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Nocturnal foraging of the Caribbean spiny lobster (*Panulirus argus*) on offshore reefs of Florida, USA

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Abstract. During night dives along randomly selected transects across sand, seagrass, and rubble on the reef flat of Looe Key, a spur-and-groove coral reef, spiny lobsters (*Panulirus argus*) from dens on the forereef were observed foraging on the reef flat, particularly on the extensive rubble ridge and also relatively frequently in *Thalassia*. Subsequent sampling of the rubble revealed hundreds of taxa of appropriate prey items, many at high densities; the density of *Cerithium litteratum*, a favoured food item, was as high as 180 individuals m^{-2}. Arthropods, especially spider crabs (*Pitho* spp.), were common in seagrass. Gut contents of 75 intermoult lobsters caught on offshore reefs at Biscayne National Park and Dry Tortugas National Park included a myriad of prey items, predominantly molluscs—especially gastropods (49%), chitons (15%), and bivalves (11%)—and arthropods (12%); many of the species in lobster guts were rubble dwellers, but some guts contained multiple prey peculiar to seagrass and sand. It is concluded that *Panulirus argus* can forage successfully wherever suitable prey items, especially molluscs, are abundant. However, where a wide range of substrata, including rubble, is available, rubble is preferred because of its abundant, accessible prey.

Extra keywords: food, feeding, marine reserves

Introduction

The Caribbean spiny lobster (*Panulirus argus*) is one of the most successful shallow-water marine invertebrates of the tropical and warm-temperate western Atlantic Ocean. The species ranges from Bermuda to central Brazil, including shelf waters of the Gulf of Mexico and the south-eastern United States, and it occurs in abundances sufficient to support major commercial fisheries throughout much of its range (Aiken 1993; Briones and Lozano 1994; Ehrhardt 1994; Fonteles-Filho 1994; Hunt 1994; Cruz *et al.* 1995). Moreover, *P. argus* is a long-lived species that is able to utilize a variety of environments. Individual lobsters change habitats several times during their ontogenetic progression from inshore nursery areas to adult habitats on offshore reefs (Herrnkind 1980; Andree 1981; Lyons *et al.* 1981; Butler and Herrnkind 1991). Any species that occupies such a wide range of environments must be capable of utilizing different food sources available throughout many foraging habitats.

Individuals of *P. argus* seek daytime shelter in the crevices and caverns of offshore reefs and in undercuts along nearby seagrass 'blowouts' (erosional features within seagrass beds; Patriquin 1975), but they leave their dens at night to forage in surrounding areas. Herrnkind *et al.* (1975) determined that adult reef-dwelling lobsters foraged opportunistically throughout their home range, feeding in rocky areas, grass, and algal flats. Reef-dwelling juveniles of *P. cygnus* forage in seagrass beds located in front of their home reef or nearby reefs (Jernakoff 1987). Movement out of dens peaks several hours after sunset, and most lobsters return to their dens several hours before dawn (Herrnkind *et al.* 1975).

Little is known regarding the foraging behaviour of any life stage of *P. argus*. Other palinurids commonly eat live molluscs and crustaceans, which they locate by contact and chemoreception (Winget 1968; Engle 1979; Joll and Phillips 1984), and a similar diet seems to be favoured by *P. argus*. Herrnkind *et al.* (1975) found that gastropods were the favoured prey of *P. argus* juveniles at St John, US Virgin Islands, whereas crustaceans were more frequently eaten by reef-dwelling adult lobsters. However, Espinosa *et al.* (1991) found that molluscs, principally gastropods, constituted most of the diet of larger *P. argus* individuals captured in seagrass and on reefs off south-western Cuba. Andree (1981) identified small gastropods and crustaceans in faecal pellets of small *P. argus* individuals at Biscayne National Park, Florida.

Herein, we describe foraging activities by reef-dwelling lobsters in the Florida Keys, based upon nocturnal surveys at Looe Key National Marine Sanctuary. We evaluate the adaptability of *P. argus* to different food availability, in

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terms of prey abundance and diversity, based upon examinations of gut contents of lobsters from other Florida reefs and surveys of benthic fauna on various substrata at Looe Key. We theorize that the relative availability of prey and its accessibility influences the nocturnal foraging patterns of *P. argus* in that lobsters tend to forage where prey is most available.

Methods

Study site

Looe Key National Marine Sanctuary (LKNMS), located 9 km south of Big Pine Key in the Florida Keys, encompasses 18·2 km^2 and includes a spur-and-groove reef (forereef) on the seaward side (Wheaton and Jaap 1988). The sanctuary is divided into seven management units that correspond to physiographic zones (Anon. 1983). The study was conducted in two of these zones: the forereef and the reef flat (Fig. 1). A 50-ha 'core area' encompassing the entire forereef and most of the reef flat is closed to commercial lobster harvesting. Recreational lobster harvesting there is discouraged by rigorous enforcement of regulations that prohibit the touching of coral.

The reef flat, located landward of the forereef, encompasses a complex mosaic of seagrass, sand, and the surrounding rubble ridge (Fig. 1). Some of the rubble ridge (about 25%) is outside the core area, so lobsters there are not protected from harvesting. The reef flat was partitioned into Region 1 and Region 2, based on proximity to the forereef (Fig. 1). The boundary between the regions is an imaginary line drawn parallel to the reef crest from the point where the northern core-area boundary crosses the western rubble ridge. Region 1 is the area between the forereef and the boundary; it contains isolated coral heads, seagrass, and sand. Region 2, landward of Region 1 and extending to the apex of the reef flat, contains sand, seagrass, and ephemeral seagrass blowouts.

Nocturnal sampling of foraging habitat

Lobsters were sampled on the reef flat at night during five periods from June 1988 to January 1989. The reef flat comprises a mosaic of potential foraging habitats for *P. argus*, but this patchiness of substrata precluded direct comparisons of lobster abundance in equivalent replicated plots. Instead, we used randomly located belt transects that crossed over all substrata in proportion to their widely disparate distributions to acquire representative samples of lobsters as they foraged.

During daylight, a 200-m tape was placed on the sea bottom at a random location on the reef flat. This tape was subdivided into five equal (40-m) lengths, and a 100-m-long belt transect (belt width: 8 m) was established perpendicular to the 200-m tape at a random location within each 40-m length. The point on the belt transect (0 m to 100 m) at which the transect crossed the 200-m tape was also randomly determined.

Belt transects were sampled between 2300 and 0100 hours for two or three consecutive nights, depending upon weather conditions. Divers recorded by substratum type each lobster they encountered on the belt transects, and they attempted to catch all lobsters observed. Lobsters residing within dens were counted and captured but were not used in foraging analyses. Each captured lobster was marked with a uniquely numbered sphyrion tag inserted into the dorsolateral extensor muscle between the cephalothorax and abdomen (Herrnkind *et al.* 1975). Size (measured as carapace length to the nearest millimetre), sex, reproductive condition of females, and tag number were recorded, and lobsters were returned to the belt transect from which they had been captured.

Divers returned during daytime after the completion of each census and documented the composition and distribution of substrata along each transect. Substratum was initially categorized as one of three seagrass types (*Thalassia testudinum*, *Syringodium filiforme*, or a mixture of the two, termed 'mixed seagrass'), sand, edge (defined as the area within 1 m on either side of a blowout cliff face), coral heads, or rubble. During the last sampling period, a mixture of small compacted rubble and short *Thalassia testudinum* was encountered and categorized as *Thalassia*–rubble. The

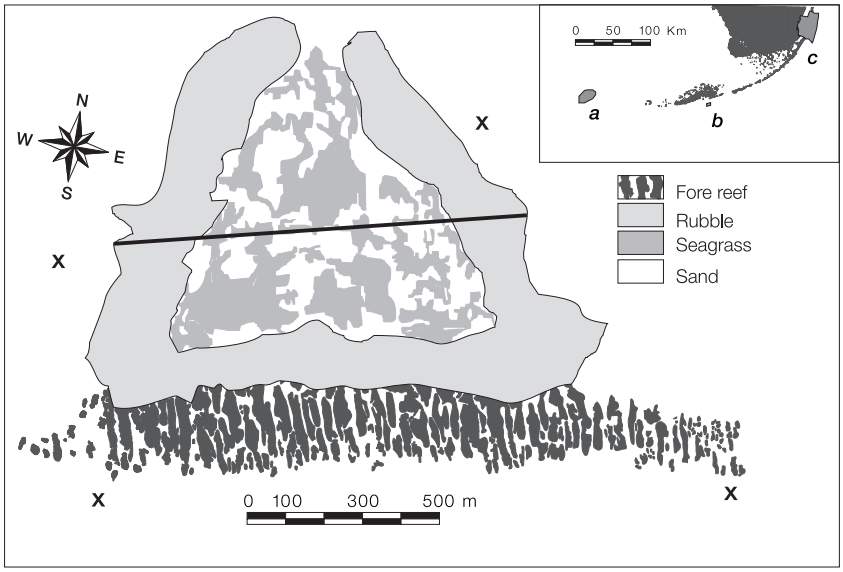

Fig. 1. Location of *(a)* Dry Tortugas National Park, *(b)* Looe Key National Marine Sanctuary (LKNMS), and *(c)* Biscayne National Park, and the forereef–reef flat complex at LKNMS. **X**s denote boundary buoys of the core area of LKNMS. The line represents the boundary between Region 1 (bottom) and Region 2 (top) of the reef flat. Small patches of rubble are interspersed throughout the sand and seagrass of the reef flat.

percentage of each substratum type along the transects was calculated for every sampling period.

To determine whether lobsters were distributed proportionately among substratum types, a preference index was calculated for each substratum in every sampling period as follows: [preference index] = [percentage of lobsters on a substratum] – [percentage of that substratum available]. A positive index indicated that more lobsters were observed on a substratum than would be expected if lobsters were distributed randomly among substrata. A negative index indicated fewer lobsters than expected. Preference indices were tested for differences among substrata by analysis of variance (ANOVA).

Not all potential foraging substrata were included in preference analyses. *Thalassia*–rubble was not encountered until the last sampling period, so data for that category were insufficient for evaluation. Only 3% of the area sampled consisted of coral heads and the only lobsters found in association with them at night were denning beneath them, not foraging upon them, so the coral heads were excluded from analyses. Additionally, early in the sampling programme we observed many lobsters walking along blowout edges, prompting us to unobtrusively observe their behaviour. None of the many lobsters observed near edges was ever seen to actively forage there, so we also excluded 'edge' (3% of the area sampled) from preference analyses.

Because each preference index could be heavily influenced by wide variability in substratum patch size, we evaluated the foraging data by an additional analysis that provided a mechanism to examine each substratum across its range of patch sizes. We predicted that there would be more lobsters on transects with higher percentages of preferred foraging substratum. For each substratum, we regressed the number of lobsters on a transect by the amount of that substratum on the transect.

A one-time nocturnal survey of the entire reef flat, including the rubble ridge, was conducted on 19 July 1989. Four sets of three 100-m-long belt transects were placed throughout the reef flat. The first transect of each set was placed on the rubble ridge, the second transect was placed adjacent to the first, primarily in seagrass or *Thalassia*–rubble, and the third transect was placed perpendicular to the others, crossing many substrata. Two sets of transects were located in Region 1; the other two sets were in Region 2. Shortly after dusk (2130 hours), all four sites were sampled simultaneously by separate teams of divers who recorded each lobster they encountered by substratum type but did not capture the lobsters. The transects were sampled again at 2300 hours, and lobsters were captured. Lobsters were measured and substratum percentages were determined as previously described.

Population dynamics and tag recapture

As part of a larger study of trends in abundance and population dynamics of spiny lobsters at LKNMS, permanent sampling sites were established on the forereef and the reef flat in 1987. Sites on the reef flat included isolated coral heads in Region 1 and seagrass blowouts (Patriquin 1975) in Region 2. Each site was sampled during daytime for two years to determine the size structure, sex ratio, and movement patterns of lobsters living in different areas of the forereef–reef flat complex. Individuals of *P. argus* were also captured at two additional sites on the forereef that were sampled regularly at night for other purposes. All lobsters were measured, sexed, tagged as previously described, and returned to their capture locations.

Gut contents and prey abundance

To elucidate the types of prey consumed by reef-dwelling lobsters in Florida, we analysed a data-set containing counts and identifications of material in *P. argus* guts collected in 1978. Lobsters were collected one to two hours before dawn from dens in shallow-water reefs at Dry Tortugas National Park and Biscayne National Park (Fig. 1). Size, sex, and moult stage were recorded for each lobster. Only intermoult lobsters were included in gut-content analyses because little, if any, foraging occurs among lobsters in late premoult through middle postmoult stages (Lipcius and Herrnkind 1982). Lobsters were sacrificed quickly to obtain relatively undigested gut contents, which were identified to the lowest feasible taxon. Identifications to species level were sometimes possible for molluscs on the basis of chitinous remains (opercula or radulae). Empty gastropod shells were assumed to have contained snails and not hermit crabs. We are confident about this assumption because of the low incidence of hermit crab parts (chelae, dactyls, etc.) in guts relative to other arthropod parts and because of the high incidence of gastropod opercula.

Prey items were enumerated and categorized as follows: molluscs (gastropods, bivalves, chitons, scaphopods), arthropods, echinoderms, plants, and 'other' (foraminiferans, sponges, polychaetes, sipunculans, amorphous tissues, spicules, etc.). Data were analysed for differences by ANOVA or, when the assumptions of ANOVA were not met, by Kruskal–Wallis test. Multiple comparisons were made with the aid of Tamhane's T2 test, which does not assume homogeneity of variance (Anon. 1996*a*).

Potential prey residing in rubble, sand, and seagrass at Looe Key was quantified to test the hypothesis that prey was more abundant in rubble than in other substrata. A suction dredge was used to sample fauna from sand and seagrass on the reef flat by removing sediments from 0·25-m^2 quadrats at seven locations selected haphazardly within each substratum type; three replicate samples were collected at each location (2 substrata × 7 locations × 3 quadrats = 42 samples). Sediments were washed through 5-mm-mesh bags (maximum stretched diameter: 6 mm), and animals retained in the bag were identified. Rubble and *Thalassia*–rubble were sampled more extensively than were sand and seagrass. To sample rubble dwellers, divers collected animals by hand from 0·25-m^2 quadrats. We sampled two haphazardly selected sites at each of four locations on the rubble ridge and at a fifth location on *Thalassia*–rubble. Nine quadrats were sampled at each site (5 locations × 2 sites × 9 quadrats = 90 samples).

Molluscs, arthropods, and echinoderms from each sample were identified to the lowest feasible taxon; arthropods were identified by D. K. Camp (Florida Department of Environmental Protection, Florida Marine Research Institute).

To facilitate comparisons across all substrata, we collapsed the prey numbers in individual rubble subsamples into an overall mean prey abundance at each site. Data were then analysed for differences among substratum types by a Kruskal–Wallis test. Multiple comparisons were made with the aid of Tamhane's T2 test. Abundance was converted to density by dividing the number of individuals for each group by the area of substratum sampled.

Results

Nocturnal sampling of foraging habitat

A total of 45 896 m^2 (4·6 ha) was sampled by the use of random transects on the reef flat. Of the 158 lobsters (22–114 mm carapace length, or CL) observed, 123 were outside their dens. Overall density of lobsters for each substratum ranged from 5·4 lobsters ha^{-1} for *Syringodium* to 94·1 lobsters ha^{-1} for edge (Table 1). As expected, densities of lobsters in a given substratum were quite variable among transects, partly because of the variable size of substratum patches. Because of the high variance, lobster density was not significantly different among substrata.

Preference indices were calculated for rubble, sand, *Thalassia*, *Syringodium*, and mixed seagrass. Despite high variance among samples, preference indices were significantly different among substrata at an α level of 0·1 (ANOVA: $F = 2{\cdot}37$, d.f. = 4, $P < 0{\cdot}1$). The preference index for rubble was positive, whereas the preference index for

Table 1. Densities of spiny lobsters in different substrata on the reef flat in Looe Key National Marine Sanctuary at night

Densities are grand means for each substratum over the entire random-transect study· *Thalassia*–rubble was sampled only during the last census

Substratum	Total area (m^2)	Total lobsters	Density (lobsters ha^{-1})
Edge	1488	14	94·1
Rubble	8848	48	54·3
Thalassia	5184	20	38·6
Thalassia–rubble	2840	8	28·2
Mixed seagrass	11592	21	18·1
Sand	6624	7	10·6
Syringodium	9320	5	5·4

sand was negative (Fig. 2). Preference indices calculated for the three seagrass categories revealed disparities among those substrata: the preference index was positive for *Thalassia*, negative for *Syringodium*, and nearly zero for mixed seagrass.

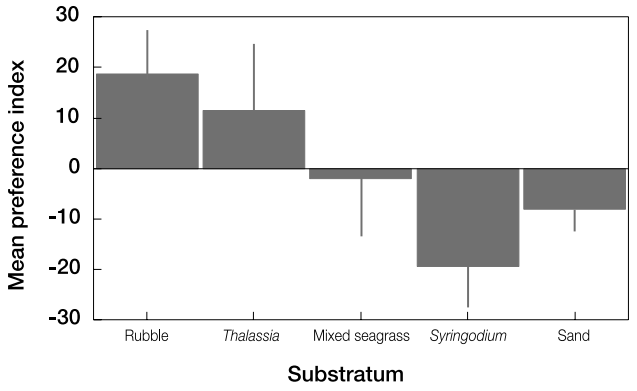

Fig. 2. Substratum preference indices for lobsters on the reef flat at night. Bars represent means from five sampling periods; vertical lines indicate ±1 s.e. of the mean.

The slope of the regression of the total number of lobsters on a transect and the percentage of rubble on that transect was significantly positive (r^2 = 0·59, d.f. = 1, F = 30·65, $P < 0·001$). In general, there were more lobsters on transects with higher percentages of rubble. In contrast, similar regressions revealed no such pattern for any other substratum; increasing percentages of other substrata did not result in correspondingly higher lobster counts. In all cases, values of r^2 were less than 0·16 and slopes were near zero.

During the single-night survey of the entire reef flat, we observed 58 lobsters on the first set of dives and 59 lobsters on the second set of dives (Table 2). Lobsters ranged in size from 59 to 107 mm CL. Contrary to our expectations, more of those lobsters were observed outside dens during the early-evening dives than later. The proportion of lobsters found in each rubble type (rubble ridge, other rubble, and *Thalassia*–rubble) was greater than the proportion of that substratum sampled in all but one instance (Dive 1: rubble ridge). The proportions of lobsters observed in other substrata were less than the proportions of those substrata sampled in all but one instance (Dive 1: *Thalassia*). Usually, however, higher proportions of lobsters were found foraging in rubble during the second dives than during the first dives, and the proportions of foraging lobsters found on sand and other substrata decreased accordingly.

Population dynamics and tag recapture

The success rate for capturing lobsters along the reef-flat transects at night was 88%. Daytime capture success rate was 94% on the reef flat and 84% on the forereef. Thus, captured lobsters are probably a representative subsample of the population.

The lobster population on the reef flat at night generally displayed characteristics intermediate between those observed on the forereef and on the reef flat during the day (Table 3). During the reproductive season, daytime sex ratios on the reef flat were nearly 1:1, whereas the sex ratio on the forereef was highly skewed toward females. At night, the sex ratio in Region 1 was intermediate between sex ratios on the forereef and in Region 1 during the day. The percentage of ovigerous lobsters on the reef flat (both Region 1 and Region 2) at night also was intermediate between percentages observed on the forereef and on the reef flat during daytime. Males were generally smaller in Region 1 at night than either on the reef flat or on the forereef during the day. Size and sex ratios during the non-reproductive season appear to follow trends similar to those observed during the reproductive season, but the number of lobsters observed was much smaller.

Lobsters found in dens on the reef flat during the day were often found foraging on the reef flat at night. We observed 20 lobsters during both day and night dives at the reef flat. Of these, 13 were observed at night in the same region (Region 1: n = 11; Region 2: n = 2) where their daytime dens were located, and seven were observed at night in the opposite region from that of their daytime shelters. An additional 10 lobsters first captured at night were recaptured only at night; five of these recaptures occurred on subsequent nights during the same census, and the other five occurred during subsequent sampling periods up to six months later.

Tagged lobsters also moved between the forereef and the reef flat. Seven female lobsters initially tagged on the reef flat at night were recaptured in shelters on the forereef during the day. Four lobsters (three females and one male) tagged on the forereef during the day were recaptured on the reef flat at night. Extensive surveys of dens on the forereef and reef flat revealed another 33 tagged lobsters (25 females

Table 2. Areas and proportions of substratum types covered by transects during simultaneous surveys throughout the reef flat, and numbers and proportions of lobsters observed on each substratum type

n, number of lobsters; 'Rubble ridge', high-relief mound of rubble bounding the reef flat; 'Other rubble', rubble observed on transects other than rubble-ridge transects

Substratum	Area		Dive 1		Dive 2	
	m^2	%	*n*	%	*n*	%
Rubble ridge	3160	33·0	15	25·9	23	39·0
Other rubble	496	5·2	5	8·6	6	10·2
Thalassia–rubble	568	5·9	17	29·3	14	23·7
Thalassia	640	6·7	4	6·9	1	1·7
Mixed seagrass	2960	30·9	7	12·1	3	5·1
Syringodium	424	4·4	2	3·4	1	1·7
Sand	1152	12·0	3	5·2	1	1·7
Edge	184	1·9	0	0	1	1·7
In den	—	—	5	8·6	9	15·3
Overall	9584	100	58	100	59	100

and 8 males) that moved between the forereef and the reef flat. Six lobsters originally tagged on either the forereef or the reef flat were recaptured from the rubble ridge just outside the core area by commercial and recreational fishers.

To assess the impacts of commercial and recreational fishing on the population of lobsters that resides within the core area, demographic parameters of abundance, sex ratio, and size were compiled for the two-month periods preceding and following the opening of the harvest season. Although mean sizes generally remained similar, lobster abundance throughout the core area declined rapidly after the season opened, and the sex ratios of lobsters on the forereef and in Region 2 shifted dramatically, indicating that more males than females were leaving the core area (Table 4).

Gut contents and prey abundance

We examined the gut contents of 55 lobsters (37 males, 18 females; size range: 49–135 mm CL) from Dry Tortugas National Park (DTNP) and of 35 lobsters (17 males, 18 females; size range: 27–104 mm CL) from Biscayne National Park (BNP). Of the 75 intermoult-stage lobsters, guts of 29 DTNP lobsters and 30 BNP lobsters each contained at least one prey item; the guts of the remaining 16 lobsters (21%) were empty. The guts contained a total of 623 prey items.

Panulirus argus at the two reef sites ate a wide variety of prey; 115 taxa (species or higher) of animals and plants were recorded among the gut contents (Table 5). The number of

Table 3. Proportion ovigerous, mean size (mm CL), and sex ratio (SR; female:male) of lobsters on the forereef and in Regions 1 and 2 in day and night samples taken during the reproductive and non-reproductive seasons

Reproductive season is March–September. *n*, number of lobsters

Zone	Time	Reproductive season				Non-reproductive season		
		Ovigerous	Size		SR	Size		SR
		(%)	Female (*n*)	Male (*n*)	(*n*)	Female (*n*)	Male (*n*)	(*n*)
Forereef	Day	66·3	80·5 (368)	89·9 (92)	4·0:1 (460)	77·5 (80)	85·0 (21)	3·8:1 (101)
	Night	67·5	77·4 (36)[A]	88·9 (7)	5·3:1 (44)	81·5 (10)	89·0 (3)	3·3:1 (13)
Region 1	Day	30·9	78·6 (175)	86·0 (130)[A]	1·3:1 (306)	77·1 (44)	79·1 (18)	2·4:1 (62)
	Night	37·1	78·7 (54)	80·8 (21)	2·4:1 (75)	80·5 (45)	79·2 (18)	2·5:1 (63)
Region 2	Day	14·1	75·3 (149)	78·2 (120)	1·2:1 (269)	71·6 (39)	65·4 (33)	1·2:1 (72)
	Night	37·9	79·4 (29)	83·7 (30)	1·0:1 (59)	71·8 (10)	55·0 (2)	5·0:1 (12)

Table 4. Abundance, mean size (mm CL), and sex ratio (SR; female:male) of lobsters during the last two months of the closed season (June and July) and the first two months of the open (harvest) season (August and September)

n, number of lobsters

Zone	Closed season				Open season			
	n	Size		SR	*n*	Size		SR
		Female	Male			Female	Male	
Forereef	211	79·7	90·3	4·0:1	50	81·9	96·7	4·6:1
Region 1	226	78·7	87·1	1·7:1	61	80·7	78·7	1·7:1
Region 2	166	76·6	80·3	0·8:1	47	77·1	78·0	2·6:1

prey consumed by individual lobsters ranged from 1 to 39 items ($\bar{X}$ = 10·9), and as many as 20 prey taxa ($\bar{X}$ = 8·4) were found in individual guts. There was no difference between sites in the number of prey items consumed (ANOVA: F = 0·743, d.f. = 1, P = 0·392). Nearly 75% of prey items were molluscs. Gastropods (49%)—especially moon snails (Naticidae: *Natica*, *Naticarius*, and *Polinices* spp.), top snails (Trochidae: *Calliostoma* and *Tegula* spp.), ceriths (Cerithiidae: *Cerithium* spp.), and dove snails (Columbellidae: principally *Columbella mercatoria*)—constituted a significantly larger percentage of lobster diet than did any other group (ANOVA: F = 24·726, d.f. = 7, P < 0·001; Tamhane: P < 0·001). Chitons (especially *Acanthochitona* spp. and *Stenoplax* spp.), bivalves, and arthropods (principally spider crabs, *Pitho* spp.) were found in similar abundances, about 11% to 15% (Tamhane: P = 1·000). Echinoderms constituted less than 4% of the items in lobster guts, but echinoderm parts (e.g. sea-urchin spines, brittle-star arms) were found in guts of 30% of the lobsters.

Table 5. Major prey categories and principal food items in guts of 59 individuals of *Panulirus argus* from reefs at Biscayne National Park (30 lobsters) and Dry Tortugas National Park (29 lobsters)

N taxa, number of species-level and higher groups; *n*, number of individuals in each prey category; *F*, number of lobster guts containing each prey category. The principal gastropod families comprise 204 of the 304 gastropods in lobster guts

Prey	*N* taxa	Items		Lobsters	
		n	%	*F*	%
Molluscs	88	465	74.6	48	81.4
Gastropods	53	304	48.9	43	72.3
Principal families:					
Naticidae		80	12·8	25	42·4
Trochidae		66	10·6	27	45·8
Columbellidae		30	4·8	23	39·0
Cerithiidae		28	4·5	23	39·0
Bivalves	28	66	10·6	31	52·5
Chitons	6	92	14·8	29	49·2
Scaphopods	1	3	0·5	3	5·1
Arthropods	8	73	11·7	38	64·4
Echinoderms	6	23	3·7	18	30·5
Plants	3	21	3·4	19	32·2
Other	10	41	6·6	26	44·1
Total	115	623	100		100

At Looe Key, many more potential prey items were found in rubble than in seagrass, *Thalassia*–rubble, or sand (Kruskal–Wallis: χ^2 = 28·638, d.f. = 3, P < 0·001; Tamhane: P < 0·05) (Fig. 3). Average density of potential prey in rubble was more than three times greater than that in seagrass and an order of magnitude greater than those in other substrata. Seagrass contained significantly more potential prey than did *Thalassia*–rubble or sand (Tamhane: P < 0·05), between which abundances of potential prey did not differ (Tamhane: P = 1·0).

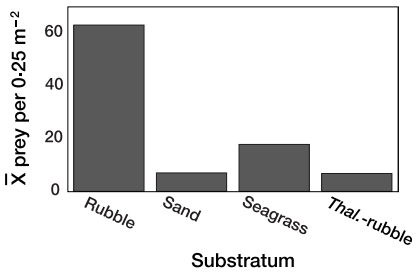

Fig. 3. Average densities of potential prey items in rubble, sand, seagrass, and *Thalassia*–rubble on the reef flat.

Gastropods were far more abundant in rubble than elsewhere (Kruskal–Wallis: χ^2 = 21·574, d.f. = 3, P < 0·001; Tamhane: P = 0·001) (Table 6) and constituted a high proportion (85%) of all molluscs there. Most of the gastropods were *Cerithium litteratum*, which occurred at densities of up to 180 individuals m^{-2}. Significantly more chitons were found in rubble than in seagrass (Tamhane: P = 0·019), and significantly more bivalves were found in seagrass than in *Thalassia*–rubble (Tamhane: P = 0·009). Among molluscs in the prey survey, 20 of 61 rubble-dwelling species (33%), 18 of 50 seagrass-dwelling species

Table 6. Average densities (m^{-2}) of potential prey in substrata sampled on the reef flat

	Rubble	Seagrass	*Thalassia*–rubble	Sand
Area sampled (m^2)	18	5·25	4·5	5·25
Molluscs	171·6	26·9	20·2	19·2
Principle classes:				
Gastropods	145·6	9·7	4·4	2·9
Bivalves	7·8	13·7	3·8	9·3
Chitons	18·2	3·0	12·0	6·1
Arthropods	65·7	40·0	4·4	6·1
Echinoderms	12·0	10·1	0·7	0·2
All taxa	249·3	77·0	25·3	25·5

(36%), 10 of 17 *Thalassia*–rubble species (59%), and 6 of 22 sand-dwelling species (27%) also occurred in lobster guts.

Most arthropods in the prey survey were hermit crabs and spider crabs. Hermit crabs, principally *Clibanarius tricolor*, were most abundant in rubble, but their abundance was highly variable. Abundance at one site ranged from 0 to 134 specimens of *C. tricolor* per 0·25-m^2 quadrat. Arthropods were more abundant than molluscs in seagrass (Table 6), and several arthropods, including spider crabs (*Pitho* spp.), that were common there were rare or absent elsewhere. Significantly more arthropods were found in seagrass than in sand or *Thalassia*–rubble (Tamhane: $P < 0{\cdot}001$). Like arthropods, echinoderms were more abundant in rubble and seagrass, and significantly fewer echinoderms were found in sand and *Thalassia*–rubble (Tamhane: $P < 0{\cdot}01$).

The distributions of prominent prey taxa on the reef flat at Looe Key were examined to ascertain the relative availabilities of those taxa among the substratum types (Table 7). Among the seven categories of prominent prey, reasonable correspondence occurred between incidence in lobster guts and incidence in *(1)* rubble for *Cerithium* spp. and *Stenoplax* spp., *(2)* seagrass for *Pitho* spp., and *(3)* both rubble and seagrass for *Columbella mercatoria*. Although *Acanthochitona* spp. constituted 3·7% of all prey in guts, these chitons were found at low density in all substrata. Trochidae and *Polinices* spp., the two groups most abundant in lobster guts, were not abundant at Looe Key.

Table 7. Prominent prey taxa in gut contents of reef-dwelling lobsters from Dry Tortugas National Park and Biscayne National Park, and average densities of those taxa in different substrata at Looe Key

Prey	Gut contents (%)	Density (m^{-2}) in substratum			
		Rubble	Seagrass	*Thalassia*–rubble	Sand
Gastropods					
Cerithium spp.	4·5	137·2	—	2·2	—
Columbella mercatoria	2·9	1·9	2·3	—	—
Trochidae	10·6	0·2	0·6	0·2	—
Polinices spp.	11·7	—	0·6	0·2	0·2
Chitons					
Acanthochitona spp.	3·7	0·2	1·3	0·2	0·4
Stenoplax spp.	2·7	3·1	0·2	0·9	—
Arthropods					
Pitho spp.	5·0	0·1	8·8	0.2	0·2

Discussion

Lobsters that foraged on the reef flat at Looe Key were more abundant in rubble than in other substrata. The rubble there also supported many more potential prey items, in terms of both abundance and diversity, than did sand or seagrass, and many of the species found in rubble, especially gastropods and arthropods, were also abundant in the guts of lobsters from other locations along the Florida reef tract.

Foraging lobsters were also relatively abundant in *Thalassia*. Likewise, guts contained substantial numbers of seagrass-dwelling prey. Lobsters were much more likely to find spider crabs in seagrass than in rubble; *Pitho* spp., which constituted 5% of lobster diets, also constituted 13% of the potential prey found in seagrass but were scarce in rubble (Table 7). Other prey, especially large snails (e.g. *Tegula fasciata*), graze on epibiota on the wide, flat blades of *Thalassia*, where they may be readily accessible to foraging lobsters. These large grazers are seldom found on *Syringodium* because its narrow, cylindrical blades provide little surface area for the snails to graze. This may explain why the substratum preference index for *Thalassia* was positive whereas the index for *Syringodium* was negative (Fig. 2). Feeding on such grazers may also explain the occasional occurrence of *Thalassia* fragments in lobster guts; the grass may be ingested incidently as grazers are consumed.

The gut contents reported here are very similar to those reported by Espinosa *et al.* (1991). Molluscs constituted 75% of the prey items found in the present study and 73% and 75% of the prey at two sites off south-western Cuba (Espinosa *et al.* 1991). Further, gastropods (primarily *Polinices lacteus*, *Tegula fasciata*, *Columbella mercatoria*, and *Cerithium litteratum*) were 57% and 66% of all molluscan prey at the two Cuban sites. In the present study, similar gastropods (Naticidae, Trochidae, Columbellidae, and *Cerithium* spp.) constituted 44% of all molluscs consumed (Table 5). Chitons (especially *Acanthochitona* spp. and *Stenoplax* spp.) constituted 12% of prey in Cuba and 15% of prey in Florida. Bivalves contributed 6% of the prey at each Cuban site, compared with 11% at the Florida sites. Similarities between gut contents from Florida and Cuba have led us to conclude that *Panulirus argus* employs similar foraging strategies and preys upon similar organisms in shallow-water reef environments throughout its biogeographic range.

Most prey items move through lobster guts within several hours of consumption (Herrnkind *et al.* 1975; Joll 1982). Even chitinous gastropod opercula (the most plentiful item we found in lobster guts) probably were ingested the night that the lobsters were captured. Joll (1982) found 135 opercula of *Littorina unifasciata* in the stomach of one individual of *Panulirus cygnus* that had been allowed to feed for only two hours after being starved. Most opercula were absent from guts within four hours of feeding. Similarly, we surmise that the many chiton radulae found were consumed the night that the lobsters were captured. Hence, the gut contents reported here probably represent prey that each lobster captured during a single night. Lobsters whose guts contained prey peculiar to a single substratum probably fed only in that substratum, whereas lobsters that consumed prey items peculiar to different substrata must have fed in several substrata in a single night. For example, the full gut of one lobster contained only five *Pitho* crabs, whereas the gut of another contained the remains of *Cerithium litteratum*, *Columbella mercatoria*, *Tegula fasciata*, and 13 *Polinices* opercula. As indicated by the substratum preferences of these prey (Table 7), the first lobster fed in seagrass but the other lobster probably fed in several substrata, including rubble and sand.

Although rubble supported more potential prey and attracted more foraging lobsters than did other substrata at Looe Key, the relative incidences of molluses in rubble, seagrass and sand were similar (27–36%) in the guts of lobsters from the other Florida reefs (BNP and DTNP), probably reflecting environmental differences between the Looe Key reef flat and the isolated reefs where lobsters in the diet study were captured. *Cerithium* spp. and *Stenoplax* spp., which were numerically dominant in rubble at Looe Key, were also frequent in lobster guts at BNP and DTNP, but lobsters at these last two sites also consumed *Columbella mercatoria* and *Pitho* spp., which were more common in seagrass, as well as trochid and *Polinices* snails, two prey categories that were relatively uncommon in the Looe Key samples (Table 7). At the reefs where this diet study was conducted, lobsters had to cross large expanses of sand (reef halos) when they moved to and from seagrass and rubble zones during foraging, and the many *Polinices* individuals in their diet were probably taken from that sand.

These results demonstrate how adaptability has enabled *Panulirus argus* to be successful. Where a wide suite of foraging substrata is available, lobsters clearly prefer rubble, and to a lesser extent *Thalassia testudinum*, over other substrata within their foraging range. However, after considering the evidence from all aspects of this study, we conclude that spiny lobsters can successfully forage in nearly any substratum they encounter. Thus, we would expect *P. argus* to forage wherever suitable prey items, especially molluscs, are most available within the foraging range of the lobsters.

Movements of lobsters to and from foraging grounds are never random (Herrnkind *et al.* 1975; Jernakoff 1987). In addition to broad orientational cues such as geomagnetic fields and water movements (Creaser and Travis 1950; Herrnkind and McLean 1971; Lohmann 1985), structural cues in the environment may be used by lobsters to find their way to and from foraging grounds. We suspect that blowout edges may serve in that capacity because lobster density was highest along edges but no lobsters were observed to feed there.

Foraging areas may be sites of important behavioural interactions among lobsters. Lobsters of different sizes, sexes, and stages of maturity that do not normally associate during daytime in the reproductive season forage in proximity to each other at night, as evidenced by our observations of the increased percentage of ovigerous lobsters (Table 3) and tagged forereef lobsters on the reef-flat foraging grounds at night. Some large males on offshore reefs guard dens containing ‘harems’ of mature females (Herrnkind and Lipcius 1989). The distribution and size structure of lobsters on the Looe Key forereef during the reproductive season is consistent with the hypothesis that polygynous males establish and defend mating territories. However, Herrnkind *et al.* (1975) reported that foraging males do not display the aggressive behaviour they show while near their dens. At night, when the lobsters leave the protection of dens to forage, the large males probably cannot defend their harems from the courtship advances of others. Small males already residing on the reef flat (Table 3) may thus gain access to reproductively receptive females when the latter arrive to forage. Although copulation characteristically occurs near dens during the day, nocturnal copulation has been documented in laboratory pools and ponds for *P. argus* (Lipcius *et al.* 1983; Lipcius and Herrnkind 1985), *P. homarus* (Berry 1970), and *Jasus edwardsii* (McKoy 1979). Nocturnal courting by *J. edwardsii* has been observed in the field (A. B. MacDiarmid, personal communication). Additional field studies on foraging and mating behaviours will be required to determine the success of harem maintenance as a reproductive strategy for spiny lobsters.

Lobsters that reside in the core area at LKNMS are afforded some protection because commercial harvesting is prohibited there, but many of those lobsters lose that protection by foraging in rubble areas outside the core-area boundary. In fact, several lobster trappers reported harvesting tagged core-area lobsters from the rubble. The impact of harvesting is evident in the swift reduction in core-area lobster abundance that occurs concurrent with the season opening. If lobsters in marine reserves are to be maintained at population levels higher than those where fisheries operate, then the reserves must protect lobster foraging grounds as well as their denning sites. The newly established (1 July 1997) Looe Key Special Protection Area has increased the protected area to about 115 ha, including

the entire reef-flat seagrass community and most of the rubble ridge (Anon. 1996*b*). However, the new area still does not fully encompass the rubble foraging grounds, nor does it provide a buffer around those grounds, so some Looe Key lobsters will remain vulnerable to harvesting during their diel activity cycle.

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