurus bahianus*, *Ocyurus chrysurus*, and *Lutjanus apodus* along transects on coral reef, seagrass, and mangrove

habitats. They found that each species exhibited habitat-specific patterns that they attributed to settlement preferences: *A. bahianus* to coral reef (and to a lesser extent seagrass); *O. chrysurus* to seagrass and mangroves; and *L. apodus* exclusively to mangroves. Since the habitat-specific patterns they observed were similar to those reported for later juvenile stages for these species, they concluded that juvenile habitat use patterns resulted primarily from settlement patterns. Adams and Ebersole (2002) censused post-settlement fishes and recruits in backreef habitat and five lagoonal habitats (seagrass, rubble, patch reef, sand, algal plain), and found two general patterns of juvenile habitat use among fishes with reef-associated adults: one group (e.g., *Acanthurus* spp., *Haemulon* spp.) used lagoon patch reef and rubble as juvenile habitats, whereas a second group (e.g., *Scarus iserti*, *Sparisoma aurofrenatum*) used backreef as juvenile habitat.

6.7.2 Recruitment Habitat Quality

For some organisms that shift habitats ontogenetically, abundances of adult populations may depend on input from lagoon nurseries, and thus show a strong connectivity to post-settlement and recruitment habitats. Finding such relationships is likely to be difficult, since variable mortality rates associated with the movement between habitats may obscure them. Robertson (1988) posited that post-settlement relocation played a large role in the difficulties of establishing a correlation between abundance of recruits and abundances of adults for three Acanthurids in the Caribbean. However, Adams and Ebersole (2004) developed a Lagoon Quality Index (LQI) to quantify recruit habitat availability and examine the relationship between recruitment habitat availability in seagrass lagoons (inshore of bank barrier reefs) and adult abundance on the nearby reefs for two genera of ontogenetic shifters in the Caribbean. An LQI that combined availability and use of recruit habitats was calculated for each of six sites for small

(< 3cm) and medium (3 - 5cm) juvenile *Haemulon* spp and for juvenile *Acanthurus* spp (small and medium size classes were combined since settlement occurs at approximately 2.5 – 3cm):

$$LQI_{ij} = \sum a_{ix} \cdot P_{jx}$$

where x = a given habitat type (e.g., patch reef, rubble, algal plain, seagrass, sand); a_{ix} = mean density of species i on habitat xj (computed from values pooled from all 6 sites); and P_{jx} = relative cover of habitat x in lagoon j . Least squares regression showed that the Lagoon Quality Index was a good predictor of adult densities on nearby reefs for *Acanthurus* spp. and for small *Haemulon* spp (Fig. 6.8, 6.9). The LQI was calculated separately for each lagoon by pooling two years of census data to reduce the impact of the storage effect (Warner and Chesson 1985) that tends to obscure the relationship between abundances of recruits and adults in fishes with ontogenetic shifts (Tolimieri 1998b). The LQI for the medium size class of *Haemulon* spp was not a good predictor because *Haemulon* spp undergo ontogenetic shifts beginning at a small size, and by the time they reach the medium size class, they are already transitioning to reef habitats (McFarland et al. 1985, Shulman and Ogden 1987, Adams and Ebersole 2004). Similar relationships between availability of recruitment habitat and adult population density have been found elsewhere for these and other fishes (Nagelkerken et al. 2001, 2002, Mumby 2006), spiny lobsters (Butler and Herrnkind 1997), and stone crabs crabs (*Menippe mercenaria*) (Beck 1995, 1997).

6.7.3 Recruitment Habitat Proximity

There may be a proximity threshold for the influence of non-reef nurseries on reef populations. In a study of mangrove shorelines in a lagoon adjacent to a fringing reef in the United States Virgin Islands, for example, Adams and Tobias (1999) found that abundance of

juveniles of species with reef-associated adults (e.g., surgeonfish *Acanthurus chirurgus*) decreased from the mangrove shorelines closest to the reef to the interior mangrove shorelines, whereas juveniles of species with a higher affinity for mangrove habitats (e.g., mangrove snapper *Lutjanus apodus*) were equally abundant throughout the mangrove lagoon. Similarly, in a lagoon studied by Nagelkerken et al. (2000b), juvenile densities of reef fish species with reef-associated adults rapidly decreased with distance from the coral reef. Densities of many species that used lagoon habitats as putative nurseries, for example, were higher on habitats nearer the reef (Fig. 6.10), whereas species with affinities for lagoon habitats were most abundant in habitats farther from the reef. Ley et al. (1999) also found differences in fish community composition across an estuarine gradient. They examined fish communities in a mangrove-fringed subtropical estuary in Florida to determine fish community composition. Juveniles and sub-adults of reef-associate species were present only in downstream, higher-salinity locations. In contrast, euryhaline residents (e.g., Poeciliidae - livebearers, Cyprinodontidae (Fundulidae) – killifishes) dominated community assemblages throughout the study area, regardless of salinity.

6.7.4 Recruit-Adult Connectivity

On a regional scale, the correlations between nursery availability and adult populations on the reef are reflected in associations between nurseries and community structure on reefs. Mumby et al. (2004) examined the distribution of mangroves and reefs in the Caribbean, and found an association between mangroves and species composition on reefs. Reefs with (more) nearby mangrove habitats had higher adult abundances of species that used mangroves as juveniles. Moreover, for many of these species, mangroves served as intermediary nursery habitat that may have increased survivorship of juvenile fishes. The effects of mangroves as

juvenile habitat was very pronounced for some fishes of commercial value, with biomass greater on reefs with nearby mangroves than reefs with fewer or no mangroves nearby. Effects were most dramatic for species with the greatest dependence on mangrove habitats: *Scarus guacamaia*, functionally dependent on mangroves, is now locally extinct in areas with high mangrove loss. The relationship between adult populations on reefs and contiguity of non-reef juvenile habitats has also been shown for seagrass (e.g., Dorenbosch et al. 2004, 2006) in the Caribbean.

Examination of fish abundances and sizes in Australia suggests a similar connection between species composition on inshore (or shallow) and offshore (or deeper) habitats. For example, at least 11 fish species in northern Australia use estuaries exclusively as juveniles and then use offshore habitats as adults (Blaber et al. 1989), suggesting selection of settlement habitats followed by ontogenetic shifts to adult habitats. Similarly, juveniles of at least 14 species of eastern Australia occur in estuarine and adjacent, shallow, turbid mangrove and seagrass-bed habitats, while the adults are found in deeper water or ocean habitats (Blaber and Blaber 1980). Sheaves (1995) also found that at least 14 species of fish with adult stages on reefs or in deeper offshore waters had juvenile stages that used estuarine mangrove habitats.

Section 6.8 Effects of Disturbance on Recruitment

6.8.1 Tropical Cyclones/Hurricanes

The most prominent natural disturbances in tropical marine ecosystems are tropical cyclones/hurricanes. The relatively few studies of hurricane effects on coral reef fishes generally report temporary, or no, measurable effects (Kaufman 1983, Lassig 1983, Letourneur et al. 1993, Aronson et al. 1994, Bouchon et al. 1994, Adams 2001, Adams and Ebersole 2004), with the

most notable effects on juvenile fishes. However, working in the Pacific, Lassig (1983) found high juvenile mortality and redistribution of subadults immediately after a tropical cyclone that occurred during the settlement season. Given the frequency of cyclones during the settlement season and the influence of recruitment on adult abundance, he postulated that cyclones might be important factors in population structure. In contrast, comparing fish abundances before and after a cyclone in the Caribbean that occurred at the end of the settlement season, Adams and Ebersole (2004) found no short-term effects on abundances or size distributions of fishes. They postulated that larger juveniles present at the end of the settlement season may be of sufficient size to be resistant to hurricane disturbances. This, however, is counter to Lassig's (1983) findings for subadult fishes. Differences in findings between these studies may have resulted from the combination of the high storm frequency and general reef degradation in the Caribbean, which may have combined to favor a community that is relatively resistant to disturbances (i.e., caused a phase shift (Done 1992, Jones and Syms 1998). Alternatively, Caribbean fish assemblages may be more resistant to hurricanes, since little or no measurable impact are common observations (e.g., Kaufman 1983, Aronson et al. 1994).

Tropical cyclones may also serve to increase larval supply to tropical estuaries and coral reefs for some species. During a multi-year study of larval tarpon (*Megalops atlanticus*), Shenker et al. (2002) experienced a tropical cyclone pass directly over their study location in Florida. The abundance of *M. atlanticus* larvae was higher in association with that tropical cyclone event than during all other sampling periods. Abnormally high settlement of juvenile honeycomb grouper (*Epinephelus merra*) occurred following a tropical cyclone on reefs of Réunion Island (Letourneur et al. 1998). However, when observations were continued after the cyclone, density-

dependent processes were found to decrease densities to more typical levels (Letourneur et al. 1998).

6.8.2 Habitat Disturbance and Degradation

Other types of disturbance also impact recruitment. Butler et al. (1995), for example, found that the distribution of juvenile Caribbean spiny lobsters (*Panulirus argus*) changed dramatically when one of their preferred habitats, sponges, suffered a massive die-off in Florida Bay (USA). Lobster density decreased in areas where few alternative shelters existed, but sites where artificial shelters were added experienced an increase in lobster density. Whether density-dependent factors acting at another stage evened out these density differences eventually – as in the honeycomb grouper – is an open question.

Studies of larger scale disturbances that impact recruitment are becoming increasingly important. These disturbances tend to cause wholesale changes in habitats, and whether it is habitat loss or degradation, loss of habitat integrity affects recruitment. Much of this habitat loss and degradation is anthropogenic. For example, the worldwide loss of mangroves between 1980 and 2000 exceeds 34% (Valiela et al. 2001). Since many species of tropical fishes and decapods use estuarine and marine mangroves as recruitment habitats, loss of these habitats likely has population-level implications that require study.

Increasingly, general degradation of coral reefs is hindering recruitment. Examination of coral reef degradation on a gradient (healthy–stressed–dead coral–algae dominated–habitat structure change) reveals a clear picture of the impacts of habitat integrity loss on fish and decapods. Coral stress (the partial degradation of coral colonies) does not appear to effect larval settlement and subsequent recruitment of fishes (Feary et al. 2007). With increasing degradation,

as coral dies, larval fish recruitment decreases (Jones et al. 2004, Munday 2004b, Feary et al. 2007), with specialists more impacted than generalists (Munday 2004b). Reef-wide coral bleaching, coral death, and change in benthic cover (e.g., live coral converts to algae) reduce fish recruitment (Garpe and Ohman 2003, 2007, Garpe et al. 2006) – moderately in the short term -- and severely in the long term (Garpe and Ohman 2003, 2007, Garpe et al. 2006). Initially, loss of coral habitats causes decreases in habitat specialists such as corallivores and coral-associated territorial species (Garpe and Ohman 2003). In the long term, a much wider array of species are impacted, including invertivores and planktivores, with Pomacentridae (damselfishes), Chaetodontidae (butterflyfishes), and Pomacanthidae (angelfishes) particularly impacted (Garpe and Ohman 2003).

Section 6.9 Greatest Knowledge Gaps

6.9.1 Connecting Larval and Juvenile Traits

Although recent research has shown the importance of settlement-stage larval condition on growth, survival, and mortality of post-settlers and juveniles (e.g., Searcy and Sponaugle 2001, Vigliola and Meekan 2002, McCormick and Hoey 2004, Nemeth 2005), the interactions between habitat quality and individual condition are less well studied. As mentioned previously, for example, Shima et al. (2006) found that juvenile *Thalassoma hardwicke* with higher lipid levels and higher growth rates were also associated with better quality habitats. These habitats had higher levels of *Pocillopora* spp coral that provided cover for juveniles and shelter from predators. In addition, the types of predators (resident vs transient) and dispersion of habitats (Overholtzer-McCleod 2006) also influence the survival of juveniles, and are independent of larval condition at settlement. Moreover, post-settlement competition, food and habitat

limitation, cohort size, timing of settlement, and priority effects all interact and contribute to recruitment success or failure. Combined, these results emphasize the need for future studies to incorporate the interactions of individual traits, habitat quality, and numerous post-settlement mechanisms influencing early life history of fishes and decapods.

6.9.2 Partitioning Mortality and Emigration

Implicit in the measures of post-settlement mortality is that the decline in post-settler abundance results from mortality (mostly from predation). For fishes and decapods with ontogenetic shifter or generalist life history strategies, future research should focus on partitioning mortality and emigration. The ability of juveniles to locate specific habitats (e.g. Blackmon & Eggleston 2001), and the ‘settle-and-move’ strategy (Robertson 1988, reviewed in Parrish 1989, Sweatman and Robertson 1994, Adams and Ebersole 2004) of many species suggests that the mobility of some species may influence effects of density-dependent mortality. Habitat shifts early in life history may be driven by site-specific densities (e.g., competition for resources) such that recruits and juveniles risk moving in search of other (better) locations. For example, Overholtzer-McCleod (2004) found that loss of *Halichoeres garnoti* from patch reef resulted from both mortality and emigration to neighboring reefs. In subsequent work (Overholtzer-McCleod 2005), she found that the degree of isolation of patch reefs was a strong factor determining emigration rates – more isolated reefs had less emigration. These results suggest caution when interpreting causes of abundance declines for recruits and juveniles of species with inherent mobility. Similarly, although not dealing with recruits, Lewis (1997a, b) also found that abundances of many fish species on isolated patch reefs were strongly influenced by post-recruitment migrations among habitats.

6.9.3 Conclusion

Clearly, much has been learned in recent decades about the processes influencing fish and decapod recruitment. For example, the planktonic life stage of marine fishes was once thought of as a black box, and recruitment was merely a reflection of larval supply. This view was modified, with Choat et al. (1988), for example, suggesting that habitat-associated variables filter larval supply, slightly modifying the settlement patterns determined by oceanographic processes. It is becoming clear with more recent research, however, that the filter effect of benthic-associated processes active during the recruitment phase can be extremely selective and severe, and require additional study.

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Table 6.1. Summary of early life history stage definitions, adapted from Adams et al. 2006. Source Citations are the references from which these definitions were derived.

Term	Definition	Source Citations
Settlement	The initial establishment of larvae onto a benthic substrate. Includes only larval processes. Important factors include larval condition and size.	Calinski and Lyons (1983) Kaufman et al. (1992), Gutierrez (1998)
Post-settlement transition	Occurs during and immediately following settlement. Late stage larvae explore and evaluate benthic habitats (and may re-enter the pelagic environment several times), undergo metamorphosis, and join the benthic population. Priority effects* are especially important during this stage.	Kaufman et al. (1992), McCormick and Makey (1997), Sancho et al. (1997)
Post-settlement stage	Time period directly after metamorphosis. A period of high benthic mortality. Duration of this stage varies among species, in part due to different susceptibility to predation. Important factors include density-dependent mortality and competition, modified by habitat complexity.	Doherty and Sale (1985), Sogard (1997), Almany 2004, Almany and Webster 2004
Recruitment	Occurs at the end of the post-settlement stage, and incorporates effects of larval and post-settlement processes. Characterized by entrance into a period of lower mortality. First record of an individual in the juvenile stage. Stage when many recruitment surveys occur.	Doherty and Sale (1985), Kaufman et al. (1992), Booth and Brosnan (1995), Gutierrez (1998), McCormick and Hoey (2004)

* Priority effect: the process by which the presence of one species in a habitat decreases the probability of invasion by another. One species can lower the recruitment of another via competition (adult and subadult residents or settling juveniles can interfere with larval settlement (interference competition) or preempting resources (interference competition) or predation (predatory adult and subadult residents can decrease settlement directly by preying on settlers or indirectly by settlers choosing sites without predators, or predatory juveniles can prevent settlement by prey species (Shulman et al. 1983).

Table 6.2. Summary of life history strategies. Strategy definitions adapted from Adams et al. 2006. Example Citations are studies that focus on species that fit this strategy category, and are listed by family.

Term	Definition	Example Citations
Habitat Specialists	<p>Larval settlement and the juvenile and adult benthic stages occur in the same location. These species tend to be site attached (e.g., Pomacentridae). Ontogenetic shifts that may occur are relatively minor, likely microhabitat changes (e.g., juveniles use microhabitats within adult habitats). Microhabitat shifts may occur to occupy areas of different complexity to reduce predation, but they occur within the same site.</p>	<p>Alpheidae: Knowlton and Keller 1986 Palaemonidae: Preston and Doherty 1990. Pomacentridae: Doherty 1983, Bergman et al. 2000, Lirman 1994, Nemeth 1998, Schmitt and Holbrook 1999b</p>
Habitat Generalists	<p>Larval settlement and the juvenile and adult benthic stages of an individual may occur in the same location, but the species is able to settle and stay, or move among, numerous habitat types (e.g., <i>Halichoeres bivittatus</i>) Species are generally not site-attached (but see – McGehee 1995, species site-attached but can use and move among many habitat types). To the extent that ontogenetic shifts occur, they don't follow a well defined pattern and/or are minor compared to Ontogenetic Shifters (e.g., Labridae).</p>	<p>Xanthidae: Beck 1995, 1997 Labridae: Green 1996</p>
Ontogenetic Shifters	<p>These species exhibit complex habitat, behavioral, and diet shifts during transitions from settlement through late juvenile stages, and again into adult. Larvae tend to settle into habitats distinct from adults and undergo notable ontogenetic shifts Larval settlement areas may differ from juvenile habitats</p>	<p>Panuliridae Herrnkind et al. 1994, Childress and Herrnkind 2001; Labridae Green 1996; Serranidae: Eggleston 1995, Dahlgren and Eggleston 2000, St. John 1999; Acanthuridae: Robertson 1988; Risk 1997, 1998, Adams and Ebersole 2002, 2004, Parrish 1989</p>

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Figure 1

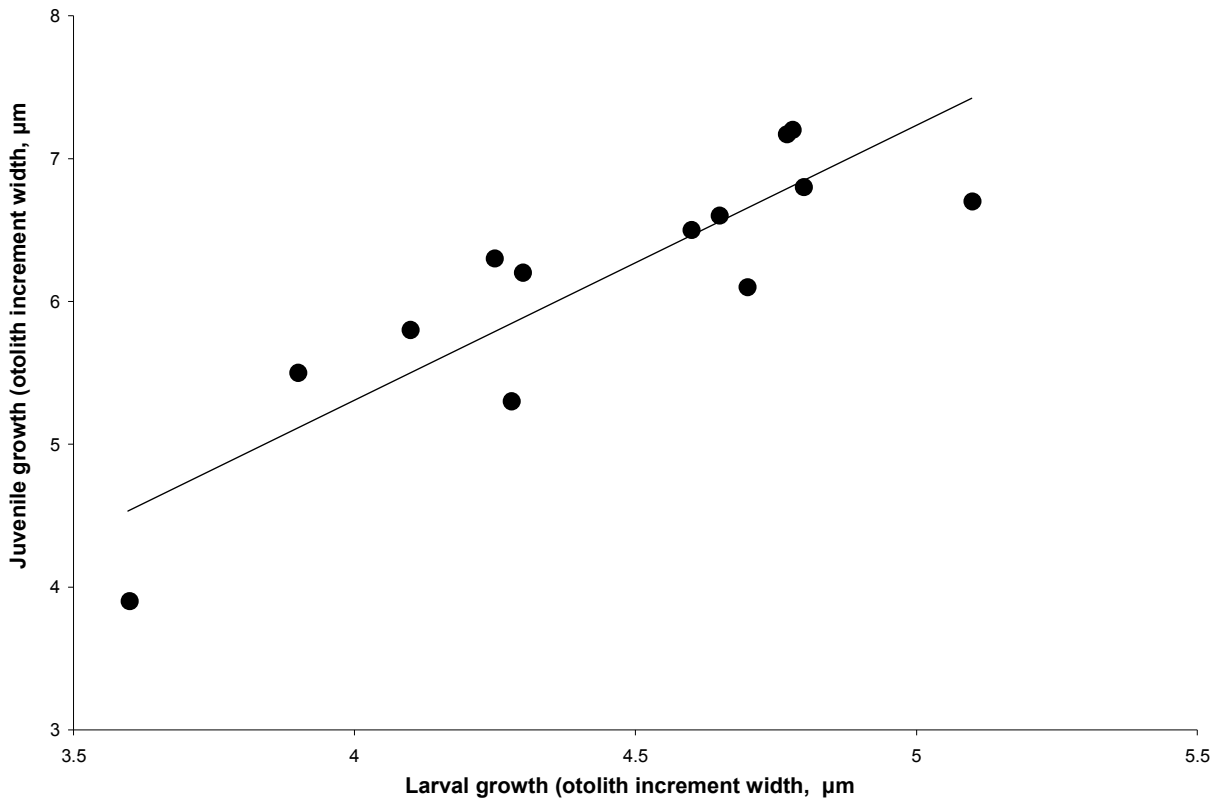
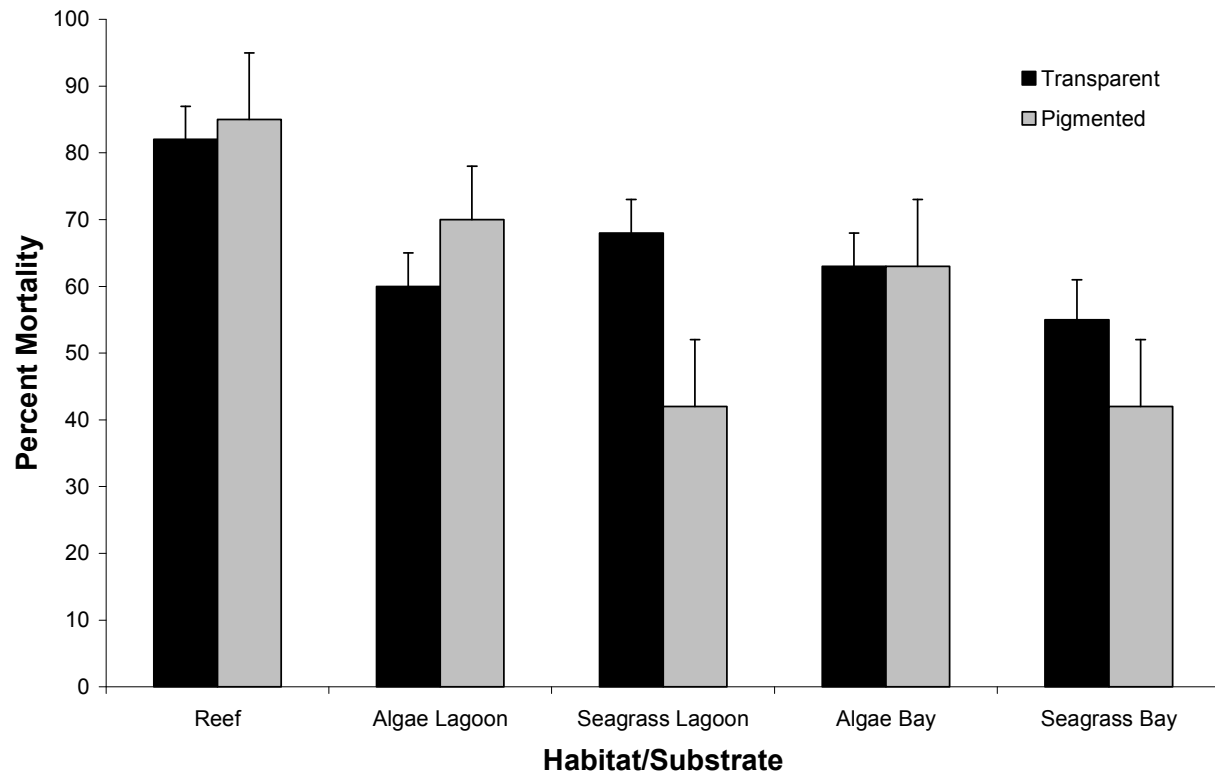


Figure 2



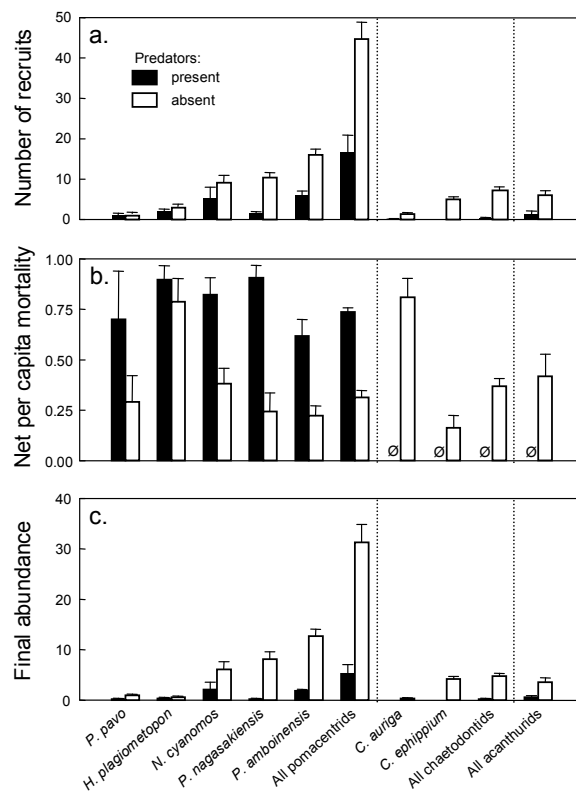


Figure 3.

Figure 4

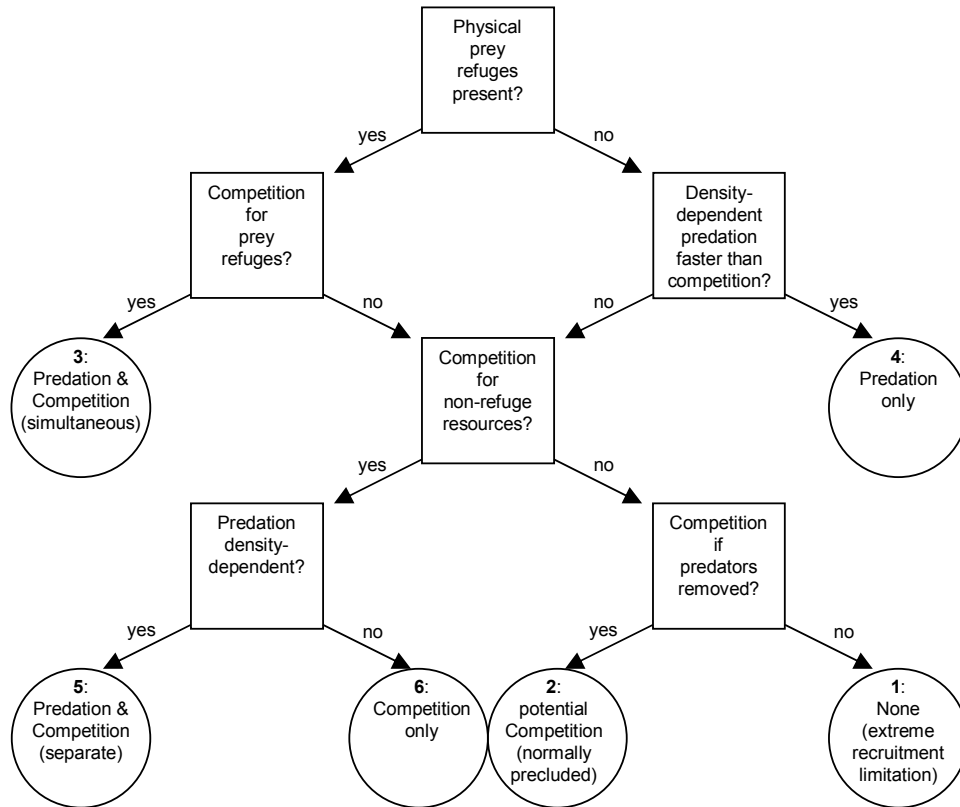
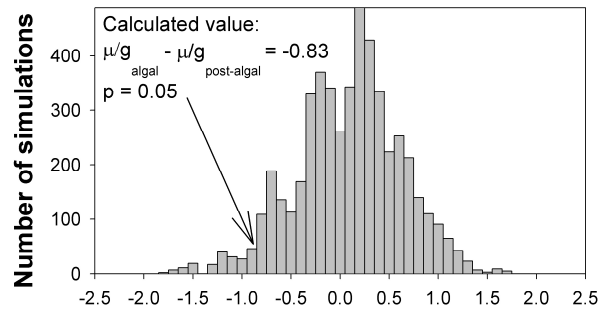


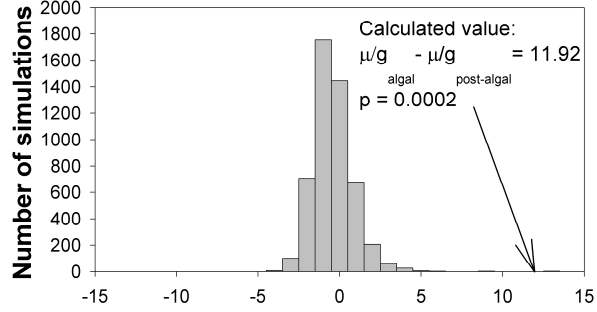
Figure 5

Number of simulations

A. Small fish



B. Medium fish



C. Large fish

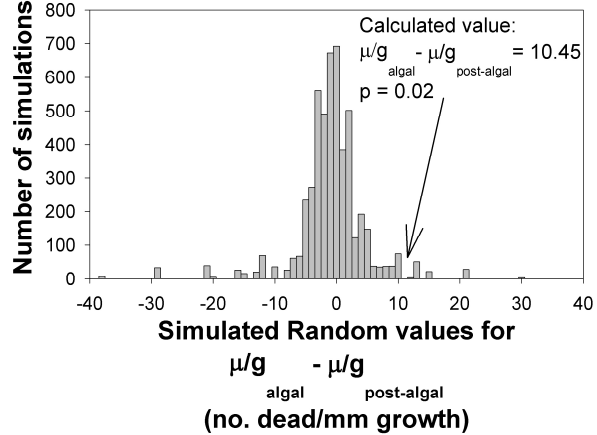


Figure 6

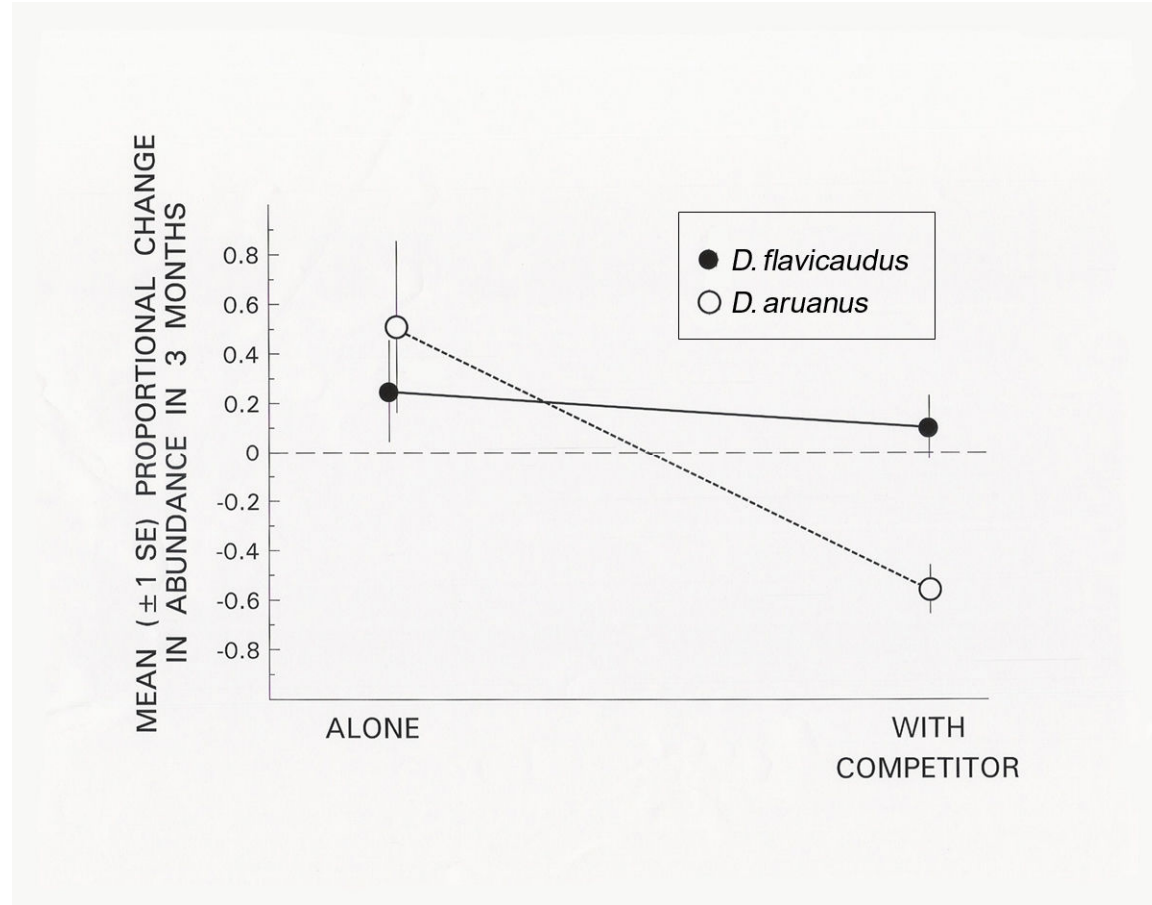


Figure 7

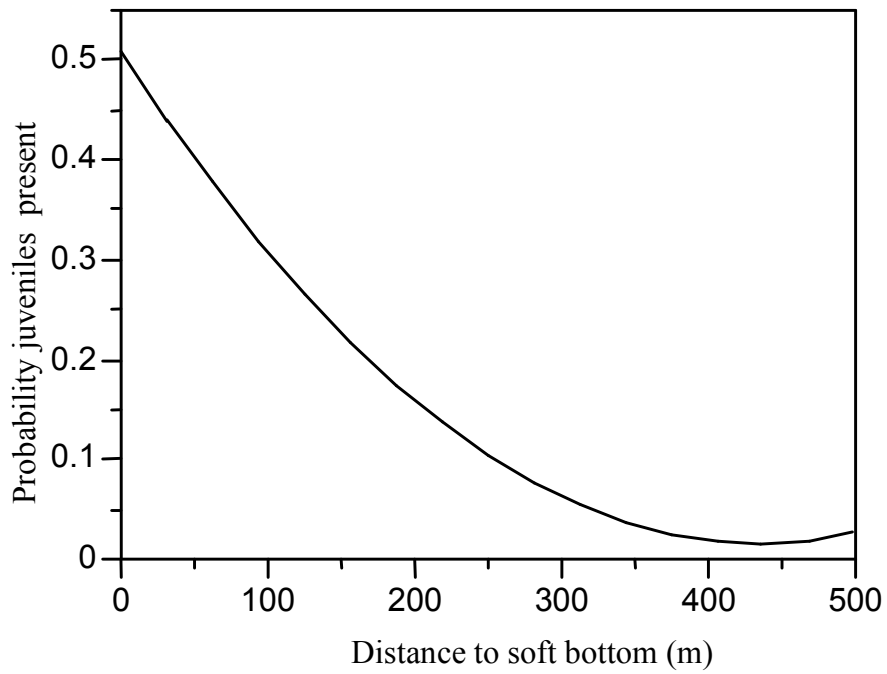
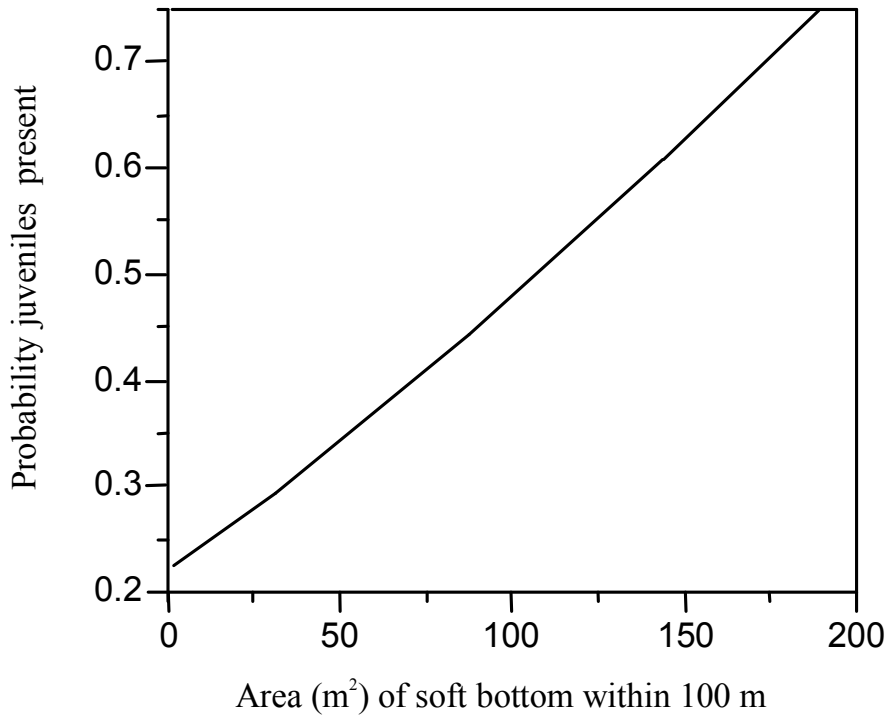


Figure 8

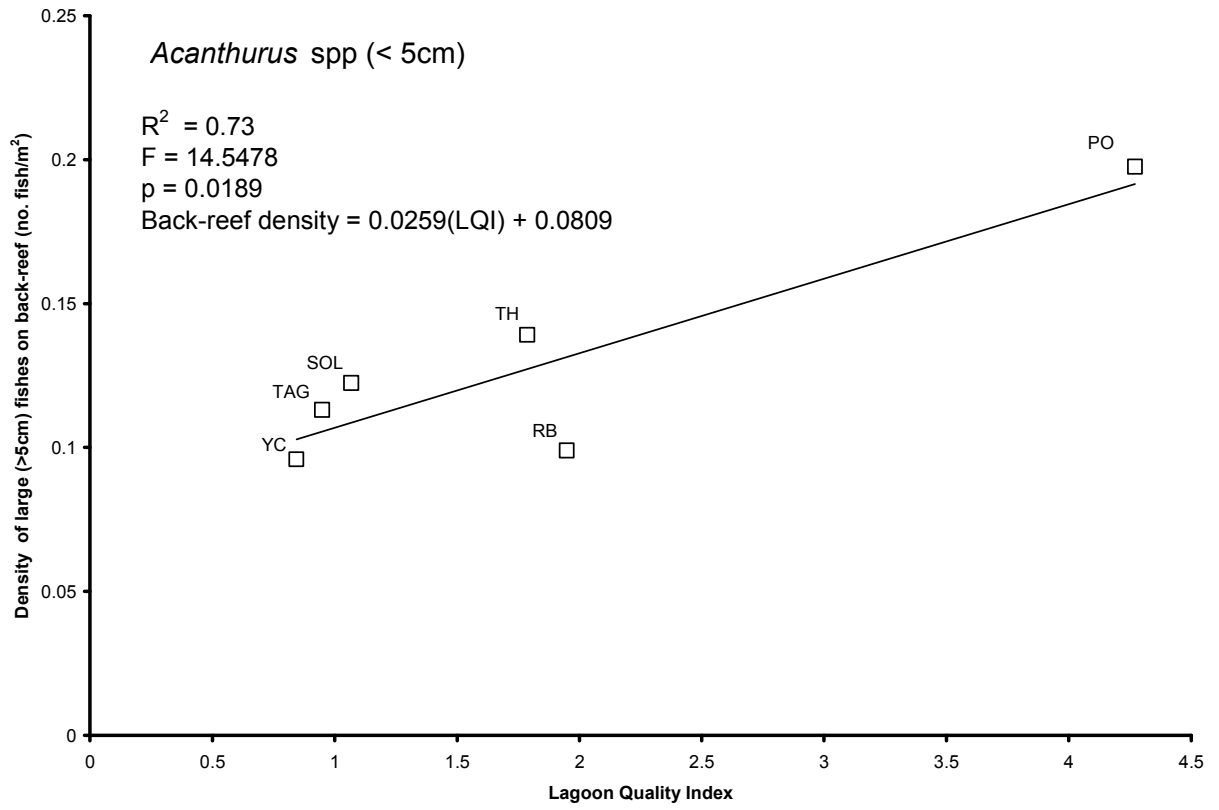


Figure 9

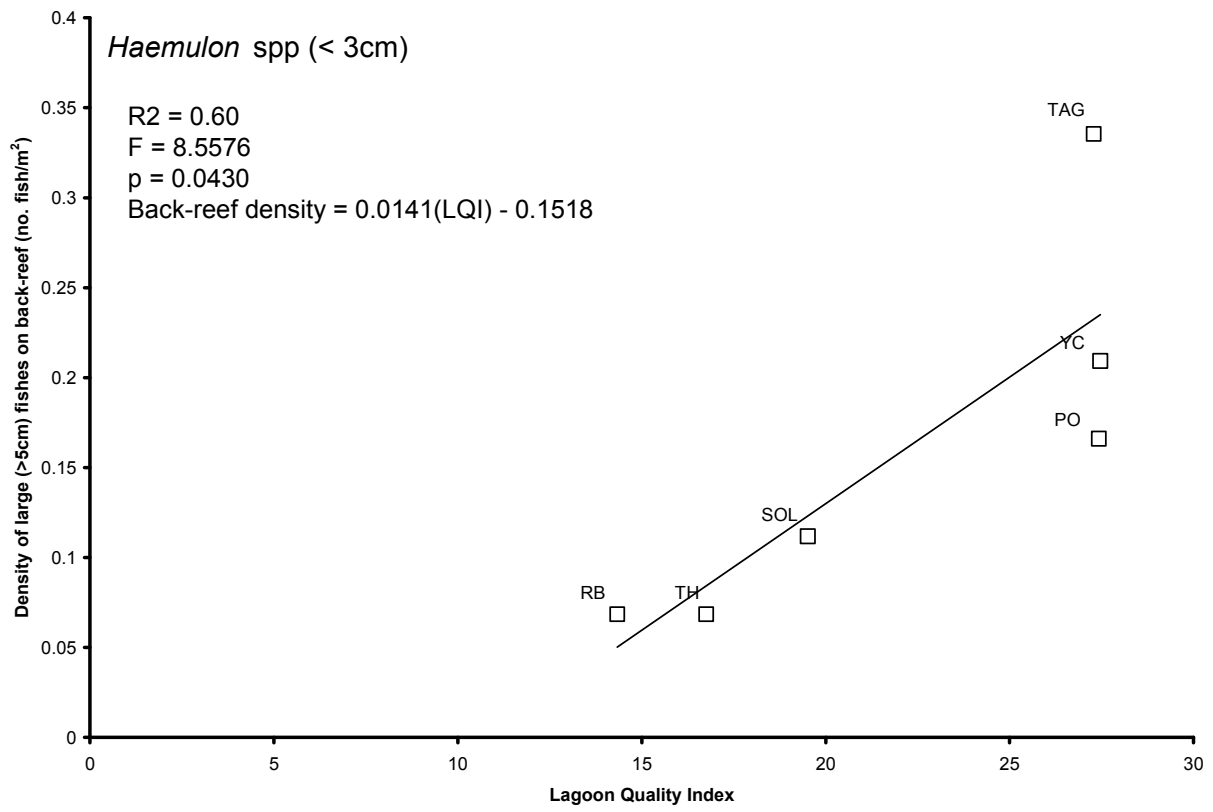


Figure 10a



Figure 10b

