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The Effects of Siltation on Recruitment of Spiny Lobsters, Panulirus argus

William F. Herrnkind

Mark J. Butler
Old Dominion University, mbutler@odu.edu

Richard A. Tankersley

THE EFFECTS OF SILTATION ON RECRUITMENT OF SPINY LOBSTERS, *PANULIRUS ARGUS*

William F. Herrnkind,[1] Mark J. Butler IV,[1] and
Richard A. Tankersley[2]

ABSTRACT

Several surveys in the Florida Keys indicated fewer juvenile spiny lobsters, *Panulirus argus*, in an area where their primary habitat, stands of benthic algae *Laurencia* spp., was heavily silted as compared with similar, less silted habitat. We tested several hypotheses explaining this relationship: 1) planktonic postlarval lobster abundances are lower in the silted area, 2) siltation of algae impedes postlarval settlement or subsequent juvenile habitat selection, or 3) siltation increases mortality at the time of metamorphosis. We also compared the time-to-metamorphosis for settling pueruli within silted and nonsilted algae, analyzed the physical character of algal silt in low-silt and high-silt regions and measured the abundances of epifauna constituting prey of juvenile spiny lobsters. Planktonic postlarval abundances were substantially higher in the high-silt area thus rejecting hypothesis 1. Likewise, results from laboratory experiments testing the effect of algal siltation on postlarval time-to-metamorphosis and early postsettlement survival showed no short-term increase in mortality. Limited postlarval settlement and avoidance of silted algal habitats by juveniles, as determined in substrate choice experiments, probably accounts for the paucity of young spiny lobsters in heavily silted localities. In addition, although juvenile spiny lobsters are nonselective predators, lower prey availability in silted algae probably promotes transiency which, in turn, causes increased mortality by predation while juveniles are exposed. Large-scale siltation exacerbated by human activity must be viewed as potentially deleterious to spiny lobster recruitment.

The western Atlantic or Florida spiny lobster, *Panulirus argus*, is the focus of an intense commercial and recreational fishery in south Florida, particularly the Florida Keys. Besides severe fishing pressure, spiny lobster populations are subject to a variety of other factors that potentially limit population size. For example, habitat degradation, like that resulting from chronic siltation, may affect not only adult lobsters but the postlarval settlement stage as well. During 1983 and 1984 we sampled numerous sites in a region of about 40 km² east of Big Pine Key which was chronically heavily silted and held low numbers of newly settled spiny lobsters despite extensive benthic algal growth typical of settlement habitat. We hypothesized that postlarval spiny lobsters either do not settle in silted habitat or settle there but do not survive. In either case, we supposed that the heavy siltation reduced the carrying capacity of otherwise suitable habitat, potentially reducing regional recruitment where siltation is widespread.

Sediment particle size, composition, and stability influence larval settlement in a variety of marine benthic invertebrates (Crisp 1974, 1976; Gray 1974; Rhoads 1974; Pearson and Rosenberg 1978). For example, heavy siltation and sediment instability, created by natural biogenic reworking of the substrate and subsequent resuspension of sediments by turbulence reduces the abundance of suspension feeding infauna (Rhoads and Young 1971; Aller and Dodge 1974). In addition, siltation from human activities (e.g., dredging, shoreline development, boat traffic, etc.) can degrade benthic community structure via anaerobiosis, direct burial, toxic poisoning, or increased turbidity (Morton 1977; Allen and Hardy 1980; Jones and Candy 1981; Cortes and Risk 1985). Most available information concerns sessile or infaunal species, but little information exists for mobile, epibenthic forms (Pearson and Rosenberg 1978). Although the habitat selection and burrowing behavior of some shrimps and juvenile clawed-lobsters has been investigated in relation to substrate character (Ruello 1973; Howard and Bennett 1979; Aziz and Greenwood 1982; Botero and Atema 1982; Pottle and Elner 1982; Roach 1983; Herrnkind and Butler 1986), we know of no research describing the effect of siltation on deca-

[1]Department of Biological Science, The Florida State University, Tallahassee, FL 32306-3050.
[2]Department of Biological Science, The Florida State University, Tallahassee, FL; present address: Department of Biology, Wake Forest University, Winston-Salem, NC 27109.

pod recruitment. Our research focuses on the impact of siltation on spiny lobster postlarvae and early benthic juveniles, stages that are morphologically and behaviorally distinct from adults.

Late stage *P. argus* phyllosome larvae drift in the oceanic plankton for 6–9 months after hatching and metamorphose offshore into nonfeeding pueruli (postlarvae) that swim inshore and settle in benthic vegetation (Marx 1986). Newly settled pueruli metamorphose into cryptically colored benthic juvenile instars after about one week. Pueruli preferentially settle in highly architectured benthic algal assemblages where subsequent survival and growth depend upon available prey and physical refuge from predators (Herrnkind and Butler 1986). Ubiquitous, widely distributed stands of bushy red algae, *Laurencia* spp., provide these essential conditions and probably serve as the most important regional settlement and nursery habitat for juvenile spiny lobsters (Marx and Herrnkind 1985a, b; Herrnkind and Butler 1986; Marx 1986). The early instars remain within the algae for several months until attaining about 20 mm carapace length (CL) (Andree 1981; Marx and Herrnkind 1985a) when they begin to occupy crevices in rubble or under sponges, coral, and exposed seagrass rhizome mats. In Florida, postlarval settlement is year-round with vernal, autumnal, newmoon, and occasionally aperiodic peaks (Little 1977; Little and Milano 1980; Marx 1986). The spatial pattern of settlement is poorly known although new recruits are widely dispersed within algal habitats; diver surveys have yielded estimates of one juvenile per 36 m^2 of profuse algal growth (Marx and Herrnkind 1985a). Yet because postlarvae settle continuously and juveniles grow rapidly, a single hectare of the above habitat is estimated to nurture about 1,000 spiny lobsters annually (Marx and Herrnkind 1985a; Marx 1986). There is no compelling evidence suggesting that benthic stage lobsters immigrate into Florida waters from other Caribbean areas, although their planktonic larvae presumably do so (Lyons 1980; Marx 1986). Recruitment is thus primarily limited to postlarval influx. Therefore, precise knowledge of the factors influencing postlarval recruitment and recruit mortality is essential to managing the intensive Florida spiny lobster fishery.

Here we report on studies undertaken to investigate the impact of the observed algal siltation on spiny lobster recruitment. We compared field abundances of both pueruli and early juveniles in a representative silted and unsilted area, examined the relationship between siltation and available epifaunal prey, determined the impact of silt load on puerulus survival from settlement through metamorphosis, and tested the preference of settling pueruli and algal-dwelling juveniles for silted and unsilted algae.

METHODS

Postlarval-Juvenile Abundance in Silted and Unsilted Habitats

During June through August 1985, we compared the natural abundance of newly settled juvenile spiny lobsters (6–20 mm CL) in previously sampled, chronically silted and unsilted areas. The silted site (No Name Key) was located approximately 30 m off the western shore of No Name Key (Monroe County, FL, U.S.A.) and the unsilted site (Burnt Point) 30 m off the northwest shore of Grassy Key at Burnt Point (Fig. 1). The benthic habitat at both sites was similar and characterized by nearly contiguous stands of algae (*Laurencia* spp.) at depths of 1.5–3.0 m. Intensive visual search in algal clumps by divers was used to estimate the relative number of benthic juveniles. Because newly settled spiny lobsters are almost exclusively found associated with algal clumps (Marx and Herrnkind 1985a), catch per unit effort (CPUE) as search time within algae, gives a more suitable estimate for our purposes of comparing abundance than density/area per se. Modified Witham-type postlarval collectors (Witham et al. 1964, 1968; Little and Milano 1980; Marx and Herrnkind 1985a) were used to compare postlarval abundance among sites. Twelve collectors were initially deployed at both sites and visited approximately every 2 weeks for 3 months. Collector results are reported in CPUE to standardize catch records biased by the loss of collectors and different sampling durations.

Algal Silt Content and Prey Content

To determine the amount of silt and macrofauna contained in algal clumps at the silted and unsilted sites, we bagged individual clumps (approximately 25 cm diameter) of *Laurencia* in the field for subsequent laboratory processing. Care was taken to ensure that loose silt present on the surface of the algae was not disturbed during collection. Ten clumps, ranging in displacement volume from 55 to 300 mL, were collected at each site. Algal samples were rinsed through a series
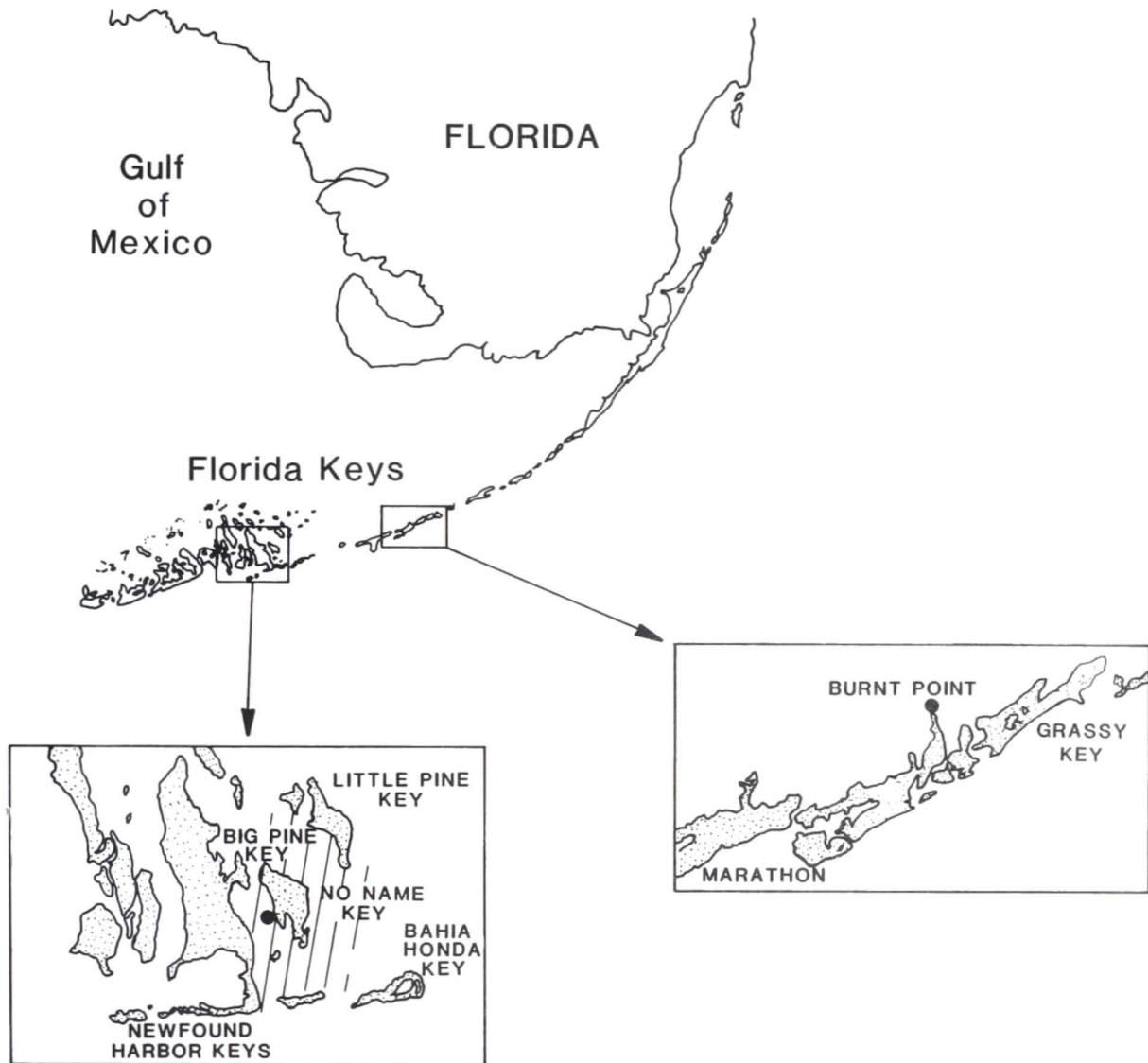
FIGURE 1.—Map of field sites in the middle and lower Keys, Monroe County, FL, U.S.A. Insets provide more detail of the areas surrounding our field sites (●). Diagonal lines depict approximate extent of the heavily silted area we surveyed.

of sieves (500 μ, 250 μ, and 63 μ; U.S. Standard Sieve Series), but only the two smallest size fractions were retained because subsamples >500 μ consisted entirely of shell and algae fragments. Silt samples were dried for 48 hours at 100°C and then weighed. The amount of algal-entrained silt at the two sites was compared using a two-sample t-test. Organic weight of the silt was derived by digesting three silt samples in 30% hydrogen peroxide for 1 week, then oven drying the remaining silt at 60°C for 48 hours (Cortes and Risk 1985). The fraction of carbonates in the silts was determined by dissolving the three samples in 5% hy-drochloric acid for 1 week, then drying the samples as above (Cortes and Risk 1985). Percent organics and carbonates (by weight) in the silts at the two sites were compared in two-sample t-tests on arcsin transformed data.

We counted the number of epifaunal prey in silted and unsilted clumps to determine the possible influence of siltation on juvenile spiny lobster food abundance. The reported estimates of prey abundance are means of two separate counts per clump; 5 clumps per treatment were processed. The volume of each *Laurencia* clump was determined by water displacement, and all silt load

and prey abundance estimates standardized by clump volume. Prey abundance data were analyzed using a two-way fixed-effects ANOVA on log transformed data and Bonferroni pairwise multiple comparisons.

Habitat Selection/Settling Experiments

We tested postlarval settlement and juvenile habitat selection in laboratory experiments using clumps of *Laurencia* spp. with high- and low-silt loads (referred to hereafter as silted and unsilted); the null hypothesis being equal selection of both habitats. Experiments were conducted in fourteen 75.7 L aquaria with subgravel filters and circulating current of 3 cm s^{-1}. Light was provided by skylights and fluorescent lights with a photoperiod of approximately 14L:10D. Two 20 cm diameter algal clumps, one silted and one unsilted, were situated 25 cm apart at opposite ends of each aquarium and at least 5 cm from aquarium walls. The number of natural prey in both silted and unsilted clumps far exceeded the number eaten daily by a juvenile. To further control food availability in experiments with juveniles we added equal amounts (10 mg) of *Tetramin*[3] fish food to each clump, providing an overabundance of food available ad libitum. If juveniles chose one type of algal clump over the other, then their selection was most likely based on the presence or absence of silt, because food abundance and quality were similar, if not strictly identical, in both types of algal clumps. Pueruli neither feed nor respond to the differential abundance of potential prey (Herrnkind and Butler 1986). Silted algae was collected from the No Name Key site (see section on Algal Silt Content and Prey Content); unsilted algae was collected just offshore of the Sea World Marine Science and Conservation Center on Long Key. Fresh algal clumps were used in each experimental replicate. An experiment was initiated by introducing a single puerulus or juvenile spiny lobster to the center of an aquarium through a 5 cm diameter PVC pipe. Once a spiny lobster settled to the substrate, the pipe was slowly withdrawn allowing the lobster to move freely about the aquarium. This technique prevented "tailflipping" by lobsters and facilitated active selection of habitats. Twenty-four hours later we located the lobsters and recorded their positions, as in previous experiments

(Herrnkind and Butler 1986). Fourteen spiny lobsters were tested on day 1, 14 more on day 2, and so on until our stock of animals was depleted. Each lobster was used only once. All pueruli were collected on the incoming tide from the plankton in interisland channels. Pueruli were either tested immediately or allowed to metamorphose for later use in experiments requiring juveniles. Data were analyzed with log-linear Goodness-of-fit tests.

Metamorphosis Experiment

The effect of siltation on the survival and time-to-metamorphosis of pueruli was tested experimentally in an outdoor, flow-through seawater system. One freshly collected puerulus was placed in each of 46 seawater-filled 1 L plastic beakers, 23 containing 5 cm diameter clumps of unsilted algae and the other 23 an equal amount of silted algae. Each container was independently supplied with flowing, filtered seawater. Algal clumps were replaced daily. Pueruli do not feed and their habitat selection operates independent of food availability (Herrnkind and Butler 1986), thus no food was added to the containers. Seawater temperature in the beakers remained between 26° and 28°C; photoperiod was approximately 14L:10D. Pueruli were monitored daily and their survival and time-to-metamorphosis recorded.

Pueruli were collected as transparent postlarvae from the plankton in interisland channels which concentrate oceanic postlarvae as they move into Florida Bay nursery areas. Time-to-metamorphosis values represent the elapsed time (in days) from puerulus collection until metamorphosis into the first benthic stage. Values are likely to differ among collections as different cohorts of pueruli arrive inshore. There are currently no techniques available to determine the actual age of pueruli (i.e., time since metamorphosis from the phyllosoma stage), but estimates of duration of the puerulus stage range from 2 weeks to 1 month (Lyons 1980; Calinski and Lyons 1983). Differences in time-to-metamorphosis between the two treatments were analyzed via a two-sample *t*-test.

Juvenile Spiny Lobster Prey Selection Experiments

Laboratory experiments were conducted to determine juvenile spiny lobster prey preference

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

and rate of consumption of algal epifauna. Prey were obtained by rinsing large clumps of *Laurencia* through a 100 μ sieve. Prey included small gastropods, amphipods, isopods, and ostracods ranging in size from 1 to 9 mm (Marx and Herrnkind 1985a). Prey were individually counted and placed in 1 L plastic beakers containing 750 mL of seawater. One starved (24-h) juvenile lobster (6–8 mm CL) was introduced to each container, allowed to feed for 12 hours, and was then removed; the remaining prey were counted. Fifteen spiny lobsters were tested in each experiment; each lobster was used once. Three experiments were conducted using different prey combinations (Table 1), but the total number of prey available remained similar and exceeded the amount a single lobster could consume in 12 hours. Electivity indices calculated for each experiment were used in multiple comparison tests to determine whether juvenile spiny lobsters fed preferentially or randomly (Johnson 1980).

TABLE 1.—Relative prey availabilities (A) and predator usage (U) values (percentages) in the three juvenile spiny lobster prey selection experiments. N = 15 lobsters per experiment. F-values calculated from Johnson (1980) indicate whether prey choice differed significantly from random in each trial; none of the tests were significant at $P = 0.05$.

| Prey type | Experiment | | | | | |
| | 1 | | 2 | | 3 | |
	A	U	A	U	A	U
Gastropoda						
Tricolia sp.	43.5	61.5	71.4	83.0	58.0	54.5
Battillaria spp.	8.7	1.0	4.3	0.2	—	—
Tegula spp.	6.5	0.0	—	—	—	—
Atys spp.	—	—	14.3	7.2	—	—
Amphipoda	32.6	33.9	10.0	9.6	7.0	7.1
Isopoda	—	—	—	—	17.4	20.0
Copepoda	—	—	—	—	11.6	13.1
Ostracoda	—	—	—	—	6.0	5.3
Decapoda	8.3	3.6	—	—	—	—
F-values	0.46		0.40		0.09	
df	4,11		3,14		4,11	

RESULTS

Postlarvae were more abundant on collectors at the silted site than at the unsilted site. Diver surveys revealed that higher numbers of algal-dwelling juveniles (<20 mm CL) resided at the unsilted site despite greater influx of pueruli into the silted area (Table 2). Only one juvenile spiny lobster collected at the silted site was <20 mm CL, most were considerably larger (25–35 mm CL) than those at the unsilted site, and some were possibly large enough to have immigrated there from adjacent unsilted areas.

Silt recovered from the algal clumps was largely calcareous and formed a cohesive cast around the algal filaments. Classifying algal-bound silts by particle size would yield irrelevant values because sieving caused fragmentation of aggregated particles. Therefore we report only the total dry weight of the silts. Algae at No Name Key carried a higher silt load than algae at Burnt Point ($\bar{x}$ = 125 vs. 65 g L algae, respectively; t = 2.90, df = 18, $P < 0.01$). Silt at No Name Key was characterized as $12.5 \pm 7.4\%$ organic and $28.1 \pm 27.6\%$ carbonate by weight, whereas Burnt Point silt was $16.9 \pm 1.06\%$ organic and $66.3 \pm 14.5\%$ carbonate (means ± 1 SD). There was no significant difference in silt composition between sites (organics: $t = 0.83$, df 4, $P > 0.05$; carbonates: $t = 1.97$, df = 4, $P < 0.05$), although sample sizes at each site were small and sample variance substantial. Algae at both sites contained primarily gastropods, amphipods, and isopods, although significantly more gastropods and echinoderms occupied unsilted clumps (Fig. 2, Table 3; $P < 0.05$ in Bonferroni pairwise multiple comparisons).

Significantly more pueruli settled in unsilted algal clumps than in silted clumps during laboratory settlement choice experiments (38 vs. 11, respectively; $G = 15.72$, $P < 0.001$). Juvenile spiny lobsters responded similarly in the habitat selection experiment (54 vs. 24; $G = 11.78$, $P < 0.001$). We excluded the open sand habitat in aquaria from our analysis because 1) juvenile spiny lobsters are never found residing on open sand in the field, presumably due to a lack of food and refuge

TABLE 2.—(A) Postlarval lobster abundances at silted and unsilted Florida Bay study areas. Postlarval catch per unit effort (CPUE) was estimated from Witham collector catches. (B) Juvenile lobster (8–20 mm CL) abundances at the two study sites in 1985 and adjacent areas sampled during 1983 and 1984. Juvenile CPUE was estimated via diver surveys.

A. POSTLARVAL ABUNDANCE

| Location | Description | CPUE[1] | | |
		June	July	August
No Name Key	silted	0.08	0.32	0.15
Burnt Point	unsilted	0.01	0.05	0.10

B. JUVENILE ABUNDANCES

Location	Description	Diving hours	CPUE[2]
No Name Key (1983–85)	silted	28	0.04
Burnt Point (1983–85)	unsilted	20	0.50

[1]CPUE $= \dfrac{\text{no. of postlarvae no. of collectors}}{\text{no. of days between collections}}$

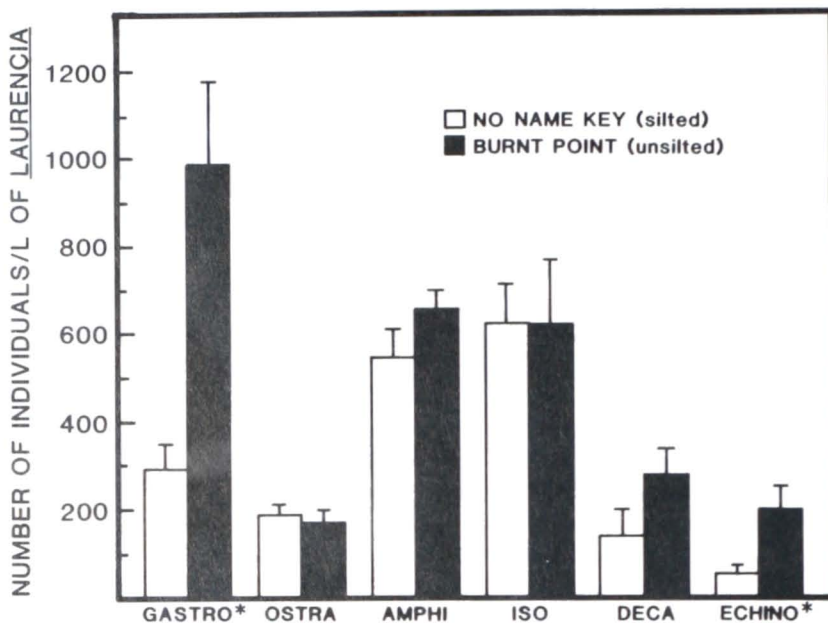[2]CPUE $= \dfrac{\text{no. of lobsters collected}}{\text{no. of diver hours}}$

FIGURE 2.—Abundances ($\bar{x} \pm 1$ SE) of the six most common prey found in algal clumps at the silted No Name Key and unsilted Burnt Point sites. Five clumps were collected at each site. Values are standardized by clump volume. Asterisks denote significant difference in Bonferroni multiple comparison tests ($P = 0.05$). Abbreviation key: GASTROpod, OSTRAcod, AMPHIpod, ISOpod, DECApod, ECHINOderm.

TABLE 3.—Two-way fixed-effects ANOVA testing for differences in the total number of individuals among six prey categories (see Table 1) at two sites, one silted (No Name Key) and one unsilted (Burnt Point). Data were log transformed.

Source	df	SS	F	P
Site	1	0.841	18.78	0.001
Prey type	5	6.242	27.89	0.001
Site X prey type	5	0.847	3.78	0.006
Error	48	2.149		

(Marx and Herrnkind 1985b; Herrnkind and Butler 1986), 2) most spiny lobsters recovered from open sand were actually in corners, indicating edge-seeking behavior rather than selection for sand per se, and 3) only 10.6% of 142 spiny lobsters tested were found on sand even though it constituted 68% of the exposed substrate in aquaria. Silt had no effect on puerulus survival through metamorphosis to the first benthic instar (13% vs. 9% mortality in silted and unsilted algae, respectively), or time-to-metamorphosis (Fig. 3; $t = 0.37$, $P > 0.05$).

The total number of prey items consumed in the juvenile prey selection experiments ranged from 19 to 57 prey per lobster per 12 hours. Juveniles fed randomly from the three different prey combinations and frequencies offered to them (Table 1).
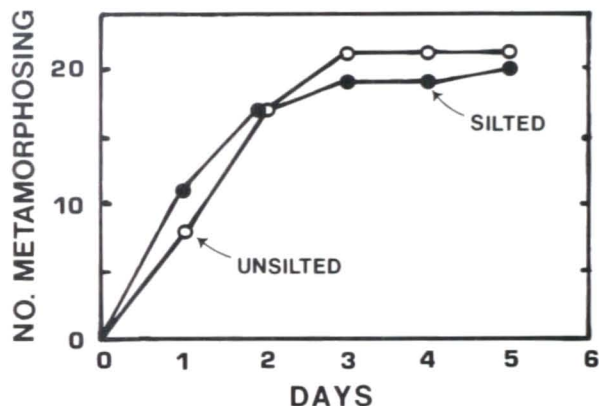

FIGURE 3.—Cumulative number of spiny lobster postlarvae metamorphosing as a function of time in one of two treatments: silted algae (*Laurencia* spp.) or unsilted algae. Twenty-three postlarvae were tested in each treatment; two postlarvae died in the unsilted treatment and three in the silted treatment.

DISCUSSION

The relative paucity of newly settled spiny lobsters in the heavily silted region around No Name Key over a 3-yr period indicates that low recruitment to benthic habitat is typical there. The absence of juveniles was apparently not due to a

lack of postlarval influx, which was higher than that at the unsilted Burnt Point site, but instead to low rates of postlarval settlement. Results from our habitat selection experiments support this hypothesis because settlement was significantly lower in silted algal clumps than in unsilted clumps. Previous studies showed that postlarvae selectively settled in highly architectured materials, like algal clumps (Herrnkind and Butler 1986). Thus, heavy silt covering an otherwise preferred habitat either masks the stimuli triggering settlement or contains stimuli that elicit rejection by pueruli. This question remains for further study. We cannot conclusively ascertain from our laboratory experiments the mechanisms governing habitat choice in the field where silted and unsilted habitats may not be adjacent, as they were in our aquaria. Yet for many species with planktonic larvae, these kinds of experiments, coupled with field observations of more general patterns of behavior and abundance, provide valuable insights into natural processes (Sulkin 1986).

Twenty percent of the pueruli we tested in laboratory tanks settled in silted clumps despite the general rejection of this habitat. Pueruli settling in silted algae probably metamorphose normally into the first benthic instar, as indicated by the equivalent time-to-metamorphosis and early post-settlement survival in both silt levels tested. However, subsequent residency by juveniles presumably is limited, given their great mobility and preference for unsilted algae with high food levels (Marx and Herrnkind 1985b; Herrnkind and Butler 1986). We found that prey abundances were significantly lower in silted algae. Thus, even if pueruli settle in the silted habitat the subsequent juveniles may leave to obtain adequate food. Frequent interclump movement by juvenile spiny lobsters, searching either for food or unsilted habitat, would predictably result in increased predatory mortality. Susceptibility to predation is much greater for juveniles in the open, than it is for individuals amidst algal clumps or dense seagrass (Herrnkind and Butler 1986). Thus, juvenile residency patterns and susceptibility to predation may, in addition to locally low settlement, contribute to the paucity of lobsters in the silted habitat.

The algal-bound silt load at No Name Key was roughly twice that at Burnt Point where spiny lobster recruitment was considerable. Our cursory surveys from Key Largo to Boca Chica Key indicate that similar silt levels are common, though geographically variable in Florida Bay. Benthic algae, including *Laurencia* spp., serve as sediment traps (Scoffin 1970) and demonstrate a remarkable resistance to siltation, growing profusely even in heavily silted areas. Silt in these areas is primarily calcareous, most of it probably a byproduct of sediment processing by deposit feeding shrimp (particularly *Callianassa*), annelids, and sea cucumbers.

We did not evaluate the geographic extent of siltation relative to spiny lobster settlement in Florida Bay. However, the demonstrated aversion to settling in naturally silted algae, characteristic of the region around No Name Key, strongly suggests that low postlarval recruitment and juvenile abundances would occur in similar conditions elsewhere. The sparse juvenile population at our silted site, one-tenth that of the unsilted site, suggests deleterious impact of high chronic silt levels in areas of potential recruitment. Human activities also cause siltation (Morton 1977; Allen and Hardy 1980). We noted that algal stands adjacent to heavily trafficked boat channels typically were more heavily silted than adjacent areas. We suspect the effect of manmade siltation to be similar to that from natural causes. Although it is now generally accepted that Florida Bay shallows serve as the main nursery grounds for the south Florida spiny lobster population (Marx 1986), the regional distribution of settlement and early juvenile habitation remains to be mapped. Future wide-area surveys by concerned researchers and agencies should include sampling of new spiny lobster recruits as well as silt levels. Meanwhile, sizable human activities such as channel construction, dredging, spoil dumping, coastal development, and mineral mining must be viewed as potentially deleterious to spiny lobster recruitment.

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