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Adaptive strategies that reduce predation on Caribbean spiny lobster postlarvae during onshore transport

Charles A. Acosta[1] *and Mark J. Butler IV*
Department of Biological Sciences, Old Dominion University, Norfolk, Virginia 23529-0266

Abstract

Like many marine species with meroplanktonic larvae, the Caribbean spiny lobster (*Panulirus argus*) has a postlarval stage that moves from the oceanic plankton to inshore nurseries only under specific environmental conditions (i.e., at night, in the surface water layer, on the flood tide, and during new moon), presumably to avoid predation or to enhance onshore transport. Using field and mesocosm experiments, we compared predation on planktonic postlarvae swimming at night near the surface and bottom over coastal habitats along typical offshore–inshore transport paths and determined whether predation rates differed between lunar periods (new moon vs. full moon) and with prey density (i.e., predator encounter rates). We also measured predation on transparent (newly settled) and pigmented (nearing metamorphosis) postlarvae sheltering in coral reef, seagrass, and macroalgal habitats during the day.

We measured predation on postlarvae swimming near the surface and bottom along typical offshore–inshore transport paths (i.e., coral reefs, coastal lagoon, and bay) by tethering postlarvae to floats that drifted on the nightly flood tide during new moon. To test the hypothesis that new-moon transport of postlarvae may have evolved as a means to avoid higher predation under the bright full moon, we repeated the pelagic tethering experiments at the reef and in the bay during full moon. Mortality was highest over coral reefs regardless of lunar phase, but it was lower nearshore, especially in the bay near the surface and during new moon. Predation on benthic, recently settled transparent postlarvae and pigmented postlarvae (nearing metamorphosis) was also higher when tethered on the reef as opposed to vegetated habitats in the lagoon and bay. In experimental mesocosms, planktivorous fish were equally efficient at consuming postlarvae under new- and full-moon conditions when postlarval density was high, as it is in the constricted water column over the reefs. However, when postlarvae were less dense, mortality was significantly lower during new moon. Collectively, these results indicate that several behavioral traits exhibited by postlarval spiny lobsters, including inshore migration during the darkest lunar phase, use of surface waters, and settlement in vegetated habitats, reduce their risk of predation, particularly in the shallow bay. No single behavioral strategy is universally advantageous across all coastal habitats, but combined, they are an effective means to reduce predation across heterogeneous environments that postlarvae must transit during recruitment.

Many marine organisms have complex life cycles, with pelagic larval stages that function in dispersal, colonization, and gene flow but that generally experience high mortality (Thorson 1950; Scheltema 1971). In both pelagic and benthic environments, predation can reduce the abundance and affect the spatial distribution of larvae (Cowden et al. 1984; Rumrill et al. 1985; Shulman 1985; Olson and McPherson 1987; Young and Chia 1987; Morgan 1992; Eggleston and Armstrong 1995) and zooplankton (Lebour 1922, 1923; Glynn 1973; Huntley and Hobson 1978; Seben and Koehl 1984). In response to predation pressure, aquatic prey have evolved a number of morphologies and behaviors to avoid detection, capture, and contact with predators (*see* reviews by Sih 1987; Morgan 1995). Cryptic coloration, for example, is an important morphological trait that may reduce the detection of prey by predators. In pelagic environments, transparent bodies can be cryptic (e.g., many pelagic larvae and zooplankton), whereas benthic stages are more often pigmented and camouflaged. Both are presumably most effective under low light conditions to counter visual predators. Behaviors that may reduce the probability of prey contact with predators include diel vertical migration by zooplankton (Hobson and Chess 1976; Zaret and Suffern 1976), horizontal migration by larvae to water masses with low predator density (Bailey and Houde 1989), reduced or restricted activity in the presence of predators (Mittelbach and Chesson 1987), and aggregative behavior (Childress and Herrnkind 1996; Butler et al. 1997).

Quantifying the severity of predation on aquatic larvae in different habitats and environmental conditions and empirically testing the effectiveness of antipredator traits under disparate situations are necessary for understanding how larvae maximize survival under overwhelming odds. Yet few studies have directly quantified the impact of predators on larvae in the field. Furthermore, the degree to which predation affects the magnitude of larval recruitment to adult populations, as opposed to mechanisms such as unfavorable transport and starvation, is still largely unknown. Predation has been inferred from prey found in predator stomach contents (Randall 1967; Theilacker et al. 1986; Bailey et al. 1993), the concordance of predator and prey distribution and abundance (Shulman 1985; Young and Chia 1987; Butler 1989), and associations between predator feeding rates, planktonic prey density, and current speed (de Boer 1978; Thresher

[1] Present address: South Florida Research Center, Everglades National Park, 40001 State Road 9336, Homestead, Florida 33034.

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1983; Hamner et al. 1988; Noda et al. 1992; Kiflawi and Genin 1997). Predation may also affect the spatiotemporal dynamics of coastal benthic populations by affecting the magnitude of larval recruitment (Watanabe 1984). For example, the magnitude of larval recruitment is negatively associated with concentrations of planktivorous fishes at offshore reefs in New Zealand (Kingsford and MacDiarmid 1988) and in kelp forests off California (Gaines and Roughgarden 1987). In only a few cases has predation on aquatic larvae been studied in situ and in such a manner that suspected antipredator adaptations of prey could be directly tested (e.g., Olson and McPherson 1987). Postlarval tropical spiny lobsters exhibit a suite of behavioral and morphological characteristics common to meroplanktonic larvae that are presumed to have some antipredator benefit. Spiny lobsters have a complex life history, with a protracted larval phase lasting up to ≥1 yr (Phillips and McWilliam 1986). Larvae metamorphose into the puerulus postlarvae near the continental shelf break (Johnson 1960; Phillips and McWilliam 1986; Yeung and McGowan 1991) and recruit to coastal habitats under very specific environmental conditions. For example, postlarvae of the Caribbean spiny lobster *P. argus* move from the Florida Current to nearshore habitats in the Florida Keys, U.S.A, at night on flood tides following the new moon (Little 1977; Acosta et al. 1997). They swim in the surface water layer (<1 m deep) during their migration to coastal settlement habitats, aided in part by wind-driven surface Ekman transport (Calinski and Lyons 1983; Acosta et al. 1997). Along a typical transport path from offshore to nearshore, *P. argus* postlarvae must traverse several distinct coastal zones (e.g., offshore reefs, seagrass and sand plains, and macroalgal-covered hardbottom) to find suitably vegetated habitats in Florida Bay in which to settle (Herrnkind and Butler 1994). During their pelagic phase, postlarvae are transparent, but they develop pigmentation within days of settling in vegetated habitats (Herrnkind and Butler 1986; Butler and Herrnkind 1991). Understanding the mechanisms by which pelagic larvae reduce predation risk may increase our understanding of recruitment to benthic habitats.

To understand the role of predation in shaping the life history traits of postlarval spiny lobsters, we tested competing hypotheses on traits that may maximize survival and recruitment success. We compared predation on planktonic postlarvae drifting near the surface and near the bottom over coastal habitats along typical offshore–inshore transport paths and determined whether predation rates differed between lunar periods (new moon vs. full moon) and with prey density (i.e., predator encounter rates). We also measured predation on transparent (newly settled) and pigmented (nearing metamorphosis) postlarvae sheltering in coral reef, seagrass, and macroalgal habitats during the day. We hypothesized that: (1) mortality of planktonic postlarvae was lower during new moon than full moon, (2) predation was highest over habitats having large resident predator assemblages (e.g., coral reefs), (3) postlarvae used surface waters for rapid transport past concentrations of predators, (4) high densities of postlarvae constricted in shallow water columns experienced higher predation than low densities, (5) shallow macroalgal beds in the Florida Bay nursery provided a higher degree of protection from predators than the coral reefs or other habitats, and (6) pigmented camouflaged settlers survived better than transparent postlarvae in benthic shelters.

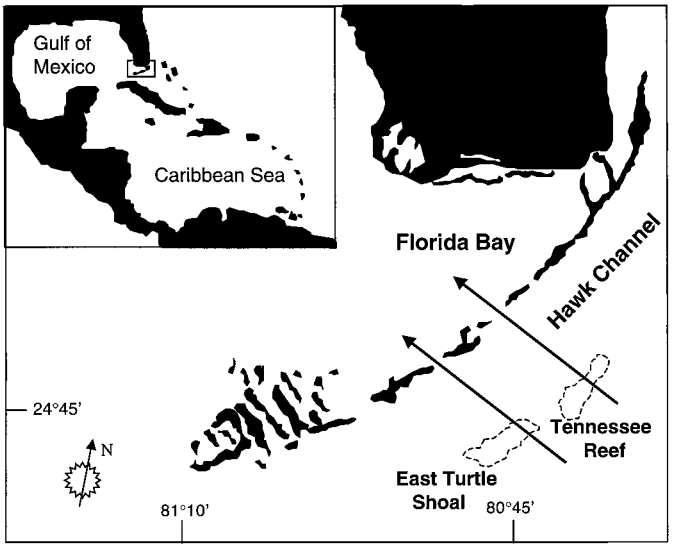

Fig. 1. Map of the Caribbean region (inset) with south Florida shown expanded. The pelagic and benthic predation experiments were conducted in the middle Florida Keys along offshore to nearshore transport paths, shown approximated by the arrows.

Methods

Predation along pelagic offshore–inshore transport paths—To measure spatially explicit predation on planktonic postlarval spiny lobsters, we conducted field experiments using postlarvae tethered to floating arrays that drifted on the new-moon flood tide over typical transport paths. Experiments were conducted at night (1000–0100 h) during the summers of 1994, 1995, and 1996 in the middle Florida Keys over representative coastal transects from offshore to inshore; replicates were run over offshore coral reefs, Hawk Channel coastal lagoon, and Florida Bay (Fig. 1).

Transparent postlarvae were collected from the plankton passing between islands in the Florida Keys using 1-m-diameter, 750-μm mesh nets (Herrnkind and Butler 1994). Postlarvae were then tethered to floating arrays consisting of a 4-m length of polyvinyl chloride pipe with several 10-cm-diameter styrofoam floats (Fig. 2). A 20-cm length of nylon thread was secured to the carapace of a postlarva by a small drop of gel cyanoacrylate glue. The thread was then attached to a length of 2-kg test, lead-weighted monofilament line that was tied to the floating array. The thin thread permitted free movement of the tethered postlarva, while the weighted monofilament line restricted the animal to a specific depth. Each floating array held six tethering lines, three each at two depths: surface (0.5 m deep) and bottom (3 m deep for reef and lagoon; 1.5 m for bay). A 2-m length of line with a fluorescent glowstick set in a funnel (to minimize light transmission to the water below) and attached to one end of the floating array served as a beacon for recovery of the arrays.

The general procedure was to release one or two floating arrays at a time from a boat positioned over the chosen hab-

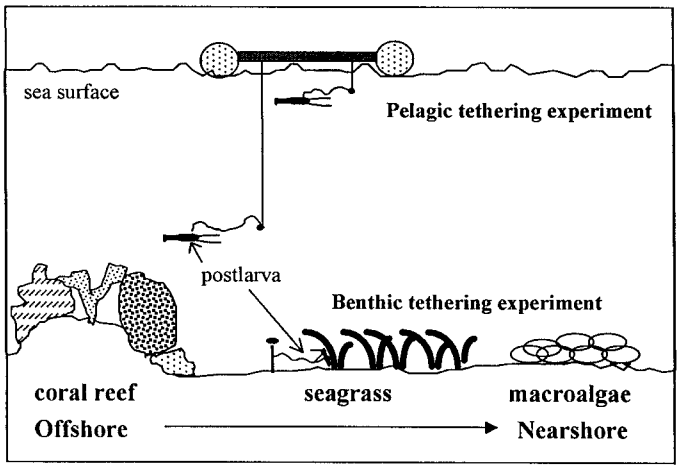

Fig. 2. Schematic diagram of technique used for tethering postlarval spiny lobster in representative pelagic and benthic habitats.

itat along the transport path. After releasing the floating arrays, the vessel was moved approximately 50 m away, and both the arrays and boat drifted along separately in the current. Results of preliminary trials indicated that a 0.5-h period was sufficient time for a measurable predation response over habitats. Points of release and retrieval of arrays were marked using global positioning satellite (GPS) coordinates, and those coordinates were retraced and checked during subsequent days to ensure that the array traveled over the intended habitat (i.e., reef, coastal lagoon, or bay). We used a depth sounder to check that the tether lines did not snag the bottom. Experiments were conducted on relatively calm nights (winds < 10 nm h^{-1}) to minimize disturbance to lobsters on tethers by wave action; this also served to reduce variability in current velocity, because surface currents are significantly affected by winds in Hawk Channel (Pitts 1994). We worked with hand-held lights at night to avoid attracting fishes. Once the floating arrays were recovered, we scored each individual postlarva as being alive or eaten. If only fragments of carapace remained on the tether, then we scored a missing individual as a kill. Postlarval lobsters were used only once in these experiments.

Each floating array traversed one of three habitats: coral reef, coastal lagoon, or bay. Floating arrays drifted over: (1) coral patch reefs (3–6-m depth) at East Turtle Shoal (24°43.18′N, 80°56.06′W) and Tennessee Reef (24°45.35′N, 80°46.14′W), (2) seagrass and sand bottom in the Hawk Channel coastal lagoon (5–8-m depth) (two sites: 24°44.47′N, 80°55.06′W and 24°45.25′N, 80°46.20′W), and (3) seagrass and hardbottom in Florida Bay (2–3-m depth) near the Long Key bridge (24°47.71′N, 80°52.29′W) and the Channel 5 bridge (24°45.30′N, 80°46.19′W). A total of 144 lobsters were used, 24 for each depth and habitat treatment (i.e., eight arrays over each habitat).

We conducted preliminary trials and behavioral observations for possible experimental bias and among-treatment artifacts in this tethering study (Peterson and Black 1994; Aronson and Heck 1995). Lobsters on floating arrays did not become entangled and could move freely on the ends of the nylon thread. We looked for trends or outliers of lobster mortality by comparing the distribution of the residuals of percent mortality within and among floating arrays, but we detected no patterns in the residual plots. Because replicates were conducted over similar habitats (coral reefs, coastal lagoon, or bay) at two locations, we first tested for a location effect within habitats in two by two contingency tables using the G^2 statistic (Zar 1984). The data from similar habitats in different locations were homogeneous, so they were pooled and then analyzed using a log-linear model for a multidimensional contingency table to model patterns of independence among habitats, depths in water column, and predation events (Fienberg 1970; Stokes et al. 1995). If there were no significant interactions between variables, the model was reduced until either differences in predation were detected or all of the first-order interactions were tested. We then constructed orthogonal contrasts using Wald χ^2 statistics to detect differences within a variable (Stokes et al. 1995).

Predation along benthic offshore–inshore transport paths—To compare predation on transparent and pigmented postlarvae sheltering in benthic habitats during the day, we conducted tethering experiments in representative benthic habitats along the same transport paths used in the pelagic tethering study. Experiments were conducted on coral reefs at East Turtle Shoal and Tennessee Reef (3–6-m depth), in seagrass and macroalgal beds (2-m depth) in the Hawk Channel lagoon near Long Key (24°45.98′N, 80°53.63′W) and Conch Key (24°46.78′N, 80°53.64′W), and in seagrass and macroalgal beds (2-m depth) in Florida Bay at Long Key (24°45.97′N, 80°57.34′W) and Grassy Key (24°44.07′N, 80°58.61′W). A total of 264 lobsters were used, 22 transparent and 22 pigmented in each habitat.

Postlarval lobsters were tethered on 0.5-m lengths of nylon thread secured to the carapace by a drop of gel cyanoacrylate glue, and we tied these threads to metal spikes in the substratum at least 1 m apart along an unmarked transect (Fig. 2). Predations on lobsters placed >1 m apart are random, independent events (Butler et al. 1997). We put the lobsters in the field near dawn and checked for survivors at dusk. Individual lobsters were used only once in these experiments. We again conducted preliminary trials and behavioral observations on tethered lobsters to evaluate the risk of treatment artifacts. Behavioral observations revealed that tethered postlarvae hidden in vegetation or coral crevices are quiescent, which enhances their crypticity. We inspected the data for trends or outliers as stated above, and the data were analyzed in a manner similar to that described above for the Pelagic Predation study. A log-linear model for a multidimensional contingency table was used to test for independence, with substrate (coral rubble, seagrass, and macroalgae), habitat (coral reef, coastal lagoon, and bay), and lobster coloration phase (transparent or pigmented) as factors and predation event as the dependent variable (Fienberg 1970).

Effect of light level and prey density on predation—We compared the effect of new- and full-moon light conditions on predation both in the field and in laboratory mesocosms to test the adaptive significance of the new-moon migration. For the field test, we compared predation on planktonic postlarvae during new and full moons at two habitat/depth treat-

ments: near the bottom at the coral reef and near the surface in the bay. These habitat/depth treatment combinations were where the highest and lowest incidence of mortality occurred, respectively, in the new-moon studies (*see Results: Predation along pelagic offshore–inshore transport paths*). Postlarvae are abundant only around the new-moon period (e.g., Little 1977). Therefore, to conduct the full-moon experiments with transparent postlarvae, we captured postlarvae during new moon, acclimated them in water chilled to 21°C, and held them at this temperature in darkened aquaria until full moon. This process retarded development of the postlarvae, so most remained in an extended transparent phase. At full moon, postlarval lobsters were reacclimated to ambient seawater temperature (near 30°C), and only those that were still transparent and actively swimming were used in the field. The methods, sites, and analyses used during this full-moon study were the same as in the new-moon study.

In laboratory mesocosms, we tested the effects of different postlarval densities and the interactive effects of different moonlight levels on predation. The mesocosms were 3-m-diameter by 1-m-deep circular tanks with flow-through seawater dispersed to create a circular flow (~5 cm s^{-1}) in the tanks. De Lafontaine and Leggett (1987) found that tank sizes of >3 m^3 are necessary for reducing artifacts in experiments on larvae or zooplankton and their predators. A ubiquitous crepuscular and nocturnal planktivorous fish (yellowtail snapper, *Ocyurus chrysurus*) was acclimated in each mesocosm at least 12 h prior to the start of the experiment. These fish were held in captivity in another tank for at least 2 weeks prior to the experiment and were not fed for 24 h prior to use in experiments. Following the predator acclimation period, we introduced lobster postlarvae into the mesocosms at 2200 h each night, and the experiment ended at 2400 h. Preliminary trials revealed that 2 h was an adequate experimental period to detect predation on postlarvae yet preclude complete depletion of prey. At the end of each trial, we removed the fish then drained the tanks and collected all the surviving postlarvae. Six replicate no-predator controls were conducted to ensure that all lobsters were recaptured by this method. Video observations revealed that postlarvae swam actively when placed in mesocosms under experimental light conditions. Individual postlarvae and fish were used only once in these experiments.

This experiment was conducted as a two-factor (postlarval density and light level), crossed design with two density treatments (low density = three postlarvae, and high density = 12 postlarvae) and two light treatments simulating full and new moons. Full-moon light conditions were simulated using artificial lighting in the laboratory, and new-moon light conditions were simulated by covering the tanks. Light level, measured with a Luna Pro Gossen light meter, was adjusted so that artificial full-moon light intensity was 0.30 lx (compared to natural full-moon intensity of 0.28 lx at the sea surface at East Turtle Shoal reef), and new-moon light intensity was 0.02 lx (compared to natural new-moon light of 0.03 lx). We conducted nine replicates for each density/light level treatment. The response variable for this study was the proportion of postlarvae killed per trial (arcsine square root-transformed data). Normality of the data was assessed graphically, and variance homoscedasticity was checked using the F_{max} test. A two-factor analysis of variance (ANOVA) was conducted on the results. A Bonferroni multiple comparison procedure was used to test for differences among treatment groups.

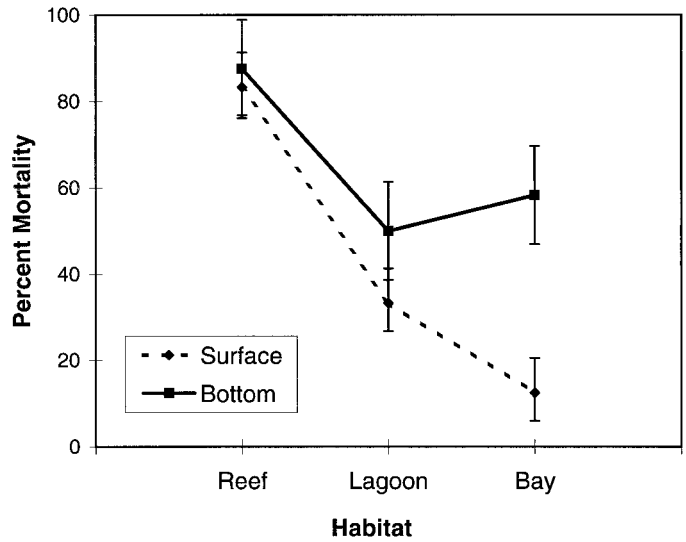

Fig. 3. Predation on postlarval spiny lobster in the water column at night during new moon along an offshore to nearshore transport path. Tethered postlarvae drifted over the coastal zones on flood tides near the surface and near the bottom. Bars are standard errors of mean percent mortality.

Results

Predation along pelagic offshore–inshore transport paths—Predation on planktonic lobster postlarvae by pelagic predators over a typical transport path from offshore to nearshore differed among habitats and depths during new moon (model $G^2 = 5.97$, df 2, $P = 0.05$) (Fig. 3). Mortality was significantly higher on tethered postlarvae floating near the surface ($\chi^2 = 8.98$, df 1, $P < 0.01$) and near the bottom ($\chi^2 = 7.67$, df 1, $P < 0.05$) over the reef than in the coastal lagoon or the bay. Within habitats, postlarval mortality was generally lower near the surface than near the bottom, but this effect was statistically significant only in the bay ($\chi^2 = 14.13$, df 1, $P < 0.001$). At least some of the predation in the coastal lagoon was by clupeid fish, because we recovered one tethered postlarvae from the mouth of a clupeid ensnared by the operculum on the tether line. These results demonstrate that predation on spiny lobster postlarvae entering the coastal waters of the Florida Keys is highest over offshore coral reefs and that their use of surface waters reduces mortality after they are transported past the reefs but not at the reef.

Predation along benthic offshore–inshore transport paths—Predation on settled postlarvae by benthic-feeding predators during daytime in representative habitats along a transport path from the reef to the bay was similar to that seen in the pelagic experiments (model $G^2 = 44.4$, df 7, $P = 0.0001$). There was a significant interaction between hab-

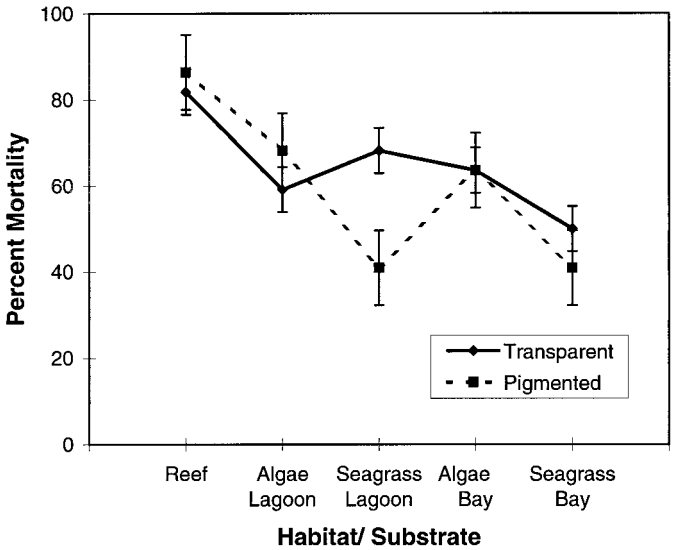

Fig. 4. Predation on transparent and pigmented postlarval lobsters in benthic habitats during the day along an offshore to nearshore transport path. Postlarvae were tethered in coral crevices on reefs and in seagrass and macroalgae in the coastal lagoon and bay. Bars are standard errors of mean percent mortality.

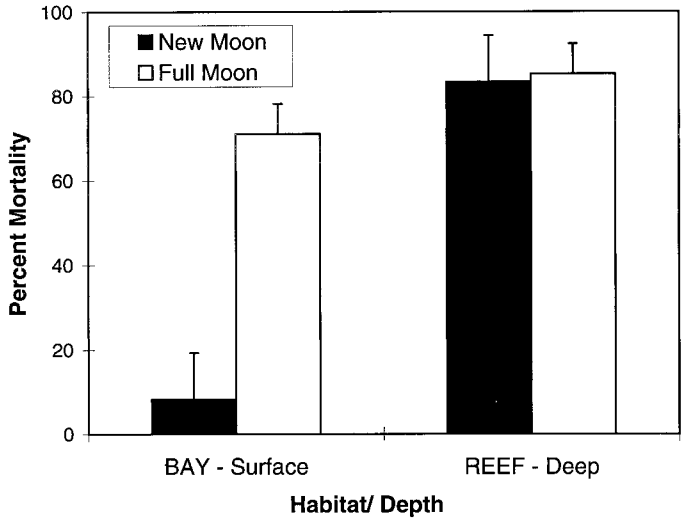

Fig. 5. Percent mortality of spiny lobster postlarvae near the bottom at reefs and near the surface in the bay during new and full moons. Bars are standard errors of mean percent mortality.

itat zone and substrate ($\chi^2 = 9.76$, df 1, $P < 0.05$). Predation was higher on coral rubble substrate on reefs for both transparent ($\chi^2 = 3.97$, df 1, $P < 0.05$) and pigmented ($\chi^2 = 13.28$, df 1, $P < 0.001$) postlarvae than in the vegetated habitats of the coastal lagoon or Florida Bay (Fig. 4). Predation on transparent and pigmented postlarvae was similar overall. These results do not support the hypothesis that pigmentation following settlement significantly reduces predation on postlarvae in these coastal benthic habitats, because transparent and pigmented individuals survived equally well.

Effect of light level and prey density on predation—Predation on planktonic postlarvae near the surface in the bay and near the bottom over the reef differed between lunar periods (model $G^2 = 8.15$, df 2, $P = 0.01$) (Fig. 5). Mortality was significantly lower near the surface of the bay during new moon compared to full moon ($\chi^2 = 12.3$, df 1, $P < 0.001$), and it was also lower in the bay than over the reef during either lunar period ($\chi^2 = 10.2$, df 1, $P < 0.01$). Mortality in the bay during full moon was similar to that over the reef during new and full moon. Thus, the surface waters of the bay appear to be safer for postlarvae than over reef habitats during new moon, but during full moon, postlarvae are equally susceptible to predation in the water column over all habitats.

In laboratory mesocosms, moonlight levels and postlarval density interacted to affect postlarval survival ($F = 14.22$, df 2, $P < 0.001$). Fish predators were equally efficient at preying on postlarvae under new- and full-moon light levels when the density of postlarval lobsters was high ($F = 1.07$, df 2, $P = 0.31$) (Fig. 6). However, when prey density was low, predation was significantly lower in new-moon conditions than in full moon ($F = 22.9$, df 2, $P < 0.0001$). A similar mechanism might be operating in nature where high densities of fish over the shallow reefs—and perhaps, a concentration of postlarvae in the reduced volume of water passing over the reef—increase predator encounters with postlarval prey.

Discussion

The survival of pelagic larvae in oceanic environments is extraordinarily poor and unpredictable, but it is difficult to study the processes affecting planktonic survival with any accuracy. Yet, as postlarvae near the coast and seek habitats suitable for settlement, these processes become more tractable. For example, we know almost nothing about the population dynamics or behavior of larval *P. argus* other than the observation that different larval instars occupy specific

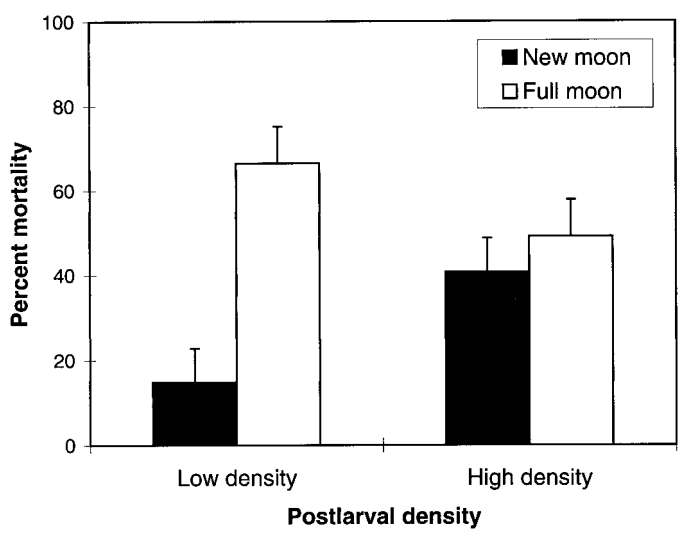

Fig. 6. Percent mortality of spiny lobster postlarvae as a function of light intensity and prey density in laboratory mesocosms. Light levels used were simulations of new- and full-moon intensities. Bars are standard errors of mean percent mortality.

depths off the Florida coast and engage in limited diurnal vertical migrations (Yeung and McGowan 1991). As they near the coast, however, the postlarvae of many decapod crustaceans exhibit a suite of behaviors that appear to maximize shoreward transport and simultaneously reduce predation risk (Forward et al. 1995; Morgan 1995). For Caribbean spiny lobster postlarvae, those characteristics include: (1) onshore migration at night on flood tides during the dark, new-moon period, and (2) use of the surface water during onshore transport. Our study reveals that postlarval spiny lobsters capitalize on these characteristics to reduce their risk of predation while in the plankton, but no single strategy is universally adaptive in all the habitats they traverse during onshore transport.

Postlarvae probably use the strong tidal current present during new moon and the rapidly moving surface water layer to speed them past dangerous habitats to the relative safety of the vegetated nursery areas in Florida Bay. While nocturnal transport in the surface water layer during new moon reduces the mortality of postlarvae in the pelagic environments of the coastal lagoon and bay, these behaviors are ineffective over coral reefs where planktivorous predators are abundant, postlarvae become concentrated in the water column, and encounter rates are high. Thus, the timing of the onshore migration of postlarvae around new moon is likely to reduce mortality in general, but the degree to which this is true depends on the amount of time postlarvae spend over dangerous habitats, such as coral reefs. The levels of mortality on planktonic postlarvae that we observed over the reef, coastal lagoon, and bay correspond with the known spatial distribution of planktivorous fishes in the region. Spiny lobster postlarvae experienced the highest mortality as they crossed the coral reefs where obligate, nocturnal planktivorous fish (e.g., Holocentridae, Priacanthidae, Apogonidae, and Pempheridae) are abundant (Starck and Davis 1966; Randall 1967; Goldman and Talbot 1976; Hobson and Chess 1978). Other wide-ranging planktivorous fish (e.g., Clupeidae, Harengulidae, and Hemiramphidae) also visit the reef tract at night, but they mainly cruise over the seagrass beds and sandflats in the coastal lagoon to forage (Starck and Davis 1966). Postlarval lobsters were safest in the shallow waters of Florida Bay, where the abundance of nocturnally active, planktivorous fish is lower (Colvocoresse unpubl. data).

Coral reefs may also affect predation rates on planktonic postlarvae by changing current velocity and constricting the water column. The dynamics of currents imposed by reef structures are potentially important to predator–prey encounter rates and predator feeding efficiency, but the effect of altered current velocity on risk of predation is difficult to predict. In laboratory flume experiments, Kiflawi and Genin (1997) observed simultaneous and nonlinear changes in the reactive volume of fish predators, predator capture efficiency, and predator confusion when current and prey density are varied. Yet, they noted that high prey density and reduced current velocity generally result in the highest predation rates. In the field, feeding rates of planktivorous fish are often correlated with prey density and current speed (de Boer 1978; Noda et al. 1992). Thus, when predators are concentrated in discrete habitats along the transport path taken by larvae (e.g., offshore kelp forests and reefs: Gaines and Roughgarden 1987; Kingsford and MacDiarmid 1988), rapid transport of larvae past these areas reduces their exposure to predators. Spiny lobster postlarvae may thus utilize the strength of the flooding new-moon tidal currents and the less turbulent surface water layer for rapid transport past the reefs that fringe the shallow coastal nurseries of the Caribbean. However, this does not explain why postlarvae do not also capitalize on the equally strong tidal transport available during full moon. Predation by nocturnal, visually acute planktivorous predators (mostly fishes) is generally, but with little evidence, offered as the explanation for greater utilization of new-moon transport by meroplanktonic larvae. Our results lend support to this hypothesis.

Lobster postlarvae may minimize their risk of exposure to planktivores that use vision to locate prey, because postlarvae are transparent and active only at night during the darkest lunar period. The notion that the predatory efficiency of nocturnal, visually acute predators is increased on bright, full-moon nights is intuitive, but the actual dynamics are unexpectedly complex. In the field, postlarvae in an artificially extended transparent phase suffered high mortality during full moon over reefs and in the bay. In contrast, predation was significantly lower in the Florida Bay nursery during the dark nights of new moon than during full moon, demonstrating the advantage of the new-moon migration. Additionally, at low postlarval densities, predation is markedly reduced during new moon. But when postlarvae are dense, planktivorous fish are equally efficient at consuming them under new- and full-moon conditions.

Coral reefs are also the most risky habitats for *P. argus* postlarvae that settle on the bottom. Predation on settled postlarvae had a similar offshore-to-inshore pattern as that observed for planktonic postlarvae, with the highest mortality occurring on coral reefs. The onshore transport of postlarvae probably takes several days, so postlarvae probably settle temporarily on the bottom during the day near the reef or in the coastal lagoon, rising into the plankton each night to continue toward the bay (Calinski and Lyons 1983). The high mortality of benthic postlarvae on the reef explains the rarity of *P. argus* juveniles there. But other species of spiny lobster settle preferentially on coral or rock reefs (e.g., *P. japonicus* and *J. edwardsii*), including a congenor (*P. guttatus*) in the Florida Keys (Sharp et al. 1997). The postlarvae of reef-dwelling lobster species presumably have other adaptations (e.g., residence in small holes; Yoshimura et al. 1994) that reduce their susceptibility to predation on reefs. Along with the reef environment, few juvenile *P. argus* occur in the coastal lagoon, and their paucity there, compared to the bay, cannot be explained by differences in predation. We suspect that factors influencing settlement (e.g., organic chemical cues; Rodriquez et al. 1993; Forward et al. 1995) differ markedly between the lagoon and bay environments and produce the observed discrepancies in juvenile abundance and distribution. Although camouflage coloration can be adaptive for reducing detection by visual predators (Owen 1980; Kiltie and Levine 1992), we also found that predation on transparent and pigmented postlarvae was similar in benthic habitats. The postsettlement transition from a transparent to a pigmented form may therefore be unrelated to predation

pressure on postlarvae. Instead, the initiation of pigmentation during the postlarval stage is probably more closely tied to the advantages of a pigmented exoskeleton (e.g., ultraviolet light protection) during subsequent benthic juvenile stages.

In summary, our study reveals that postlarval spiny lobsters exhibit characteristics that reduce their risk of predation during recruitment, but no single antipredator strategy is universally effective in all habitats traversed by postlarvae during the risky onshore migration process. Postlarvae probably use the strong tidal current in the surface water layer present during new moon to speed them past dangerous habitats to the relative safety of the vegetated nurseries in Florida Bay. This theme—that the intensity of selection can be spatially heterogeneous, thereby focusing adaptations to specific circumstances—is echoed in a number of investigations of natural selection in the wild (*see* Endler 1986), but it is often overlooked in the search for general processes and unifying themes. A key element of this study was the development of a unique, pelagic tethering technique whereby free-swimming, planktonic postlarvae could be maintained at specified depths while they drifted onshore with the tidally driven current. Coupled with mesocosm experiments, these studies permitted direct tests of the hypothesis that the nocturnal onshore transport of postlarvae in the surface water layer during new moon is advantageous for reducing mortality due to predation.

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