CSIRO PUBLISHING

www.publish.csiro.au/journals/mfr *Marine and Freshwater Research*, 2005, **56**, 1037–1045

Determination of preferred habitats of early benthic juvenile California spiny lobster, *Panulirus interruptus*, on the Pacific coast of Baja California Sur, Mexico

Verónica Castañeda-Fernández de Lara[A], *Mark Butler*[B], *Sergio Hernández-Vázquez*[A], *Sergio Guzmán del Próo*[C] *and Elisa Serviere-Zaragoza*[A,D]

[A]Centro de Investigaciones Biológicas del Noroeste (CIBNOR), La Paz, B.C.S. 23090, Mexico.
[B]Department of Biological Sciences, Old Dominion University, Norfolk, Virginia 23529-0266, USA.
[C]Escuela Nacional de Ciencias Biológicas, Laboratorio de Ecología, Instituto Politécnico Nacional, México, D.F. 02800, Mexico.
[D]Corresponding author. Email: serviere04@cibnor.mx

Abstract. The habitat requirements of early benthic stage juveniles of California spiny lobster *Panulirus interruptus* are known only from studies conducted near its northernmost geographic range, where environmental conditions differ markedly from those along the Pacific coast of the southern Baja California Peninsula (Mexico). We determined the natural habitat of this stage of *P. interruptus* in the central portion of their range from sampling the available dominant vegetated habitats included various seagrasses and macroalgae. Additionally, experiments on habitat selection by early benthic juvenile *P. interruptus* were performed under laboratory conditions to test natural substrate selection and whether selection of substrata is affected by odour signals. Despite the abundance of different macrophytes as habitat, 93% of the juvenile lobsters were found at the base of the blades of *Phyllospadix* spp. in the intertidal zone at 0 to 3 m. The highest juvenile densities were found in September at both sites. In laboratory experiments, juvenile lobsters preferred, in order of preference, *Gelidium robustum*, *Phyllospadix*, *Plocamium pacificum*, and holdfasts of the kelp *Macrocystis pyrifera.* A second laboratory experiment showed that these preferences were affected by odour signals. Results indicate that the ecology of juvenile *P. interruptus* off the coast of the Mexican Baja is similar to that observed off the coast of southern California.

Extra keywords: early benthic stage juveniles, habitat preference, *Panulirus interruptus*, *Phyllospadix*, spiny lobster.

Introduction

The California spiny lobster *Panulirus interruptus* Randall, 1840 is a temperate-subtropical species distributed from coastal San Luis Obispo County, California at ~35°N to Isla Santa Margarita, Bahía Magdalena, México at ~24.5°N (Vega *et al*. 1996); its greatest abundance is centred along the central part of the Baja California Peninsula of Mexico (Johnson 1960; Pringle 1986; Vega and Lluch-Cota 1992). Throughout its range, *P. interruptus* is found in rocky areas from the low intertidal zone to depths of 100 m (Lindberg 1955). The state of Baja California Sur contributes around 50% of the total lobster catch in México (Vega *et al.* 1996), but 95% of which is *P. interruptus* and the rest is *Panulirus inflatus* and *Panulirus gracilis* (Briones-Fourzán and Lozano-Álvarez 2000). In Mexico, the value of the lobster catch stands at US$24 million based on production of 1970 t (SAGARPA 2003), making the spiny lobster fishery the sixth most valuable fishery in Mexico after shrimp, tuna, bream, octopus, and grouper.

Some studies of the early life history and ecology of *P. interruptus* were conducted over a quarter century ago in California (USA) at the northern limit of its range (Mitchell 1971; Parker 1972; Serfling 1972; Engle 1979), but little research on early life history has since been published, especially along the coast in Mexico, where the species is most abundant. The early life history of *P. interruptus* begins with a protracted oceanic larval period (*c*. 7 to 8 months; Johnson 1960; Ortuño-Manzanarez 2003), after which the final larval phase (Stage 11) metamorphoses into a 'puerulus' postlarva, measuring 2 to 3 cm long (6.5 mm carapace length; CL). Postlarvae return to the coast between May and September (Serfling and Ford 1975; Guzmán del Próo *et al.* 1996; Vega *et al.* 2000) and settle in shallow, rocky vegetated areas (Parker 1972; Engle 1979; Ayala-Martínez and Chávez 1985). After settlement, they acquire pigmentation in 9–10 days, moult to the early benthic juvenile (EBJ) stage, and take up residence within vegetated habitats for a few months (Serfling and Ford 1975).

10.1071/MF04284 1323-1650/05/071037

Mechanisms of habitat selection by pueruli are unknown for most species of spiny lobster (Palinuridae) (Kanciruk 1980; Butler and Herrnkind 2000). This is partly a consequence of puerulus characteristics and behaviour (Krebs and Kacelnik 1992), such as their sparseness in natural habitats, small size, and crypticity (Marx and Herrnkind 1985*a*; Herrnkind and Butler 1986), and partly owing to the complex topographic microhabitat where they reside (Caddy and Stomatopoulos 1990; Boudreau 1992). These characteristics conspire to make the early post-settlement phases of nearly all spiny lobsters challenging to study (Butler and Herrnkind 2000). Despite this, others have demonstrated that survival of the EBJ stage of *Panulirus argus* is directly related to habitat quality, including food supply and shelter (Marx and Herrnkind 1985*a*, 1985*b*; Butler and Herrnkind 1986; Butler *et al.* 1997).

Our general knowledge of the spiny lobster's early life history was summarised by Butler and Herrnkind (2000), indicating that natural habitats for newly settled pueruli and EBJ stages are either dense vegetation such as red or brown macroalgae or seagrass (e.g. *P. argus* and *P. interruptus*), or small holes in rocks or reefs that are scaled to body size of the EBJ (e.g. *P. cygnus*, *P. homarus*, *P. japonicus*, *P. ornatus*, *P. versicolor*, *P. guttatus*, and *Jasus lallandii*), or both as in *J. edwardsii*. However, the primary habitat of EBJ stage palinuridae often depends on ecological characteristics of the particular region (Serfling and Ford 1975; Marx and Herrnkind 1985*a*). As an example, for one of the most studied species, *P. argus*, EBJ and recently settled pueruli occurred on seagrass in Florida Bay (Holmquist *et al.* 1989), mangrove roots in Belize coastal waters (Acosta and Butler 1997), clumps of red macroalgae *Laurencia* spp. in the Florida Keys (Marx and Herrnkind 1985*a*, 1985*b*), and mats of brown algae *Lobophota variegata* in a barrier reef lagoon in the Mexican Caribbean (Briones-Fourzán and Lozano-Álvarez 2001). Experimental studies with *P. argus* suggest that postlarval and EBJ lobsters may respond to both chemical and architectural cues (Herrnkind and Butler 1986).

Even thought seaweed habitat is available for most species of palinuridae, many prefer hard habitats. For example, EBJ *P. japonicus* occupy holes on coral reefs (Norman *et al.* 1994) instead of readily available seaweeds, such as the various species of Laminareaceae or *Sargassum* spp. (Yoshimura *et al.* 1994). Although the presence of large kelps near rocky reefs appears to enhance settlement of *P. japonicus* in Japan (Norman *et al.* 1994; Yoshimura *et al.* 1994), as well as *J. edwardsii* in Tasmania (C. Gardner, personal communication). Dennis *et al.* (1997) observed juvenile *P. ornatus* inhabiting holes or crevices in a limestone substratum partially cover by seagrass or macroalgae, as was observed with juvenile *P. cygnus* by Jernakoff (1990). Early benthic juvenile *J. edwardsii*, which typically occupy holes or crevices on rocky reefs in New Zealand (Butler *et al.* 1999), apparently require bio films on the substrate for it to be attractive to them (Booth 2001).

Off Santa Catalina Island in California, subtidal surveys indicate that juvenile *P. interruptus* occupy two habitats: (*a*) shallow, rubble-rocky areas with algae such as *Sargassum*, *Pterocladia*, *Plocamium*, and unidentified corallines; or (*b*) large *Phyllospadix* beds and low-lying red algae growing on consolidated substrates (Parker 1972). Exploratory habitat surveys at different places in California indicated that small juveniles, although difficult to find, commonly inhabited rocky habitats with dense plant cover at depths from 0 to 4 m; most were encountered in *Phyllospadix* beds (Engle 1979). Some EBJ *P. interruptus* have been found in Bahía Sebastián Vizcaíno within tide pools during low tide where calcareous algae were abundant (Ayala-Martínez and Chávez 1985).

Laboratory studies of habitat selection by *P. interruptus* pueruli and EBJ suggested that both stages prefer *Phyllospadix* over rubble rock and *Macrocystis*, but pueruli showed no preference among *Phyllospadix*, *Zostera marina*, *Plocamium*, *Halidrys*, and other red algae. On the other hand, juveniles preferred *Plocamium* to *Phyllospadix* and showed equal preference among *Phyllospadix*, *Halidrys*, and other red algae (Parker 1972; Engle 1979).

Our objective was to determine the natural habitat of EBJ *P. interruptus* in Baja California Sur, Mexico where the species is most abundant and where seagrass and macroalgal substrates are present. We also conducted laboratory experiments to test: (*a*) substrate selection by EBJ *P. interruptus* and (*b*) their response to odour produced by various natural substrates.

Materials and methods

Study sites

Our field studies were conducted at two sites. 'Queen' is located at the south end of a large bay, Bahía Sebastián Vizcaíno (27°46′33″–27°46′47″N, 114°38′00″–114°38′20″W). 'Arvin' is located to the south in a cove at the north end of Bahía Tortugas (114°51′59″–114°52′17″N, 27°38′51″–27°38′59″W) (Fig. 1). These sites were selected because older juveniles (40–60 mm CL) were seen and captured during two previous exploratory surveys. In addition to the studies described here, we also examined the feeding ecology of juvenile *P. interruptus* at these same sites and sample periods (Castañeda-Fernández de Lara *et al.* 2005). The two sites experience different oceanographic conditions and are dominated by different flora because they are separated by a peninsula that juts north–west into the Pacific and diverts prevailing currents (Lluch-Belda 2000). This in turn generates differences in seawater temperature at the two sites, and creates a near permanent gyre that may retain *P. interruptus* larvae in the region (Pringle 1986). Seawater temperature at the Arvin site is generally cooler and temperate seagrasses and macroalgae are the dominant benthic flora there, whereas at the Queen site, seawater temperature is higher and the benthic flora more indicative of warmer seas.

From Bahía Sebastián Vizcaíno to Punta Abreojos (26°45′00″N, 113°37′30″W), which corresponds to the centre of lobster capture (Vega and Lluch-Cota 1992), well known locally as the 'North Pacific fishing region', the dominant flora are the brown algae *Macrocystis pyrifera*,

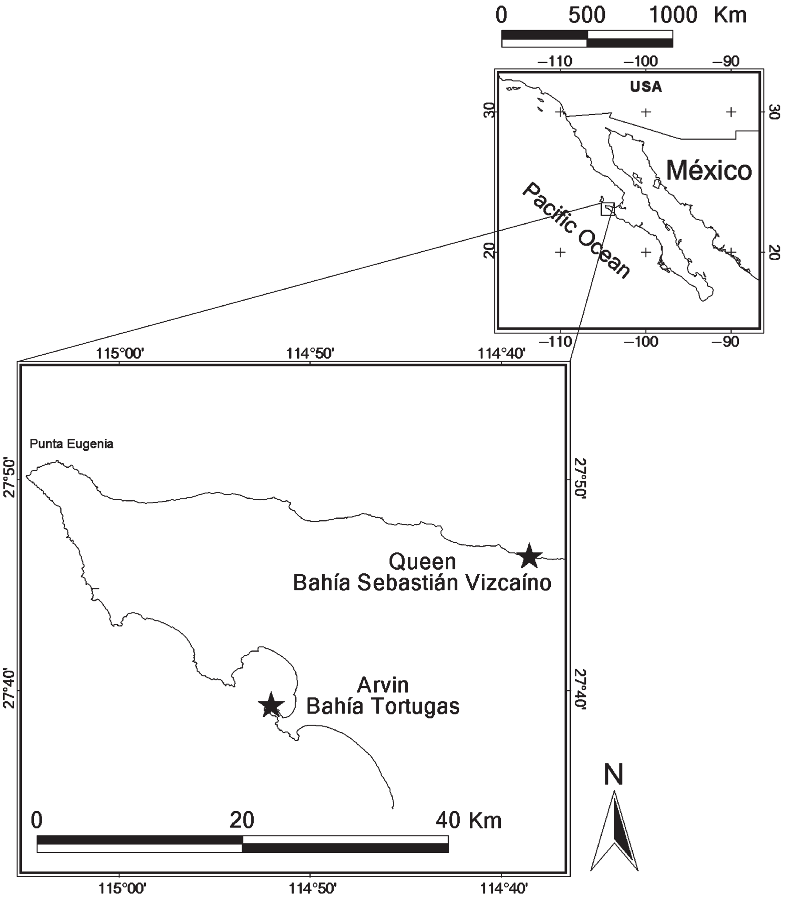

Fig. 1. Location of field sites in Baja California Sur, México.

Pelagophycus porra, and *Eisenia arborea*; the red alga *Gelidium robustum*, numerous species of calcareous red algae, and the surfgrasses *Phyllospadix torreyi* (Guzmán del Próo *et al.* 1972) and *P. scouleri* (Ramírez-García *et al.* 1998, 2002).

Field sampling

To locate EBJ spiny lobsters in their natural habitat and assess shifts in benthic flora, we acquired quantitative samples of the benthic flora at both sites once per quarter-year, in September 2001 (nominal autumn), January 2002 (nominal winter), April 2002 (nominal spring), and June 2002 (nominal summer). At each site, a 2000 m^2 area was surveyed. Several 200-m transects running parallel to the shore were made at $\leq$1 m, 2–3 m, and 4–6 m depth during each sampling. All biological materials in five quadrats (0.25 m^2) were randomly sampled along each transect, yielding a total sample surface area of 3.75 m^2 at each site per sampling time. All vegetation with a quadrat was collected by hand, and placed in 1-mm^2 mesh bags. After collection, the biomass sample was placed in labelled plastic bags and preserved with a 10% formalin seawater solution. The geographic position of quadrats was recorded with a GPS unit. Seawater temperatures were recorded every hour from September 2001 to September 2002. Measurements were taken at a depth of 3 m with a continuous recording thermograph (Hobo-Temp, Onset Computer Corporation, Cape Cod, MA), ~200 m from the shore. The nominal seasonal variability was determined by the average of the daily temperature for that quarter-year (nominal season).

In the laboratory, we separated floral species and searched for juvenile *P. interruptus* among the vegetation. The wet weights of the dominant floral (seagrass and macroalgae) species were determined using an electronic balance (±0.1 g), and carapace length (CL, base of the supraorbital spines to the posterior edge of the carapace) of juvenile lobsters was measured using a calliper (±0.1 mm). We identified the most conspicuous floral species in the samples using description keys of species of the region (Dawson 1951; Mason 1957; Abbot and Hollenberg 1976; Phillips 1979; Hickman 1993; Ramírez-García *et al.* 1998, 2002). Taxonomic identification of surfgrass was confirmed (P. Ramírez-García, National Herbarium, Universidad Nacional Autónoma de México, personal communication).

Habitat selection experiments

Laboratory experiments to test EBJ lobster habitat preference were performed in September 2002 and 2003 within circular tanks (150 cm diameter, 80 cm deep) that were supplied with filtered seawater with opened flow and constant aeration. A total of 179 early benthic juvenile lobsters were obtained from artificial collectors and from collections that we made within natural habitat, ranging from 6.6 to 29.6 mm CL.

Natural substratum selection by EBJ California spiny lobsters

We tested EBJ preference for *Macrocystis pyrifera*, *Phyllospadix scouleri*, *Plocamium pacificum*, and *Gelidium robustum* because: (*1*) these plants are abundant in the study area; and (*2*) other authors

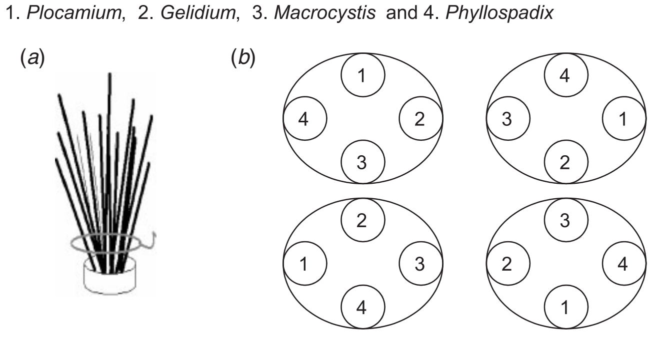

Fig. 2. Diagram showing (*a*) method for constraining vegetation in the tanks and (*b*) position of each vegetation type in experimental tanks where habitat selection of early benthic juvenile California spiny lobster *Panulirus interruptus* was tested.

had implicated these genera as critical components of juvenile California spiny lobster nursery habitat (Parker 1972; Serfling and Ford 1975). Divers at the Arvin location, using SCUBA collected the macrophytic test substrata. In the laboratory, the substrata were washed under moderate pressure with filtered seawater and then shaken to eliminate epifauna that could serve as food and modify the preference for structural features of the natural substrata (Marx and Herrnkind 1985*b*). To standardise the size of the substratum, vegetation was constrained within a 15-cm diameter PVC pipe and in the case of surfgrass *Phyllospadix*, the leaves were also held together with a galvanised thread to better mimic its true form (Fig. 2*a*).

In each tank, the four substrata were simultaneously offered as settlement habitat as multiple-choice trials. To avoid any positional bias, each substratum, was repositioned after each trial, within each tank ($n = 90$) (Fig. 2*b*). We also added an equal portion of crushed gastropods (i.e. 2 g of *Tegula* spp.), an abundant community member at the site, to equalise the available food in each substratum. To initiate a trial, one juvenile lobster was released in the centre of the tank. During daylight hours on the following day, each substratum was isolated within an acrylic enclosure and covered with a net. The substrate was then carefully extracted from the reservoir to reduce disturbance to the juveniles that may have selected another refuge location. Each substratum was checked, and when the specimen was found, its CL was measured and recorded.

Substratum selection by EBJ California spiny lobsters affected by odour signal

To determine if juveniles preferred substrata based on odours, a similar trial was conducted with artificial substrata supplied with different natural odour cues ($n = 99$). We used the same synthetic rope fibre used in GUSI and Phillips artificial collectors design for postlarvae (Phillips and Booth 1994; Guzmán del Próo *et al.* 1996; Vega *et al.* 2000). We made a clump of this fibre similar to the way we prepared the natural substrata (Fig. 2*b*) and to each clump, we added 10 g of natural substratum to generate an odour signal.

Statistical analysis

We used a non-parametric Kruskal–Wallis (K–W) analysis to assess if there were significant differences in mean biomass of the principal macrophytes among sample periods because the raw data did not meet the assumptions of ANOVA (i.e. homogeneity of variances and normality). To test for significant differences in sea bottom temperature between sites and sample periods, we used Student's *t*-test. We also used a χ^2-square goodness-of-fit test comparing the observed numbers of juveniles of various sizes to the expected number in each size class among sites and sample periods.

For the behaviour experiments, we used a 1-factor model I ANOVA to determine if there were significant differences in the size of juvenile lobsters that selected specific natural substrata, and to determine if choice of substrate was affected by odour. A χ^2-square goodness-of-fit test was used to determine if choice of habitat differed significantly among the habitats (Sokal and Rohlf 1981).

Results

Field site characteristics

At the Queen site at Bahía Sebastián Vizcaíno, the bottom slopes gradually towards the continental shelf; the seafloor near the coastline is composed of a series of overlapping, thin, but large angular rocks arranged in a step-like arrangement. In the spaces between the angular blocks, fine sediments accumulate and provide a substrate for the flora. At this site, the dominant species is the surfgrass *Phyllospadix torreyi*, contributing ~80% of the biomass in the year of the survey. This is followed by *Padina caulescens* (7%) and *Sargassum agardhianum* (4%). The biomass varied between 1.6 and 3.3 kg m^{-2} for *P. torreyi*, 0.001 and 0.6 kg m^{-2} for *P. caulescens*, and 0.01 and 0.3 kg m^{-2} for *S. agardhianum*. The biomass was significantly different among the nominal seasons for *P. torreyi* ($K\text{–}W = 15.4$: $df = 3, 56$: $P < 0.05$), and for *P. caulescens* ($K\text{–}W = 14.4$: $df = 3, 29$: $P < 0.05$). In the three strata, *P. torreyi* was the dominant species.

The Arvin site at Bahía Tortugas is well protected from currents and wind. The near shore bottom is rocky, but becomes more silted with depth. From the shore to moderate depths, fine sediment is a matrix interspersed with rounded boulders, cobbles, and gravel. Two species, surfgrass *P. scouleri* (39% of the total biomass during the year) and seagrass *Zoostera marina* (17%) and two brown algae, *Sargassum muticum* (34%) and *Macrocystis pyrifera* (6%) were the dominant species. Their biomass ranged between 2.2 and 3.2 kg m^{-2} for *P. scouleri*; 1 and 1.5 kg m^{-2} for *Z. marina*; 0.2 and 7 kg m^{-2} for *S. muticum*, and 0.03 and 1 kg m^{-2} for *M. pyrifera*. The *S. muticum* biomass was significantly different among the nominal seasons ($K\text{–}W = 12.4$: $df = 3, 21$: $P < 0.05$), but this was not the case for the other species. The intertidal stratum, ≤ 1 m, was dominated by *P. scouleri*; the second stratum by the two species of brown algae, and the third stratum by *Z. marina.*

At Queen, the annual mean seawater bottom-temperature is 19.9°C with a minimum of 16.1°C in July and a maximum of 26°C in September (Fig. 3*a*). At Arvin, the annual mean seawater bottom-temperature was 17.3°C, ranging from a minimum of 13.3°C (August) to a maximum of 23.1°C (October). Seasonal mean seawater temperature was significantly different between sites (T test $= -2.8$, $df = 6$, $P < 0.05$); the Arvin site was cooler than the Queen site, but the greatest difference between the two sites was during the summer (Fig. 3*a*).

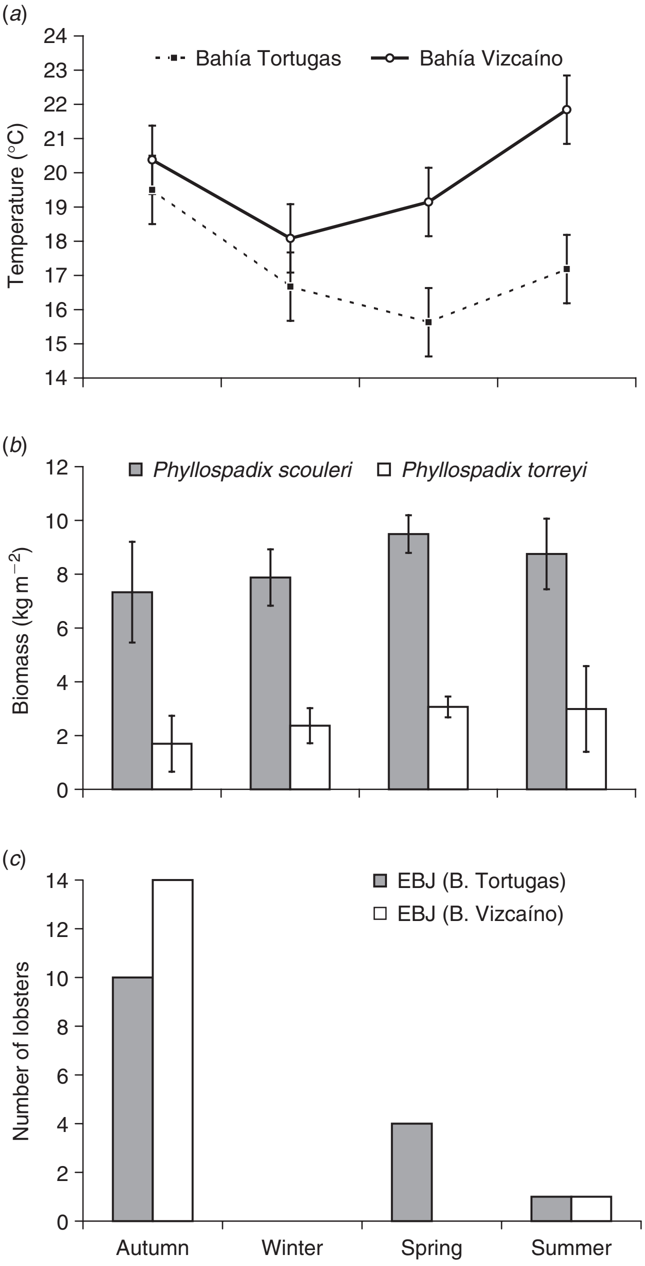

Fig. 3. (*a*) Seasonal mean sea water temperature (mean ± s.d.) in - ▪ - (Bahía Tortugas) and —o— (Bahía Vizcaíno). (*b*) Seasonal biomass per m^2 (mean ± s.d.): (*Phyllospadix torreyi*, Stratum 1, Bahía Vizcaíno) and (*Phyllospadix scouleri*, Bahía Tortugas). (*c*) Total number by season of early benthic juvenile (EBJ) California spiny lobster *Panulirus interruptus* caught in (Bahía Tortugas) and (Bahía Vizcaíno).

Table 1. Size distribution of early benthic juvenile California spiny lobster *Panulirus interruptus* at two locations in Baja California Sur, Mexico

Size class (CL, mm)	Bahía Vizcaíno *Phyllospadix torreyi* Frequency (*n*)	Zone IT	Zone ST	Bahía Tortugas *Phyllospadix scouleri* Frequency (*n*)	Zone IT	Zone ST
6–7	4	3	1	5	5	–
8–9	4	3	1	7	7	–
10–11	5	5	–	2	2	–
12–13	2	2	–	–	–	–
>14–<22	–	–	–	1	1	–
Total	15	13	2	15	15	–

Dwelling resource and zone (of capture): IT = intertidal, ST = subtidal, CL = carapace length.

Number and size of EBJ spiny lobsters

Of 30 EBJ lobsters found in natural settlement habitats during the study, all were found at the base of the blades of *Phyllospadix* spp.; 15 EBJ lobsters were found in *P. torreyi* at Queen and 15 were found in *P. scouleri* at Arvin. Most of these (28) were collected in samples from the intertidal beds of *Phyllospadix* spp. ($\leq$1 m depth) and the others from subtidal beds of *Phyllospadix* at Queen (2–3 m depth) (Table 1). The intertidal biomass of *P. torreyi* varied between 1.7 and 3.1 kg m^{-2} and from 7.3 to 9.5 kg m^{-2} for *P. scouleri* (Fig. 3*b*).

The mean carapace length of EBJ lobsters did not differ significantly between sites ($\chi^2 = 5.2$, $df = 4$, $P > 0.05$): 9.8 mm (range: 7–13.7 mm) at Queen and 9.3 mm (range: 6.6–21.3 mm) at Arvin (Table 1). At both sites, most EBJ lobsters were found during the nominal autumn sampling (September) and no EBJ lobsters were found in the survey during nominal winter ($\chi^2 = 53.7$, $df = 3$, $P < 0.005$) (Fig. 3*c*). Across all three depth strata, EBJ density was estimated to range between 0 and 3.7 individuals per m^2. However, if we use only the intertidal samples (Stratum l), where most EBJ lobsters were found, the density varied from 0 to 11.2 individuals per m^2 (Table 2).

Habitat selection experiments

Lobster size had no effect on substrate selection (Table 3). *Gelidium robustum* was preferred (61.1%) over the three other available substrates ($\chi^2 = 70.8$, $df = 3$, $P < 0.001$) (Table 4). When the effect of habitat architecture was controlled, EBJ were drawn more to the odour of *P. scouleri* ($\chi^2 = 12.6$, $df = 3$, $P < 0.005$) than the other three substrata (Table 4). Again, choice of habitat based on odour was unaffected by lobster size (Table 3).

Discussion

The dominant vegetated habitats available to EBJ lobsters differed appreciably between the field sites used in the present study and included various seagrasses and macroalgae. Some of these macrophytes have been described as being possible nursery habitats for EBJ lobsters, including: *Sargassum*, *Plocamium*, unidentified corallines, *Phyllospadix* beds, and low-lying red algae (Parker 1972). However, the EBJ lobsters (6.6 to 21.3 mm CL) that we recovered from the field were

Table 2. Density of early benthic juvenile California spiny lobster *Panulirus interruptus* caught at two sites along the Baja California Peninsula coast

Season	Bahía Tortugas *Phyllospadix scouleri*			Bahía Vizcaíno *Phyllospadix torreyi*			
	Frequency (*n*)	Density		Frequency (*n*)	Density		Total
		TA^A (ind m^{-2})	I^B (ind m^{-2})		TA (ind m^{-2})	I (ind m^{-2})	
Autumn	10	2.7	8	14	3.7	11.2	24
Winter	0	0	0	0	0	0	0
Spring	4	1.1	3.2	0	0	0	4
Summer	1	0.3	0.8	1	0.3	0.8	2
Total	15			15			30

^{A}Total benthic area sampled by season (TA = 3.75 m^2). ^{B}Area within intertidal stratum sampled (I = 1.25 m^2).

Table 3. Selection of vegetation feature of habitat by early benthic juvenile California spiny *Panulirus interruptus*

Results of ANOVA among sizes that select any of the substrata by natural or odour signal

Substrata	Natural		Odour signal	
	n	CL (mm) Mean ± s.d.	*n*	CL (mm) Mean ± s.d.
Gelidium robustum	55	12.9 ± 5.9	25	15.5 ± 1.1
Phyllospadix scouleri	22	10.9 ± 4.5	39	13.9 ± 5.5
Plocamium pacificum	10	10.5 ± 3.0	19	14.8 ± 4.9
Macrocystis pyrifera	3	10.6 ± 3.6	16	13.0 ± 1.3
F	1.128		0.8622	
df	3/86		3/95	
P	0.342		0.464	

CL = carapace length.

Table 4. Resume of substratum selection by early benthic juveniles *Panulirus interruptus* both experiments type

Substrata to be selected	(Natural)	(Odour signal)
Gelidium robustum	55	25
Phyllospadix scouleri	22	39
Plocamium pacificum	10	19
Macrocystis pyrifera	3	16
Total	90	99
	$\chi^2 = 70.8$, $df = 3$, $P < 0.001$	$\chi^2 = 12.6$, $df = 3$, $P < 0.005$

found almost exclusively (93%) at the base of the blades of *Phyllospadix* spp. in the intertidal zone, despite the abundance of the other macrophytes as habitat. Although *P. torreyi* was distributed from the intertidal to the subtidal zones (0 to 6 m) at Queen, EBJ lobsters were present only in samples from 0 to 3 m. The use of intertidal habitat by EBJ lobsters has been described for other lobster species, for example, *J. edwardsii* (Booth *et al.* 1991) in New Zealand, *Homarus gammarus* in Europe (Linnane *et al.* 2000*a*, 2000*b*), and in *H. americanus* in Canada (Cowan 1999; Sainte-Marie and Chabot 2002). Along the east coast of North America, juvenile *H. americanus* are voracious predators of mussels (Sainte-Marie and Chabot 2002). In fact, adult California spiny lobsters have been described as keystone predator on wave-exposed sites, intertidal zones where they can alter sessile community assemblages by preying on competitively dominant juvenile mussels (*Mytilus californianus* and *M. galloprovincialis*) (Robles *et al.* 1990; Robles and Robb 1993; Robles 1997).

We estimated the natural density of EBJ *P. interruptus* to be between 0 and 3.7 individuals per m^2 if one considers the entire depth spectrum that we sample, and between 0 and 11.2 individuals per m^2 if only samples from the intertidal zone are considered. These densities are higher than those reported in studies conducted near the species' northern limit (1 m^{-2}) (Parker 1972), and considerably higher than EBJ densities estimated for other species: as in *P. argus*, between 0.01 and 2.5 individuals per m^2 (Marx and Herrnkind 1985*a*; Forcucci *et al.* 1994; Acosta and Butler 1997; Butler and Herrnkind 1997; Briones-Fourzán and Lozano-Álvarez 2001); in *P. ornatus*, 0.01 m^{-2} (Dennis *et al.* 1997); in *P. cygnus*, 0.1–1.7 m^{-2} (Jernakoff 1990); in *J. edwardsii*, 2.2 m^{-2} (Butler *et al.* 1999); and in *P. japonicus*, 0.21–0.32 m^{-2} (Norman *et al.* 1994). The highest density that we observed was in September, which is consistent with other studies that suggests that *P. interruptus* has a well defined seasonal settlement peak. In Bahía Tortugas, Guzmán del Próo *et al.* (1996) and Vega *et al.* (2003) have reported that settlement of *P. interruptus* peaks in autumn, although settlement on artificial collectors occurs year-round. Serfling and Ford (1975) also reported the highest catch of *P. interruptus* postlarvae on floating traps filled with *Phyllospadix* and red algae during this season. Engle (1979) caught greater numbers of EBJ lobsters using night light traps in September, which coincides with the time of the year for settlement reported by Ayala-Martínez and Chávez (1985).

We employed a different design in our habitat selection experiments that permit us to test four substrata simultaneously, rather than two substrata at a time, as did Parker (1972) and Engle (1979). However, our observations are in agreement with the findings of those authors. The juvenile lobsters preferred *Phyllospadix* and red algae *Gelidium* to *Macrocystis* and *Plocamium*, but showed no preference between *Phyllospadix* and red alga *Gelidium.* In our extensive field explorations, we did not find EBJ *P. interruptus* in *Gelidium* or *Plocamium*, although fisherman collecting macroalgae for sale say that they some time do. *Gelidium* was overwhelmingly preferred in the experiment with natural substrata, while *Phyllospadix* was moderately preferred in the experiment with odour-seeded artificial substrata. Odour reception as a potential mechanism of orientation during the habitat selection process at settlement has been determined in postlavae of *H. americanus* (Boudreau *et al*. 1993). In *P. argus*, experimental behaviour studies have shown that, whereas postlarvae use algal architecture as a cue for settlement, juveniles use architecture and food abundance for selecting habitat (Herrnkind and Butler 1986).

There are a few plausible explanations for the observation that EBJ *P. interruptus* show no preference between these two substrates (*Phyllospadix* and *Gelidium*) in the laboratory, yet were found dwelling almost exclusively within *Phyllospadix* in the field. It is possible that settlement or 'choice' for these substrates is similar in nature, but mortality may be lower for individuals choosing the cover of *Phyllospadix*, particularly when it occurs intertidally or in the shallow subtidal zone. *Phyllospadix* spp. occurs along the full distributional range of *P. interruptus*, but it does not occur with *Gelidium robustum*, whose distribution is patchy, occurring on points or rocky keys as far south as Punta Prieta, in southern Baja California (Casas-Valdez and Hernández-Guerrero 1996). Evolutionary maintenance of choice for *Gelidium* under such negative selection may be balanced by the fact that *Gelidium* can be locally more abundant at rocky sites where *Phyllospadix* is absent, offering better protection in those habitats than other available substrates. Alternatively, one could argue that our recovery of EBJ *P. interruptus* was more effective in *Phyllospadix* than in *Gelidium*, thus giving the false impression of density differences. Although possible, we removed all the vegetation from within all of the quadrats we sampled and thoroughly searched this material in the laboratory to avoid field-based bias in detection. Therefore, we believe that the most parsimonious explanation for our results is the 'multiple cue' hypothesis described above.

Other decapod crustaceans with broad geographic distributions are known to respond to multiple cues in their search for coastal nursery habitats that vary locally in environmental features. Perhaps the best studied of these is the blue crab, *Callinectes sapidus*, which occurs along the east and Gulf coasts of the United States. Depending on the local conditions, that species responds to temperature, salinity, pressure, or odour cues during selective tidal stream transport up estuaries to find nursery habitat (Forward and Tankersley 2001). Response to such a broad range of nursery habitat cues has not been tested for spiny lobsters, although the postlarvae of at least one species (*P. argus*) are known to respond differentially to offshore *v.* inshore water masses, seawater of different salinity, and seawater conditioned with different types of coastal vegetation (e.g. seagrass *v.* red macroalga) (Goldstein 2005). Similar studies on *P. interruptus* and other species are needed to assess the generality of these behaviours. Studies that compare behavioural responses among species that vary in geographic range or settlement habitat variability may be particularly revealing.

Phyllospadix spp. beds in the lower intertidal zone, as habitat of EBJ *Panulirus interruptus* on the Pacific coast of Baja California Sur, Mexico, is instructive and complements the available ecological information of the species. Juvenile assessments need to be done to understand the use of intertidal habitat at this lobster stage. For economic considerations, as well as basic ecological value, our findings serve as a cautionary finding related to coastal management. The intertidal zone is a particularly vulnerable habitat because it is close to the major anthropogenic impacts from land sources of pollution, fresh water, and erosion leading to sediment deposition.

Acknowledgments

This research was supported by the National Counsel of Science and Technology (CONACYT 35151-B) and a CIBNOR institutional project, and partial supported by the project (NSF-0410439/CIBNOR 995–0). V. Castañeda received a fellowship from CONACYT Grant 112870. We thank Carlos Gomez-Rojo and Armando Vega-Velázquez, Coordinator of the lobster programme at the Regional Fishery Research Centre (INP-CRIP, La Paz), for logistical assistance, Juan José Ramírez for technical support in the field, and Alma Rosa Rivera for assistance with algae analysis in the laboratory. To 'INP-CRIP, La Paz' and 'Escuela Nacional de Ciencias Biológicas, Laboratorio de Ecología, IPN' for the supply of juveniles from artificial collectors. Fishing cooperatives 'La Purísima' and 'Bahía Tortugas', and especially Ignacio Villavicencio, and Alejandro Villa Bastida provided assistance in the field. The editor at CIBNOR improved the English text.

References

Abbot, I. A., and Hollenberg, G. J. (1976). 'Marine Algae of California.' (Stanford University Press: Palo Alto, CA.)

Acosta, C. A., and Butler, M. J. (1997). Role of mangrove habitat as a nursery for juvenile spiny lobster, *Panulirus argus*, in Belize. *Marine and Freshwater Research* **48**, 721–727. doi:10.1071/MF96105

Ayala-Martínez, Y., and Chávez, H. (1985). Note on the collection of larvae and juveniles of the red lobster *Panulirus interruptus* (Randall) in the west coast of Baja California, Mexico. *Ciencias Marinas* **11**, 93–100.

Booth, J. D. (2001). Habitat preference and behaviour of newly settled *Jasus edwardsii* (Palinuridae). *Marine and Freshwater Research* **52**, 1055–1065. doi:10.1071/MF01089

Booth, J. D., Carruthers, A. D., Bolt, C. D., and Stewart, R. A. (1991). Measuring depth of settlement in the red rock lobster, *Jasus edwardsii. New Zealand Journal of Marine and Freshwater Research* **25**, 123–132.

Boudreau, B. (1992). Bases comportementales du déterminisme des sites de déposition chez le Homard Américain (*Homarus americanus*). Ph.D. Thesis, Université Laval, Québec, Canada.

Boudreau, B., Bourget, E., and Simard, Y. (1993). Behavioural responses of competent lobster postlarvae to odor plumes. *Marine Biology* **117**, 63–69. doi:10.1007/BF00346426

Briones-Fourzán, P., and Lozano-Álvarez, E. (2000). The spiny lobster fisheries in Mexico. In 'Spiny Lobster: Fisheries and Culture'. (Eds B. F. Phillips and J. Kittaka.) pp. 169–188. (Blackwell Science Ltd.: Oxford.)

Briones-Fourzán, P., and Lozano-Álvarez, E. (2001). The importance of *Lobophora variegata* (Phaeophyta: Dictyotales) as a habitat for small juveniles of *Panulirus argus* (Decapoda: Palinuridae) in a tropical reef lagoon. *Bulletin of Marine Science* **68**, 207–219.

Butler, M. J., IV, and Herrnkind, W. F. (1986). Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters *Panulirus argus. Marine Ecology Progress Series* **34**, 23–30.

Butler, M. J., IV, and Herrnkind, W. F. (1997). A test of recruitment limitation and the potential for artificial enhancement of spiny lobster (*Panulirus argus*) populations in Florida. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 452–463. doi:10.1139/CJFAS-54-2-452

Butler, M. J., IV, and Herrnkind, W. F. (2000). Puerulus and juvenile ecology. In 'Spiny Lobster: Fisheries and Culture'. (Eds B. F. Phillips and J. Kittaka.) pp. 276–301. (Blackwell Science Ltd.: Oxford.)

Butler, M. J., IV, Herrnkind, W. F., and Hunt, J. H. (1997). Factors affecting the recruitment of juvenile Caribbean spiny lobsters dwelling in macroalgae. *Bulletin of Marine Science* **61**, 3–19.

Butler, M. J., IV, MacDiarmid, A. B., and Booth, J. D. (1999). The cause and consequence of ontogenetic changes in social aggregation in New Zealand spiny lobsters. *Marine Ecology Progress Series* **188**, 179–191.

Caddy, J. F., and Stomatopoulos, C. (1990). Mapping growth and mortality rates of crevice-dwelling organisms onto a perforated surface: The relevance of "cover" to the carrying capacity of natural and artificial habitats. *Estuarine Coastal and Shelf Science* **31**, 87–106.

Casas-Valdez, M., and Hernández-Guerrero, C. J. (1996). Pesquería de *Gelidium robustum*. In 'Estudio del potencial pesquero y acuícola de Baja California Sur'. (Eds M. Casas-Valdez and G. Ponce-Díaz.) pp. 419–429. (Centro de Investigaciones Biológicas del Noroeste: La Paz, B.C.S., Mexico.)

Castañeda-Fernández de Lara, V., Serviere-Zaragoza, E., Hernández-Vázquez, S., and Butler, M. J., IV (2005). Feeding ecology of juvenile spiny lobster, *Panulirus interruptus*, on the Pacific coast of Baja California Sur, Mexico. *New Zealand Journal of Marine and Freshwater Research* **39**, 425–435.

Cowan, D. F. (1999). Method for assessing relative abundance, size distribution, and growth of recently settled and early juvenile lobsters (*Homarus americanus*) in the lower intertidal zone. *Journal of Crustacean Biology* **19**, 738–751.

Dawson, E. Y. (1951). A further study of upwelling and associated vegetation along Pacific Baja California, México. *Journal of Marine Research* **10**, 39–58.

Dennis, D. M., Skewes, T. D., and Pitcher, C. R. (1997). Habitat use and growth of juvenile ornate rock lobsters, *Panulirus ornatus* (Fabricius, 1798), in Torres Strait, Australia. *Marine and Freshwater Research* **48**, 663–670. doi:10.1071/MF97184

Engle, J. (1979). Ecology and growth of juvenile California spiny lobsters (*Panulirus interruptus*, Randall). Ph.D. Thesis, University of Southern California, Los Angeles, CA.

Forcucci, D., Butler, M. J., IV, and Hunt, J. H. (1994). Population dynamics of juvenile Caribbean spiny lobster, *Panulirus argus*, in Florida Bay, Florida. *Bulletin of Marine Science* **54**, 805–818.

Forward, R. B., Jr, and Tankersley, R. A. (2001). Selective tidal-stream transport of marine animals. *Oceanography and Marine Biology Annual Reviews* **39**, 305–353.

Goldstein, J. S. (2005). Nursery habitat selection and settlement behavior of postlarval Caribbean spiny lobster, *Panulirus argus*. M.S. Thesis, Old Dominion University, Norfolk, VA.

Guzmán del Próo, S. A., De la Campa-Guzmán, S., and Pineda-Barrera, J. (1972). Flora macroscópica asociada a los bancos de abulón (*Haliotis* spp.) en algunas áreas de la costa occidental de la Península de Baja California. In 'Memorias IV Congreso Nacional Oceanografía'. pp. 257–263. (México.)

Guzmán del Próo, S. A., Carrillo-Laguna, J., Belmar-Perez, J., De la Campa, S., and Villa, B. A. (1996). The puerulus settlement of red spiny lobster (*Panulirus interruptus*) in Bahia Tortugas, Baja California, Mexico. *Crustaceana* **69**, 949–957.

Herrnkind, W. F., and Butler, M. J., IV (1986). Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters, *Panulirus argus. Marine Ecology Progress Series* **34**, 23–30.

Hickman, J. D. (1993). 'The Jepson Manual Higher Plants of California.' (University of California Press: Berkeley, CA.)

Holmquist, J. G., Powell, G. V. N., and Sogard, S. M. (1989). Decapod and stomatopod assemblages on a system of seagrass-covered mud banks in Florida Bay. *Marine Biology* **100**, 473–483. doi:10.1007/BF00394824

Jernakoff, P. (1990). Distribution of newly settled western rock lobsters *Panulirus cygnus. Marine Ecology Progress Series* **66**, 63–74.

Johnson, M. W. (1960). The offshore drift of larvae of the California spiny lobster, *Panulirus interruptus. California Cooperation Oceanic Fishery Investigation Report* **7**, 147–161.

Kanciruk, P. (1980). Ecology of juvenile and adult Palinuridae (spiny lobsters). In 'The Biology and Management of Lobsters'. Vol. II (Eds S. J. Cobb and B. F. Phillips.) pp. 59–96. (Academic Press: New York.)

Krebs, J. R., and Kacelnik, A. (1992). Exploitation of resources: decision-making. In 'Behavioural Ecology: An Evolutionary Approach'. (Eds J. R. Krebs and N. B. Davies.) pp. 105–136. (Blackwell Science: Oxford.)

Lindberg, R. G. (1955). Growth, population dynamics, and field behavior in the spiny lobster *Panulirus interruptus* (Randall). *University of California Publication in Zoology* **59**, 157–249.

Linnane, A., Ball, B., Munday, B., and Mercer, J. P. (2000*a*). On the occurrence of juvenile lobster *Homarus gammarus* in intertidal habitat. *Journal of the Marine Biological Association of the UK* **80**, 375–376. doi:10.1017/S0025315499002039

Linnane, A., Mazzoni, D., and Mercer, J. P. (2000*b*). A long-term mesocosm study on the settlement and survival of juvenile European lobster *Homarus gammarus* L in four natural substrates. *Journal of Experimental Marine Biology and Ecology* **249**, 51–64. doi:10.1016/S0022-0981(00)00190-8

Lluch-Belda, D. (2000). Centros de Actividad Biológica en la Costa Occidental de Baja California. In 'Centros de Actividad Biológica del Pacífico Mexicano. Centro de Investigaciones Biológicas del Noroeste'. (Eds D. Lluch-Belda, J. Elourduy-Garay, S. E. Lluch-Cota and G. Ponce-Díaz.) pp. 49–64. (CIBNOR, CICMAR, CONACYT.)

Marx, J. M., and Herrnkind, W. F. (1985*a*). Macroalgae (Rodophyta: *Laurencia* spp.) as habitat for young juvenile spiny lobsters *Panulirus argus. Bulletin of Marine Science* **36**, 423–431.

Marx, J. M., and Herrnkind, W. F. (1985*b*). Factors regulating microhabitat use by young juvenile spiny lobsters, *Panulirus argus*: food and shelter. *Journal of Crustacean Biology* **5**, 650–657.

Mason, H. L. (1957). 'Flora of the Marshes of California.' (University of California Press: Berkeley, CA.)

Mitchell, J. R. (1971). Food preferences, feeding mechanisms, and related behavior in phyllosoma larvae of the California spiny lobster, *Panulirus interruptus* (Randall). M.Sc. Thesis, San Diego State University, San Diego, CA.

Norman, C. P., Yamakawa, H., and Yoshimura, T. (1994). Habitat selection, growth rate and density of juvenile *Panulirus japonicus* (Von Seibold, 1824) (Decapoda, Palinuridae) at Banda, Chiba Prefecture, Japan. *Crustaceana* **66**, 366–383.

Ortuño-Manzanarez, G. (2003). Abundancia y distribución de larvas filosoma de langosta roja (*Panulirus interruptus*) en la parte sur de la corriente de California durante el 2000. M.Sc. Thesis, Centro de Investigación Científica y de Educación Superior de Ensenada, Baja California, México.

Parker, K. P. (1972). Recruitment and behavior of puerulus larvae and juveniles of the California spiny lobster, *Panulirus interruptus*. M.Sc. Thesis, San Diego State University, San Diego, CA.

Phillips, R. C. (1979). Ecological notes on *Phyllospadix* (Potamogetonaceae) in the Northeast Pacific. *Aquatic Botany* **6**, 159–170. doi:10.1016/0304-3770(79)90059-7

Phillips, B. F., and Booth, J. D. (1994). Design, use, and effectiveness of collectors for catching the puerulus stage of spiny lobsters. *Reviews in Fisheries Sciences* **2**, 255–289.

Pringle, J. D. (1986). California spiny lobster (*Panulirus interruptus*) larval retention and recruitment: A review and synthesis. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 2142–2152.

Ramírez-García, P., Lot, A., Duarte, C. M., Terrados, J., and Agawin, N. S. R. (1998). Bathymetric distribution, biomass and growth dynamics of intertidal *Phyllospadix scouleri* and *Phyllospadix torreyi* in Baja California (Mexico). *Marine Ecology Progress Series* **173**, 13–23.

Ramírez-García, P., Terrados, J., Ramos, F., Lot, A., Ocaña, D., and Duarte, C. M. (2002). Distribution and nutrient limitation of surfgrass, *Phyllospadix scoueleri*, and *Phyllospadix torrey*, along the Pacific coast of Baja California (México). *Aquatic Botany* **74**, 121–131. doi:10.1016/S0304-3770(02)00050-5

Robles, C. D. (1997). Changing recruitment in constant species assemblages: implications for predation theory in intertidal communities. *Ecology* **78**, 1400–1414.

Robles, C. D., and Robb, J. (1993). Varied carnivore effects and the prevalence of intertidal algal turfs. *Journal of Experimental Marine Biology and Ecology* **166**, 65–91. doi:10.1016/0022-0981(93)90079-4

Robles, C. D., Sweetnam, D., and Eminike, J. (1990). Lobster predation on mussel shore-level differences in prey vulnerability and predation preference. *Ecology* **71**, 1564–1577.

SAGARPA (2003). ‘Anuario Estadístico de Pesca 2002.’ (Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación: México.)

Sainte-Marie, B., and Chabot, D. (2002). Ontogenetic shifts in natural diet during benthic stages of American lobster (*Homarus americanus*), off the Magdalen Islands. *Fishery Bulletin (Washington, D.C.)* **100**, 106–116.

Serfling, S. A. (1972). Recruitment, habitat preference, abundance and growth of the puerulus and early juvenile stages of the California spiny lobster *Panulirus interruptus* (Randall). M.Sc. Thesis, San Diego State University, San Diego, CA.

Serfling, S. A., and Ford, R. F. (1975). Ecological studies of the puerulos larval stage of the California spiny lobster *Panulirus interruptus. Fishery Bulletin (Washington, D.C.)* **73**, 361–368.

Sokal, R. R., and Rohlf, F. J. (1981). ‘Biometry. The Principles and Practice of Statistics in Biological Research.’ 2nd edn. (W. H. Freeman: New York.)

Vega, V. A., and Lluch-Cota, D. B. (1992). Análisis de las fluctuaciones en los volúmenes de langostas (*Panulirus* spp.), del litoral oeste de la Península de Baja California, en relación con el desarrollo histórico de la pesquería y la variabilidad del marco ambiental. In ‘Memorias del Taller Internacional México-Australia sobre reclutamiento de los recursos marinos bentónicos de la Península de Baja California’. (Ed. S. Guzmán del Proó.) pp. 191–212. (Escuela Nacional de Ciencias Biológicas, Centro Interdisciplinario de Ciencias Marinas, Instituto Nacional de la Pesca, La Paz, Baja California Sur, México.)

Vega, V. A., Espinoza-Castro, G., and Gómez-Rojo, C. (1996). Pesquería de langosta *Panulirus* sp. In ‘Estudio del potencial pesquero y acuícola de Baja California Sur’. (Eds M. Casas-Valdez and G. Ponce-Díaz.) pp. 227–261. (Centro de Investigaciones Biológicas del Noroeste: La Paz, B.C.S., Mexico.)

Vega, V. A., Espinoza-Castro, G., and Gómez-Rojo, C. (2000). Langosta. In ‘Sustentabilidad y pesca responsable en México, evaluación y manejo’. (Ed. SEMARNAP.) pp. 263–298. (Secretaria del Medio Ambiente Recursos Naturales y Pesca.: D.F., México.)

Vega, V. A., Gómez-Rojo, C., Del-Valle-Manríquez, A., Ayala-Murillo, R., and Villa-Bastida, A. (2003). Reclutamiento de estadios tempranos de langosta roja (*Panulirus interruptus*) y su relación con factores ambientales en la costa noroccidental de Baja California Sur. In ‘Caracterización-temporal del hábitat de los Primeros estadios bentónicos de la langosta roja *Panulirus interruptus* (Randall) en su área de mayor abundancia’. (Ed. G. Ponce-Díaz.) pp. 39–66. Consejo Nacional de Ciencia y Tecnología (CONACT), Technical Report, Project 35151-B, Mexico, D.F.

Yoshimura, T., Yamakawa, H., and Norman, C. P. (1994). Comparison of hole and seaweed habitats of post-settled pueruli and early benthic juvenile lobsters, *Panulirus japonicus* (Von Siebold, 1824). *Crustaceana* **66**, 356–365.

Manuscript received 30 November 2004; revised 16 June 2005; and accepted 11 August 2005.