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Feeding ecology of juvenile spiny lobster, *Panulirus interruptus*, on the Pacific coast of Baja California Sur, Mexico

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Abstract Many aspects of the early life history of the red lobster *Panulirus interruptus* are little known, including the relationship between habitat structure, food resource availability, and nutrition of juveniles. We investigated the spatial and temporal differences in food intake, diet composition, and nutritional condition of juveniles at two sites along the Pacific coast of the Baja California Peninsula (Mexico) with contrasting oceanographic and biological conditions. One site (Arvin) is located inside a protected bay, Bahía Tortugas, where the waters are cooler and temperate seagrasses and macroalgae are the dominant benthic flora. The second site (Queen) in Bahía Sebastián Vizcaíno was located along a more open coastline where seawater temperatures were higher and the benthic flora more indicative of warmer seas. At both sites, we randomly sampled epifauna within vegetated habitats to estimate the seasonal

availability of food resources for juvenile lobsters from autumn 2001 until summer 2002. Concurrently, we used traps to sample *P. interruptus* juveniles for stomach content analysis. At both sites, Amphipoda, Gastropoda, and Polychaeta dominated the epifauna assemblages, as determined by an Index of Importance. Juvenile *P. interruptus* primarily consumed crustaceans (mostly amphipods and isopods) and vegetal material (surf-grass *Phyllospadix* spp. and calcareous algae), but their food spectrum was wide. Manly's Index of Resource Selection indicated that lobsters preferred some prey (e.g., Brachyurans) over others despite their low Index of Importance. Despite marked differences in the types of food and their availability between sites, there were no significant differences in the nutritional condition (e.g., relative weight of the digestive gland) of lobsters at the two sites. However, the nutritional condition of lobsters was effected during some seasons. In particular, their condition deteriorated during the spring (April 2002) at Arvin, as did the proportion of individuals with empty stomachs. This study shows the feeding adaptation capacity of the juvenile California spiny lobster *P. interruptus* to different environmental conditions prevalent in Centre Baja California Peninsula.

Keywords feeding ecology; spiny lobsters; *Panulirus interruptus*; juveniles

INTRODUCTION

Spiny lobsters are a commercially important resource in Mexico. Profits from these fisheries are the fifth most valuable in Mexico, and are estimated to be worth US\$18 million from a catch of 744 t (SAGARPA 2003). Along the Pacific coast of the Baja California Peninsula, three spiny lobster species are exploited: red lobster *Panulirus interruptus* (Randall, 1840), blue lobster *P. inflatus* (Bouvier, 1895), and green lobster *P. gracilis* (Streets, 1871). *P. interruptus* represents 95–97% of total production (Vega et al. 2000).

The red lobster, *P. interruptus*, occurs along the west coast of the Baja California Peninsula as far south as Isla Margarita (c. 24.5°N) (Vega et al. 1996), and small populations are also found along parts of the east coast of the Peninsula (Ayala et al. 1988). However, it is most abundant off the central part of the Baja California Peninsula from Punta Abreojos (c. 26.7°N) to Isla Cedros (c. 28.3°N) (Johnson 1960a,b; Vega et al. 1996, 2000), where it lives in rocky areas from the low intertidal zone to depths of c. 150 m. Our understanding of the biology and ecology of *P. interruptus* along the Mexican Pacific coast is limited to a few studies on reproduction, puerulus settlement, growth, and genetic structure (e.g., Ayala 1976; Pineda et al. 1981; Guzmán del Prío & Pineda 1992; Guzmán del Prío et al. 1996; Perez-Enriquez et al. 2001).

Information on the natural diet and feeding habits of *P. interruptus* is scarce, although the species has been characterised as omnivorous with a diet consisting of gastropods, fish remains, decapods, and red and brown algae (Díaz-Arredondo & Guzmán del Prío 1995). This is true of palinurid lobsters in general (Kanciruk 1980), which are omnivorous and consume, among other things, crustaceans, gastropods, fish, and marine plants (Lindberg 1955; Engle 1979; Colinas-Sánchez & Briones-Fourzán 1990; Díaz-Arredondo & Guzmán del Prío 1995; Briones-Fourzán et al. 2003); although *P. inflatus* and *P. gracilis* do not appear to eat plants (Lozano-Alvarez & Aramoni-Serrano 1996). In this study, we compared spatial and seasonal differences in food intake, diet composition, and nutritional condition of juvenile *P. interruptus* at two sites on the central part of the Baja California Peninsula.

MATERIALS AND METHODS

Study sites

Our two study sites on the Pacific coast of the Baja California Peninsula (Mexico) occur within the zone where *P. interruptus* is most abundant (Vega & Luch-Cota 1992). The "Arvin" site lies inside a protected bay, Bahía Tortugas whereas the second site ("Queen") is located on the coast of Bahía Sebastián Vizcaíno, a more open coastline (Fig. 1). We selected these sites because older juvenile lobsters (40–60 mm carapace length (CL)) had previously been observed there, and because the two sites have different physiographic and marine conditions (Lluch-Belda 2000) that are indicative of those that occur along the western Baja California

coast. Mean bottom seawater temperature at Arvin (17.3°C) was cooler than at Queen (19.9°C) during September 2001 and October 2002 and the dominant benthic flora also differ. At Queen, one surf-grass species *Phyllospadix torreyi* and two brown algae *Padina caulescens* and *Sargassum agardhianum* are the dominant species. At Arvin, two marine grass species *P. scouleri* and *Zoostera marina* and three brown algae *Macrocystis pyrifera*, *Sargassum muticum*, and *Cystoseira osmundacea* are the dominant species. Along Bahía Sebastián Vizcaíno, tropical species of macroalgae related to an oceanographic gyre have been described (Dawson 1951, 1952), as has the absence of the kelp *M. pyrifera* for c. 300 km of coastline within its broad distribution range (Ladah & Zertuche-González 1999).

Sampling of *P. interruptus* juveniles

To determine the feeding habits of juvenile *P. interruptus* and whether those habits varied among seasons and sites, we sampled both sites during four seasons: September 2001 (autumn), January 2002 (winter), April 2002 (spring), and June 2002 (summer). In each season, juveniles were caught with octopus traps made with galvanised wire and baited with fish (*Scomber japonicus*). Ten traps were set in the afternoon (1900 h) because lobsters feed actively during the night (Herrnkind et al. 1975; Lipcius & Herrnkind 1982). At 0800 h, we checked the traps and collected juveniles under 65 mm CL (measured from between the rostral horns to the posterior margin of the carapace). For each lobster we recorded: sex, CL (± 0.1 mm), and total weight (TW ± 0.1 g). Individuals were dissected in the field to extract their stomach, pleopods, and digestive gland. Stomachs were preserved in 10% formaldehyde in sea water and pleopods in 70% ethanol for later analysis. The digestive gland was blotted dry and weighed (WDG = weight of digestive gland ± 0.01 g), and its relative weight (RWDG = WDG/TW ($\times 100$)) was obtained as an index of the nutritional condition of individuals. Starved or poorly fed individuals have significantly lower values of RWDG than do well-fed individuals (Dall 1974).

In the laboratory, juveniles were classified as postmoult, intermoult, or premoult, based on the determination of their stage in the moulting cycle from observation of a pleopod under a microscope (Lyle & MacDonald 1983). The percentage fullness of the stomach was visually calculated and categorised according to the following scale: 0% (0–5%), 10% (6–15%), 25% (16–35%), 50% (36–65%),

Fig. 1 Study area on the Pacific coast of northern part of Baja California Sur, México.

75% (66–90%), and 100% (91–100%) (Briones-Fourzán et al. 2003). Diet analysis was performed only on juveniles with stomachs 10% full (Joll 1984). Stomach contents were obtained and stored in 70% ethanol until sorting and identification under a stereo-microscope to the lowest taxonomic level possible (Smith & Carlton 1975; Brusca 1980; Morris et al. 1980; Kozloff 1987). Frequency of occurrence (FO = number of stomachs containing a given food category/total number of stomachs examined ($\times 100$)) was determined for each food category.

For each individual stomach, the total volume of the contents was determined using a 10-ml graduated glass cylinder ($\text{ml} \pm 0.1$). The stomach contents were then squashed to a uniform depth on a large Petri dish on which 100 squares (each one: 40.96 mm^2) were imprinted (VWR®). Thirty of these squares were randomly selected and the number of squares covered by each type of food was measured under a stereo-microscope to estimate the percentage

contribution by volume (V%) of each food type in each stomach (Krebs 1999). This technique standardises estimates of volume, irrespective of the size of the lobsters (Hyslop 1980; Joll & Phillips 1984; Briones-Fourzán et al. 2003). Finally, we calculated an Index of Relative Importance (IRI) to assess the importance of each food category in the stomachs of lobster by season and site (Yáñez-Arancibia et al. 1976). The IRI per trophic group is calculated as:

$$\text{IRI} = (\text{FO} \times \text{V})/100$$

where FO = percentage frequency of occurrence, and V = volumetric percentage of each trophic group.

Sampling of epifauna

We also compared the resources consumed by juvenile *P. interruptus* to the availability of food in the habitats frequented by juvenile lobster during different seasons. In the same areas where juveniles were caught for stomach analysis, we established

three 200-m transects running parallel to the shore at depths of 1 m, 2–3 m, and 4–6 m. Along each transect, all biological material in five randomly positioned 0.25-m² quadrats was collected at both the Arvin and Queen sites during each sampling time. Samples for quantitative analysis were collected by hand, using a net bag with a 1-mm² mesh. In the field, biological material was placed in plastic bags, labelled, and preserved with a 10% formalin seawater solution. In the laboratory, the samples were washed with fresh water and the macrofauna retained on a 1-mm² mesh sieve were kept for identification based on taxonomic keys for the region (Smith & Carlton 1975; Brusca 1980; Morris et al. 1980; Kozloff 1987).

For each sample, 10% of the total macrofauna weight was analysed according to previous minimum-weight calculations performed on five samples (Margalef 1998). We used a stereo-microscope to separate the epifauna into the taxonomic groups that we observed in the stomach contents (Marx & Herrnkind 1985). For each group, the relative frequency and biomass (± 0.01 g) percentages by season and site were calculated to generate an Index of Importance Value (IIV) defined as:

$$\text{IIV} = (\text{RF} \times \text{RB})/100$$

where RF = relative frequency (%) of the macrofauna group, and RB = relative biomass (%) of the same group.

Data analysis

Contingency table analyses were used to test the association between stomach fullness and sex, moult stage (intermoult or premoult), season (autumn, winter, spring, or summer), and sampling area (Queen or Arvin) (Oh et al. 2001). Comparisons of the logarithmic transformation of the relative weight of digestive glands over moult stage, seasons, and

sites were made with a three-way factorial ANOVA (Sokal & Rohlf 1998). The logarithmic transformation was needed to yield data that were normally distributed with homogeneous variances (Zar 1999).

Manly's alpha index was used to estimate the preference of juvenile lobsters for each faunal group (Manly et al. 1993; Krebs 1999). We compared both IRI of the trophic group and IIV of the same taxon category in the environment by season and site. We obtained these estimates for each season by site combination, using "Programs for Ecological Methodology" (Charles J. Krebs 2000[®]).

RESULTS

We caught 377 juvenile *P. interruptus*, of which 215 were from Arvin (size and weight range: 30.0–61.9 mm CL and 36.7–237.2 g) and 162 from Queen (size and weight range: 39.4–65.5 mm CL and 55.5–272.0 g). Of the total, 67 were caught in summer, 80 in autumn, 98 in winter, and 132 in spring (Table 1). There were 122 females and 255 males. Based on moult stage, 169 were in premoult and 208 in intermoult. Postmoult individuals were absent in both study sites. There were significant differences in stomach fullness of lobsters between sites, seasons, and moult stage, but sex had no effect on stomach fullness (Fig. 2).

There was no significant difference in the RWDG in relation to site ($P = 0.8$) or moult stage ($P = 0.5$). However, the RWDG was greater in juveniles caught in autumn (390.1 g) and statistically different from juveniles caught in spring (306.5 g), but not in winter or summer (main effect: $P < 0.05$), regardless of the site. However, the specimens were affected by season in relation to the site (interaction: $P < 0.05$). The greatest RWDG was for juveniles collected from

Table 1 Summary of measurements of *Panulirus interruptus* juveniles arranged by site and season. Mean $\pm$ SD. (CL, carapace length; WDG, weight of digestive gland.)

Site	Season	<i>n</i>	CL (mm)	Total length (mm)	Total weight (g)	WDG (g)
Arvin	Autumn	40	56.7 $\pm$ 4.3	183.4 $\pm$ 15.0	174.9 $\pm$ 35.5	7.7 $\pm$ 2.3
	Winter	60	55.4 $\pm$ 5.9	182.3 $\pm$ 20.3	173.4 $\pm$ 40.2	6.9 $\pm$ 2.3
	Spring	83	54.0 $\pm$ 4.4	172.3 $\pm$ 13.9	144.3 $\pm$ 30.3	4.3 $\pm$ 1.2
	Summer	32	55.9 $\pm$ 3.4	178.1 $\pm$ 11.6	165.4 $\pm$ 29.4	6.1 $\pm$ 1.7
Queen	Autumn	40	56.1 $\pm$ 4.5	179.5 $\pm$ 14.9	158.1 $\pm$ 29.3	5.8 $\pm$ 1.6
	Winter	38	53.8 $\pm$ 6.2	176.2 $\pm$ 20.8	151.3 $\pm$ 49.9	5.6 $\pm$ 2.2
	Spring	49	57.0 $\pm$ 5.1	184.9 $\pm$ 16.3	167.8 $\pm$ 42.3	6.2 $\pm$ 2.3
	Summer	35	55.8 $\pm$ 3.2	176.9 $\pm$ 9.6	161.2 $\pm$ 24.1	6.2 $\pm$ 0.9

Fig. 2 Juvenile *Panulirus interruptus*. Comparison of the degree of stomach fullness by: **A**, site; **B**, season; **C**, sex; and **D**, moult stage. Results of contingency table analysis (χ^2) appear below each graph (d.f. = degrees of freedom). Numbers above bars represent sample size.

Arvin in autumn, and the lowest was from juveniles caught in Arvin in spring (Fig. 3).

At both sites, a large percentage of the juvenile stomach contents was the bait used in the traps to collect them. At Arvin, it varied from 28 to 61% (FO) and 9 to 25% (V); at Queen, it varied from 12 to 67% (FO) and 5 to 47% (V). The percentage of unidentified organic matter varied from 0 to 63% (FO) and 0 to 10% (V) at Arvin. At Queen, it varied from 6 to 26% (FO) and from 1 to 6% (V). Bait and organic material were not considered in the statistical analysis of diet.

A total of 26 taxa and unidentified crustacea were identified in the diet; 18 were from stomach contents of juveniles caught at Arvin and 24 from juveniles caught at Queen. At Arvin, according to the IRI, the most important animal trophic groups (10) were Amphipoda during autumn and spring, Isopoda in summer, and Gastropoda in spring. Of marine plants, the surf-grass *P. scouleri* was important in winter, spring, and summer. In juveniles from Queen, the most important faunal stomach contents were Isopoda during autumn and winter. Coralline algae were important in spring and the seagrass *P. torreyi* in summer (Table 2).

We identified 35 macrofauna groups at the sites where juveniles were caught; 30 at Arvin and 32 at

Fig. 3 Mean $\pm$ standard error in vertical bars of the relative weight of the digestive gland (RWDG) of juvenile *Panulirus interruptus* among seasons at two sites (Arvin and Queen). Results of three-way ANOVA are inserted above in the figure. Factors considered in the analysis were seasons, sites, and moult stage. The main effects are shown only when there was statistical significance. Different letters indicate significant differences (Tukey analysis).

Queen (Table 3). At Arvin, the groups with greatest importance were Amphipoda in all seasons and Polychaeta in autumn, winter, and summer. At Queen, Polychaeta and Gastropoda had the greatest importance in all seasons and Amphipoda was important from winter to summer (Table 3). Estimates of IIV of Bryozoa was not possible because relative frequency estimates are not achievable for colonial organisms. However, this group was present in many samples at both sites (73–100%); its relative biomass was lowest in spring at Arvin (0.5%) and highest in autumn at Queen (36%).

Combining the stomach content results with the availability of food resources in the environment, we compared the selectivity of lobsters for various prey types using the selection index of Manly. Although some groups were estimated as being preferred, preferences varied inconsistently among sites and seasons (Table 4).

DISCUSSION

This study of the feeding ecology of small juvenile *P. interruptus* in Baja California Sur, Mexico complements previous studies in the same region but conducted on larger specimens (57–132 mm CL) (Díaz-Arredondo & Guzmán del Prío 1995). In both studies, crustaceans, molluscs, and vegetal material were the main trophic groups exploited by juveniles; however, the relative importance of the groups was different. Crustacea were more important than Mollusca in this study, but Díaz-Arredondo & Guzmán del Prío (1995) found that the pattern was reversed. This difference may be related to the size of the juvenile specimens in the two studies. Changes in diet preferences between size classes or stages in lobsters have been observed in other species, as in *P. cygnus* (Joll & Phillips 1984), *P. argus* (Andrée 1981; Marx & Herrnkind 1985; Herrnkind & Butler

Table 2 Index of Relative Importance (IRI) of trophic groups of juvenile *Panulirus interruptus* during seasons at Arvin in Bahía Tortugas and Queen in Bahía Sebastián Vizcaíno. Bold type represents up to 10 of the IRI value.

Trophic group Type		Arvin, Bahía Tortugas				Queen, Bahía Sebastián Vizcaíno			
		Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer
		= 28 IRI	n = 22 IRI	n = 30 IRI	n = 29 IRI	n = 27 IIR	n = 34 IIR	n = 25 IIR	n = 21 IIR
Crustacea	Brachyura	2.31	1.17	3.74	<0.01	<0.01	0.31	0.13	0.08
	Amphipoda	14.63	9.28	20.61	1.08	8.17	9.60	6.05	1.13
	Isopoda	1.69	3.79	0.70	17.40	26.34	30.09	1.42	4.81
	Ostracoda	4.85	—	0.11	0.1	—	0.39	—	—
	Tanaidacea	—	—	—	—	—	0.002	—	—
	Cumacea	—	—	—	—	—	—	0.01	—
	<i>P. interruptus</i>	—	—	—	—	0.06	—	—	—
Mollusca	Unidentified	<0.01	0.04	0.58	—	—	0.02	0.12	—
	Gastropoda	0.34	0.33	10.93	2.48	4.20	5.22	6.19	1.62
	Bivalvia	0.05	0.01	0.95	0.72	<0.01	0.38	3.24	—
	Polyplocophora	—	—	0.02	—	0.12	0.01	<0.01	—
	Monoplacophora	—	—	0.05	—	—	—	<0.01	—
Porifera	Demospongia	<0.01	0.13	0.03	0.02	0.11	—	0.95	0.20
Annelida	Polychaeta	—	<0.01	0.05	0.09	<0.01	<0.01	—	—
Ectoprocta	Bryozoa	4.00	2.10	<0.01	0.27	0.38	0.33	0.42	1.78
Nemata	Nematoda	<0.01	—	—	0.05	—	—	<0.01	0.09
Sarcodina	Foraminiferida	<0.01	—	—	—	—	0.14	0.05	0.06
Echinodermata		—	—	—	—	—	0.33	0.01	—
Cnidaria	Coelenterata	—	—	—	—	—	—	—	0.07
Algae	Coralline algae	9.54	2.64	5.01	9.98	0.57	4.54	17.33	0.26
	Red algae	0.41	0.05	0.17	0.18	0.01	0.2	0.33	0.80
	Brown algae	0.22	—	0.35	0.1	1.49	0.1	0.85	0.23
	Filamen algae	—	—	—	—	—	—	0.12	—
	Dictyota	—	—	—	—	—	—	0.21	—
	<i>Macrocystis pyrifera</i>	—	0.34	—	—	—	—	—	—
Plantae	<i>Phyllospadix scouleri</i>	4.83	15.95	10.50	18.71	—	—	—	—
	<i>Phyllospadix torreyi</i>	—	—	—	—	2.08	9.63	4.23	37.46

1986; Lalana & Ortiz 1991), *J. edwardsii* (Edmunds 1995), and *P. elephas* (Goñi et al. 2001). This general change in prey choice with ontogeny probably reflects an expanded foraging range and thus ability to exploit different habitats and unique prey (Andrée 1981; Edgar 1990; Briones-Fourzán et al. 2003).

In California coastal populations, Engle (1979) found a high proportion of molluscs in the juvenile

P. interruptus diet, which could be related to the availability of molluscs in the study site or to the method used for analysis (faecal rest analysis), because digestion can lead to overestimation of the importance of groups with harder parts (Joll 1982). Like us, Engle (1979) reported differences in the diet of *P. interruptus* that depended on local habitat characteristics. This implies that local habitat

Table 3 Index of Importance Value (IIV = Relative frequency $\times$ relative biomass/100) of the epifaunal groups by season at Arvin in Bahía Tortugas and Queen in Bahía Sebastián Vizcaíno. (*, Not possible to estimate colonial organisms.) Bold type represents up to 1 of the IIV value.

Phylum/ Subphylum	Class/Order	Arvin, Bahía Tortugas				Queen, Bahía Sebastián Vizcaíno			
		Autumn IIV	Winter IIV	Spring IIV	Summer IIV	Autumn IIV	Winter IIV	Spring IIV	Summer IIV
Crustacea	Brachyura	0.008	0.022	0.001	0.004	0.005	0.007	0.013	0.003
	Amphipoda	30.872	21.963	56.222	29.124	0.743	1.332	1.121	1.717
	Amphipoda tube	—	0.001	<0.001	<0.001	0.001	0.002	<0.001	<0.001
	Isopoda	0.076	0.115	0.004	0.343	0.055	0.043	0.076	0.07
	Ostracoda	0.001	0.001	<0.001	<0.001	0.001	0.002	0.017	0.001
	Tanaidacea	0.04	0.157	0.004	0.01	0.005	0.002	0.002	<0.001
	Paguroidea	—	—	—	<0.001	—	—	<0.001	<0.001
	Caridea	<0.001	<0.001	<0.001	<0.001	—	—	<0.001	<0.001
	Cumacea	0.018	<0.001	<0.001	<0.001	—	—	—	—
	Picnogonida	0.003	0.001	<0.001	<0.001	0.005	0.002	0.001	<0.001
Chelicerata	Gastropoda	0.062	0.035	0.028	0.013	6.061	8.199	14.782	10.206
Mollusca	Bivalvia	0.012	0.001	<0.001	0.009	0.054	0.003	0.008	0.018
	Polyplacophora	—	<0.001	<0.001	<0.001	0.001	—	<0.001	0.001
	Monoplacophora	0.008	0.025	0.007	0.096	0.055	0.155	0.032	0.02
	Opisthobranchia	—	<0.001	—	—	—	0.001	—	—
Porifera	Demospongia	0.001	0.003	<0.001	<0.001	0.006	0.001	<0.001	0.001
Annelida	Anelidae	0.11	0.056	0.001	0.009	0.002	0.01	0.013	0.003
	Polychaeta	1.427	2.478	0.237	1.799	7.896	3.944	1.557	2.513
	Clitellata	—	—	—	—	—	—	—	—
	(Oligochaeta)	0.013	<0.001	0.001	<0.001	0.001	0.049	0.124	0.001
Ectoprocta	Gymnolaemata	—	—	—	—	—	—	—	—
	(Bryozoa)	*	*	*	*	*	*	*	*
Nemata	Nematoda	—	—	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Protozoa	Sarcodina	—	—	—	—	—	—	—	—
	(Foraminiferida)	<0.001	<0.001	<0.001	<0.001	0.004	<0.001	0.001	0.001
Echinodermata	Asteroidea	—	—	—	—	—	—	<0.001	—
	Ophiuroidea	<0.001	<0.001	<0.001	<0.001	0.025	0.009	0.006	0.003
	Holothuroidea	<0.001	<0.001	<0.001	<0.001	0.007	0.001	0.002	0.002
	Echinoidea	—	—	—	—	—	—	—	<0.001
Cnidaria	Anthozoa	—	—	—	—	—	—	—	—
	(Coelenterata)	0.073	0.624	0.081	0.109	0.022	0.031	0.035	0.01
	Anthozoa	—	—	—	—	0.002	<0.001	—	—
	(Gorgonoacea)	—	—	—	—	—	—	—	—
Platyhelminthes	Turbellaria	0.174	0.024	0.007	0.021	0.001	0.001	0.002	0.002
Nemertea	Nemertinos	0.012	0.029	0.004	0.006	0.001	0.002	0.007	0.001
Sipuncula	Sipunculidae	—	—	0.000	0.012	—	<0.001	—	<0.001
Entoprocta	Entoprocto	—	—	—	—	—	—	—	<0.001
Chordata	Tunicata	—	—	—	—	—	—	—	—
	(Ascidieacea)	0.002	<0.001	<0.001	<0.001	0.002	0.001	<0.001	<0.001
Echiura	—	—	—	—	<0.001	—	—	—	—

information is fundamental for understanding the feeding ecology of spiny lobsters (Edgar 1990), as is the inclusion of a range of lobster sizes even among juveniles.

We attribute differences in stomach fullness among individuals in different moult stages to be a consequence of altered foraging activity. Intermoult lobsters forage more actively than individuals in premoult condition (Lipcius & Herrnkind 1982), whereas postmoult juveniles typically remain hidden in crevices and are consequently less likely to be caught in baited traps (Herrera et al. 1991; Jernakoff et al. 1993). Briones-Fourzán et al. (2003) handcaught a similar number of intermoult and premoult juvenile *P. argus* in their study, suggesting that trap capture selects for the more active intermoult lobsters.

Using IRI analysis, we found that Amphipoda and Isopoda were important in stomach contents in some seasons and also more abundant in the environment (IIV analysis), and thus were not considered preferred food items by the Manly Index. Similarly, Díaz-Arredondo & Guzmán del Prío (1995) described seasonal variations in trophic groups related to abundance of benthic components, which suggests trophic plasticity of *P. interruptus* as in other spiny

lobsters (Andrée 1981; Joll & Phillips 1984; Jernakoff et al. 1993; Briones-Fourzán et al. 2003). In contrast, the Manly Index suggests that juvenile *P. interruptus* prefer Brachyurans despite their low availability in the environment. A searcher characteristic was reported in other lobsters (Andrée 1981; Joll & Phillips 1984; Jernakoff et al. 1993; Briones-Fourzán et al. 2003).

At Arvin, the nutritional status of juveniles as determined by RWDG differed significantly among seasons, but at Queen the nutritional condition of lobster varied little seasonally. We suspect that this disparity among sites is related to differences in local environmental conditions, specifically, the warmer and less variable seawater temperatures at Queen. Like juveniles from Queen, *P. argus* juveniles caught in a tropical reef lagoon showed no seasonal differences in mean RWDG (Briones-Fourzán et al. 2003).

At Arvin, we observed the lowest value for RWDG in juveniles caught in spring, which coincided with the largest number of lobsters with empty stomachs. Baited traps promote the capture of starved animals (Dall 1975), which is related to a lack of available food (Chittleborough 1975; Colinas-Sánchez & Briones-Fourzán 1990). In this

Table 4 Selective index (Manly's alpha index (α_i)) of trophic groups by season from data of Index of Importance Value (IIV) of the group in the environment versus Index of Relative Importance (IRI) in the stomach contents of juvenile *Panulirus interruptus* for the seasons at Arvin in Bahía Tortugas and Queen at Bahía Sebastián Vizcaíno. Bold type indicates preferred groups using the Manly α_i .

Fauna	Trophic group	Arvin, Bahía Tortugas				Queen, Bahía Sebastián Vizcaíno			
		Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer
Crustacea	Brachyura	0.052	0.334	0.101	—	—	0.03	0	0.01
	Amphipoda	0	0.003	0	0	0.016	0.005	0	0
	Isopoda	0.004	0.208	0.006	0.017	0.71	0.452	0	0.023
	Ostracoda	0.942	—	0.274	0.491	—	0.116	—	—
	Tanaidacea	—	—	—	—	—	0.001	—	—
	Cumacea	—	—	—	—	—	—	—	—
	<i>P. interruptus</i>	—	—	—	—	—	—	—	—
	unidentified	—	—	—	—	—	—	—	—
Mollusca	Gastropoda	0.001	0.059	0.016	0.064	0.001	0	0	0
	Bivalvia	0.001	0.094	0.1	0.026	—	0.077	0.004	—
	Polylapophora	—	—	0.457	—	0.245	—	—	—
	Monoplacophora	—	—	0	—	—	—	—	—
Porifera	Demospongia	—	0.303	0.046	0.029	0.027	—	0.995	0.084
Annelida	Polychaeta	—	—	0	0	—	—	—	—
Ectoprocta	Bryozoa	—	—	—	—	—	—	—	—
Nemata	Nematoda	—	—	—	0.373	—	—	—	0.842
Sarcodina	Foraminiferida	—	—	—	—	—	0.32	0.001	0.039
Echinodermata	—	—	—	—	—	—	—	—	—
Cnidaria	Coelenterata	—	—	—	—	—	—	—	0.002
	Manly α_i	0.17	0.17	0.1	0.13	0.2	0.125	0.143	0.125

study, significant differences in stomach fullness of lobsters among seasons could not be related to availability of food items because the dominant and preferred trophic groups of epifauna did not change drastically in any season at either site. Changes in seasonal nutrition may be related to differences in the quantity and quality (Dall 1975) of trophic groups eaten one season earlier. Although crustaceans and gastropod prey are protein sources essential to the structure and overall function of lobsters (Kanazawa 2000), vegetal material may also be important in the diet of lobsters. Joll & Phillips (1984) state that cellulose fibre stimulates growth and the assimilation of nitrogen in lobsters on high protein diets. When on low protein diets, the plant material acts as an extender, making a low protein diet adequate for normal growth and survival. Coralline algae may also serve as a source of calcium for the juveniles as suggested by Lindberg (1955) and Engle (1979). Joll & Phillips (1984) observed that coralline algae (*Corallina cuvieri*) can be digested by *P. cygnus*, with absorption efficiencies up to 35%.

In *P. inflatus*, Aramoni-Serrano & Lozano-Alvarez (1995) found higher densities of lobsters with diminished nutritional condition in winter. They mentioned that this impoverishment could be the result of intra-species competition for food by migration of lobsters to the coastal habitat. Vega et al. (1996) found a migration of reproductive females to shallow waters (1–25 m) into the juveniles' habitat (<4 m) to carry out egg extrusion and hatching during spring-summer. This suggests that further research on possible trophic competition among size classes from migration patterns of *P. interruptus* needs to be clarified.

Our study shows local and seasonal changes in natural diet, preferences and nutritional condition of small lobsters, a phase poorly studied in Palinuridae, which complements the knowledge of *P. interruptus* feeding ecology in the region.

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