Squat lobsters (Decapoda: Anomura: Galatheidae) from deepwater Pacific Costa Rica: species diversity, spatial and bathymetric distribution

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Abstract

Galatheids are abundant, speciose and often commercially exploited decapods, which are distributed worldwide in marine habitats. In Central America, our knowledge concerning these squat lobsters is rather limited. Here we examined a large collection of galatheids to provide information about species diversity and distribution of these decapods in deep waters along the Pacific coast of Costa Rica. The material analyzed herein was retrieved from (a) commercial deepwater shrimp trawls (2004-2009) and (b) specimens deposited in the collection of the Museo de Zoología, Universidad de Costa Rica. The material contained six species of squat lobster (*Munida gracilipes, M. mexicana, M. obesa, M. refulgens, Munidopsis hamata,* and *Pleuroncodes monodon*), with *P. monodon* (1600 ind.) and *M. gracilipes* (651 ind.) being the most abundant. This is the first record of *M. mexicana* for Costa Rica, confirming its geographic distribution from Mexico to Panama and Galapagos. All four *Munida* species were encountered in depths between 30-384 m; *P. monodon* occurred between 150 and 350 m, while *M. hamata* was collected substantially deeper (1190-1281 m). Three species (*M. gracilipes, M. obesa* and *P. monodon*) showed a spatial distribution covering practically the entire Pacific coast of Costa Rica, while *M. refulgens* was absent along the central-southern and southern parts of this coast. Body size varied significantly among the four most common species. The material examined contained ovigerous females from all four *Munida* species, but in contrast, we did not retrieve any egg-bearing females of *P. monodon* nor of *M. hamata.* We provide a list of all galatheid deepwater species so far reported from Costa Rica and conclude that the species diversity of these squat lobsters in Costa Rican deepwater zones is surprisingly high.

Key words: deep water, *Pleuroncodes, Munida, Munidopsis,* Eastern Tropical Pacific.

Introduction

Crustacean decapods play an influential ecological and economic role in marine ecosystems, and the Galatheidae is no exception (Aurioles-Gamboa *et al.,* 2004; Fierro Rengifo *et al.,* 2008). Members of the Galatheidae family represent an important component of marine food webs, and can reach high densities on soft bottoms (Fierro Rengifo *et al.,* 2008). The commercial use of galatheid species is multiple: from cocktail shrimps to a source of astaxanthin for the pigmentation of chicken eggs and cultured salmon (Calvo-Carrillo *et al.,* 1995). Other squat lobsters are considered as the main food source for species such as fish, turtles, birds and marine mammals (Abitia-Cárdenas *et al.,* 1997; Aurioles-Gamboa *et al.,* 2004; Boyle and Limpus, 2008).

Squat lobster is the common name for members of the family Galatheidae, including the genera *Munidopsis* Whiteaves 1874, *Galathea* Fabricius 1793, *Pleuroncodes* Stimpson 1860, and *Munida* Leach 1820, among others. These crabs comprise one of the most species-rich families of the anomuran decapods. Currently, the family is known to accommodate 34 genera and 680 species (Baba and Fujita, 2008; Baba *et al.,* 2008; Macpherson and Baba, 2009). According to Macpherson *et al.* (2010), galatheids are most diverse in the Pacific Ocean, including 476 species in 32 genera. These decapods are commonly present on coral reefs, rocky, sandy or muddy substrates, and can be encountered from the surface to over 5000 m depth (Baba, 2005). Squat lobsters can be found worldwide (Baba *et al.,* 2008), and many species are known to occur in American waters (Hendrickx and Harvey, 1999; Boschi, 2000; Melo-Filho and Melo, 2001; Fierro Rengifo *et al.,* 2008).

During many decades, our information on species diversity, spatial distribution and ecology of galatheids has been concentrated in North and South American waters (*i.e.* Haig, 1955; Bahamonde, 1964; Pequegnat and Pequegnat, 1971; Mayo, 1972; Retamal, 1981; Hendrickx, 1995; Boschi, 2000; Melo-Filho and Melo, 2001; Hendrickx, 2003; Campos *et al.,* 2005). Regarding the Mesoamerican Province of the Pacific, including Central America, Macpherson *et al.* (2010) mentioned the presence of 28 galatheid species in depths down to 2000 m. Fierro Rengifo *et al.* (2008) indicated 137 species of Galatheidae for the Neotropics, with representatives of *Munida* and *Munidopsis* comprising 91% of the total of these species. Regarding Central America, Wehrtmann and Echeverría-Sáenz (2007) provided information on four galatheids associated with the deepwater fishery. However, our knowledge on squat lobsters from Central America is still scarce and often simply nonexistent.

Concerning Costa Rica, the presence of 12 species of squat lobsters has been reported for the Pacific coast, distributed within the genera *Munida, Munidopsis* and *Pleuroncodes* (Vargas and Wehrtmann, 2009). Since 2003, we had the opportunity to sample monthly deepwater shrimp fishing grounds between 150 and 400 m depth along the Pacific coast of Costa Rica (Wehrtmann and Nielsen-Muñoz, 2009), which provided an excellent opportunity to obtain abundant material of squat lobsters associated with this shrimp fishery (Wehrtmann and Echeverría-Sáenz, 2007). Here we present the results of this long-term study, documenting the species diversity as well as spatial and bathymetric distribution patterns of squat lobsters collected from deepwater areas from Pacific Costa Rica. The results may contribute to a better understanding of the ecology of these ecologically and economically important decapods.

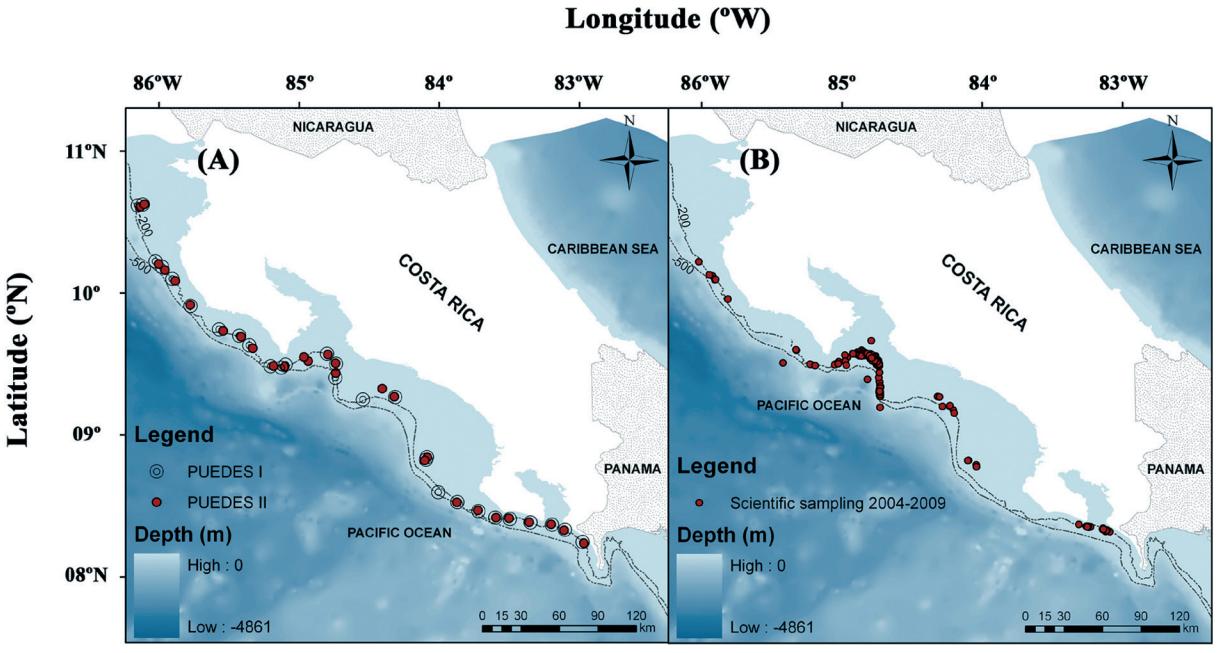

Figure 1. Study site locations (A: campaign PUEDES, 2008 and 2009; B: monthly monitoring program) of the Pacific coast of Costa Rica where specimens of squat lobsters were collected.

Table I. Range and mean of the total and carapace length, sex ratio (1:1), and percentage of ovigerous females in six species of galatheids of the Pacific coast of Costa Rica. N: number of individuals, SD: standard deviation. M: males; F: females.

Species	N	Total length (mm)		Carapace length (mm)		Sex ratio	Ovigerous females
		Range	Mean ± SD	Range	Mean ± SD	(M:F)	(% of all females)
Munida gracilipes	651	3.5-55.0	37.6 ± 5.30	10.0-21.9	15.4 ± 1.91	286:365*	48
M. mexicana	9	7.0-11.0	8.1 ± 2.93	2.9-4.6	3.9 ± 0.64	3:6	66
M. obesa	67	32.2-66.1	48.2 ± 7.67	14.0-29.8	21.2 ± 3.42	31:36	14
M. refulgens	49	8.0-75.0	42.5 ± 15.69	3.4-31.0	18.2 ± 6.59	36:13*	46
Munidopsis hamata	2	38.0-39.8	—	15.0-16.6	—	2:0	0
Pleuroncodes monodon	1600	39.6-83.2	63.5 ± 5.69	16.0-40.2	29.3 ± 2.71	1045:555*	0

*Differs statistically from the expected 1:1 ratio (χ^2, P > 0.05).

Material and Methods

Samples from commercial deepwater shrimp fishery

We analyzed samples taken between 2004 and 2009 with commercial shrimp trawlers operating along the Pacific coast of Costa Rica, equipped with two standard epibenthic nets; each net was 20.5 m long and had a mouth opening of 5.35 x 0.85 m. The mesh size was 4.45 cm, that of the cod-end 3.81 cm. The sampling area (Fig. 1) covered the principal fishing grounds for the two target shrimp species, *Heterocarpus vicarius* Fazon, 1893 (Decapoda, Pandalidae) and *Solenocera agassizii* Faxon, 1893 (Decapoda, Solenoceridae). Moreover, we included material obtained during two cruises (August 2008 and May 2009) in the frame of the project PUEDES ("Programa Universidad Empresa para un Desarrollo Sostenible", http://puedes.csuca.org). These campaigns covered the entire Pacific coast of Costa Rica (Fig. 1), and were carried out simultaneously (one boat covering the southern part of the coast, the second one the northern part) by two commercial shrimp trawlers of The Rainbow Jewels S.A. company (Puntarenas, Costa Rica). The depth range during this campaign was from 150 to 350 m. Representative samples of the collected galatheids were brought to the laboratory of the Unidad de Investigación Pesquera y Acuicultura (UNIP) of the Centro de Investigación en Ciencias Marinas y Limnología (CIMAR), Universidad de Costa Rica (UCR), San José; species were identified according to the descriptions and keys provided by Hendrickx (1995, 2000). As a complementary source of information, we examined the entire collection of Pacific galatheids of the squat lobster species collected below 100 m depth deposited in the Museo de Zoología of the UCR; a total of 95 individuals were analyzed.

Laboratory analyses

In the case of the field samples, after extracting the squat lobsters, each individual was sexed and classified into one of the following categories: male, non-ovigerous female, or ovigerous female. The sex determination was based on the presence of the first and second pairs of pleopods in males and the presence from the second to the fifth pairs of pleopods in females (Baba *et al.,* 2009); when these criteria did not allow a definitive sex determination, the location of the gonopores was revised, too. The following morphometric measurements (± 0.1 mm) were taken: total length (TL: from the posterior edge of the orbital arch to the mid-dorsal posterior region of the telson), and carapace length (CL: from the posterior edge of the orbital arch to the mid-dorsal posterior margin of the carapace).

Sex ratio was estimated as the number of females divided by the number of males. Departures from the expected 1:1 ratio were tested statistically using a chi-square test ($p < 0.05$, Sokal and Rohlf, 1995). However, interpretations of these data were carried out with care as the number of individuals showed marked variations among species, and the test has a low power with species represented by few individuals (Sokal and Rohlf, 1995).

Results

Spatial and bathymetric distribution

We analyzed a total of 2376 individuals obtained from the above-mentioned sampling programs and additional 95 specimens from the material deposited in the Museo de Zoología. These combined collections were comprised of a total of six species: *Munida gracilipes* Faxon, 1893, *M. mexicana* Benedict, 1902, *M. obesa* Faxon,

1893, *M. refulgens* Faxon, 1893, *Munidopsis hamata* Faxon, 1893, and *Pleuroncodes monodon* Stimpson, 1860 (Table I). However, the following two species were encountered exclusively in the material deposited in the Museo de Zoología: *Munida mexicana* and *Munidopsis hamata*. Most

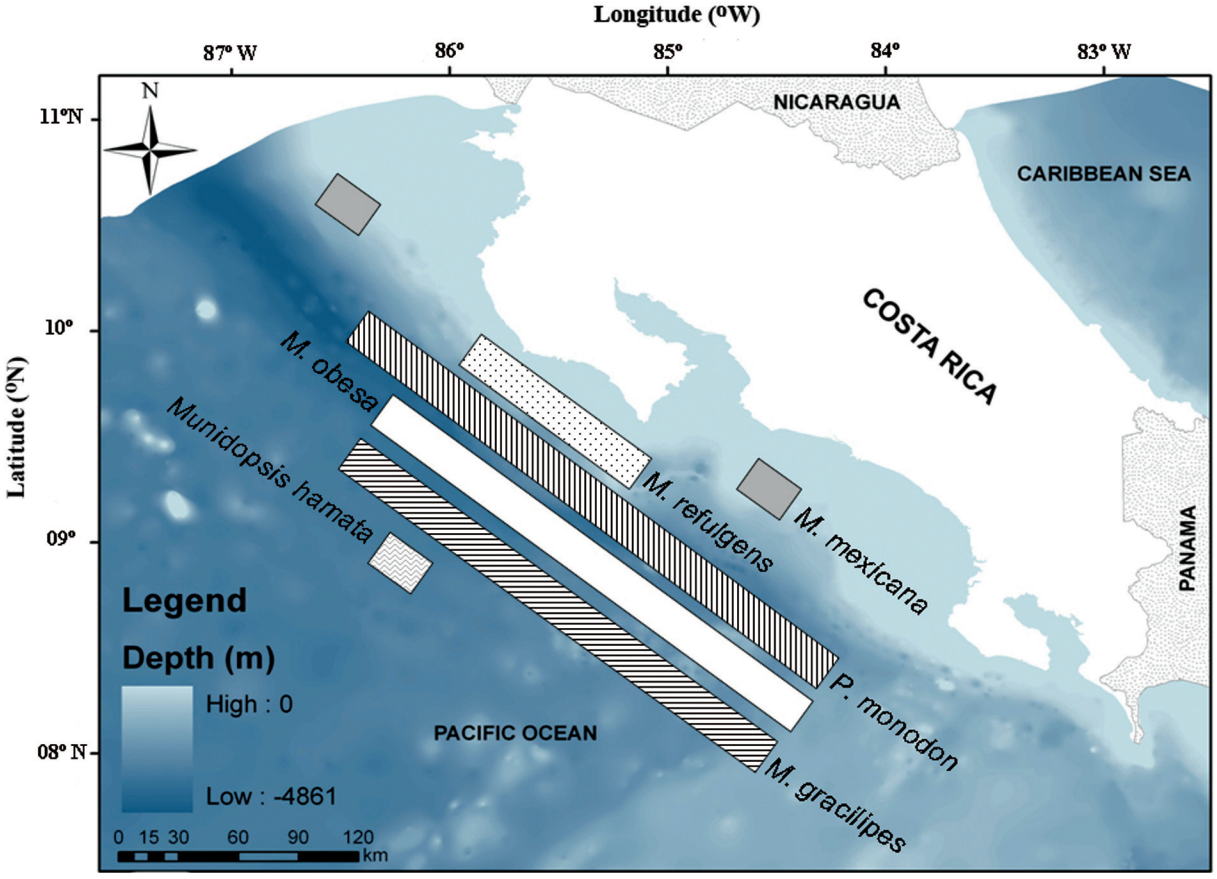

Figure 2. Approximate latitudinal distribution of the deepwater squat lobsters along the Pacific coast of Costa Rica.

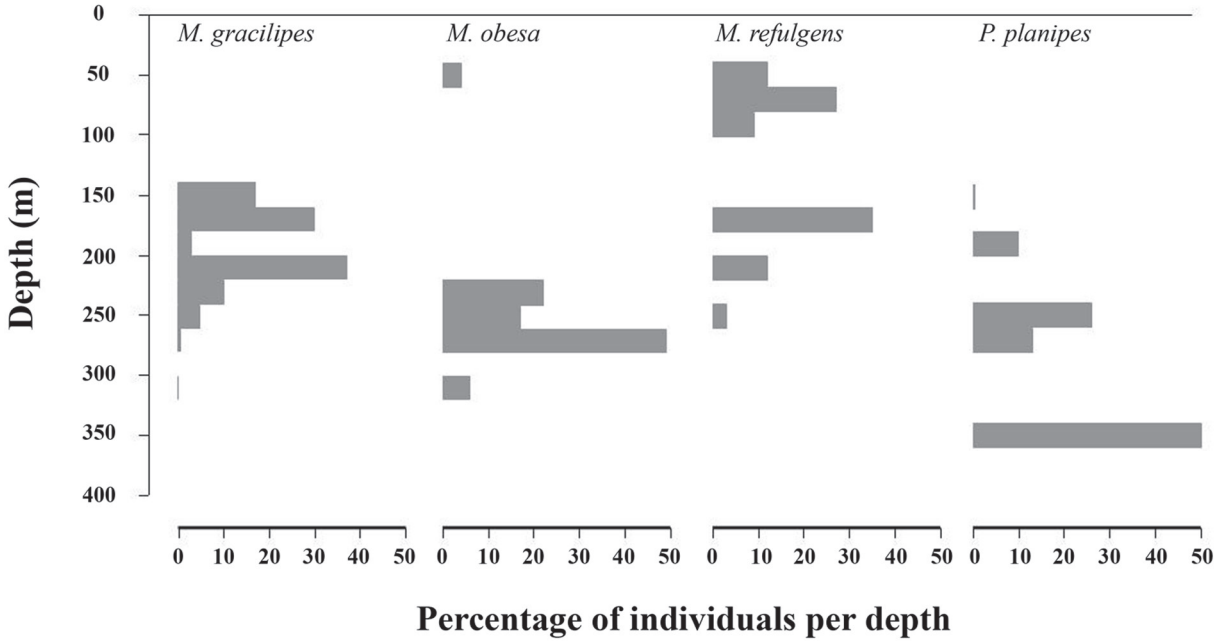

Figure 3. Bathymetric distribution and percentage of occurrence per depth range of the four most common squat lobster species collected during our field campaigns (2004-2009) along the Pacific coast of Costa Rica.

Table II. Summary of galatheid deepwater species so far reported from Pacific Costa Rica. The bathymetric range includes the information obtained during the present study as well as published information, indicated in "Reference". Presence/absence refers to the material examined within the present study (field samples and species deposited in the collection of the Museo de Zoología, Universidad de Costa Rica). The inclusion of species in one of the four depth range categories is based on the maximum depth recorded per species.

Depth range	Species	Bathymetric range (m)		Presence/absence	Reference
		Present study	Literature		
0-400 m	*Munida gracilipes*	140-320	180-280	present	Hendrickx, 2000; Baba, 2005; Vargas and Wehrtmann, 2009
	Munida mexicana	30-97.5	11-198	present	Hendrickx, 2000; Baba, 2005
	Munida obesa	40-320	117-385	present	Wicksten, 1989; Hendrickx, 2000; Baba, 2005; Vargas and Wehrtmann, 2009
	Munida refulgens	40-290	37-205	present	Wicksten, 1989; Hendrickx, 2000; Baba, 2005; Vargas and Wehrtmann, 2009
401-900 m	*Pleuroncodes monodon*	150-350	172-523	present	Faxon, 1893; Baba, 2005; Vargas and Wehrtmann, 2009
901-2000 m	*Munidopsis aspera*	—	104-1431	absent	Baba, 2005; Vargas and Wehrtmann, 2009
	Munidopsis hamata	1190-1281	396-1337	present	Baba, 2005; Vargas and Wehrtmann, 2009
> 2001 m	*Munida perlata*	—	1160-3292	absent	Wicksten, 1989; Hendrickx, 2000; Baba, 2005; Vargas and Wehrtmann, 2009
	Munidopsis albatrossae	—	2850-3680	absent	Baba, 2005; Vargas and Wehrtmann, 2009
	Munidopsis antonii	—	366-4010	absent	Baba, 2005; Vargas and Wehrtmann, 2009
	Munidopsis diomedeae	—	768-3790	absent	Wicksten, 1989; Baba, 2005; Vargas and Wehrtmann, 2009
	Munidopsis nitida	—	2030-2875	absent	Hendrickx, 2000; Baba, 2005;Vargas and Wehrtmann, 2009
	Munidopsis vicina	—	3063-3885	absent	Wicksten, 1989; Hendrickx, 2000; Baba, 2005; Vargas and Wehrtmann, 2009

specimens (n = 1600) referred to *P. monodon,* and all individuals originated from the two PUEDES – campaigns; the analysis of the monthly sampling program regarding this abundant species has not yet finished.

Three species (*M. gracilipes, M. obesa* and *P. monodon*) showed a spatial distribution covering practically the entire Pacific coast of Costa Rica. In contrast, *M. refulgens* was absent along the central-southern and southern Pacific coast of Costa Rica (Fig. 2); one additional record from the Museo de Zoología material indicated offshore Isla del Coco as a collection site. The few individuals of the remaining two species were collected in the central-northern region (*M. hamata;* n = 2) and in the central as well as in the northern part of the Pacific coast (*M. mexicana;* n = 9).

Three species analyzed (*M. mexicana, M. obesa* and *M. refulgens*) were recorded from both deep and shallow waters (30-40 m), while the other three species were collected exclusively in waters deeper than 140 m, reaching a maximum depth of 1281 m (*M. hamata;* Table II). Figure 3 reveals the bathymetric distribution of the four squat lobster species obtained during our field campaigns (2004-2009); *Munida mexicana* and *Munidopsis hamata* were excluded from this analysis due to the few specimens available. *Munida gracilipes* was common between 140 to 220 m, while the majority of individuals from *M. obesa* was collected between 220 and 280 m depth (Fig. 3). In the case of *M. refulgens,* although a large group of individuals was detected around 170 m, the species was generally more abundant in shallower waters (50 to 80 m). In contrast, *P. monodon,* the most frequent and abundant squat lobster species in our material, was especially abundant below 240 m of depth (Fig. 3).

Demographic patterns

Body size varied significantly among the four most common species (*M. gracilipes, M. obesa, M. refulgens,* and *P. monodon:* ANOVA, $p < 0.01$). An analysis *a posteriori* revealed significant differences between CL of all four species (Tukey, $p < 0.01$). The smallest species was *M. mexicana,* the largest one *P. monodon* (Table II). With the exception of *M. obesa,* the sex ratio was significantly different from the usual 1:1 (χ^2, $p < 0.05$) in the remaining three species (Table I). In *M. refulgens* and *P. monodon,* the number of males was significantly higher (< 60% of all individuals examined per species) than that of females (Table I).

The material examined herein contained ovigerous females from all four *Munida* species (Table I); however, only the samples of *M. gracilipes* included a substantial number of egg-bearing females (n = 173). In contrast, we did not retrieve any ovigerous females of *P. monodon* nor of *M. hamata* in the material revised by us (Table I). The smallest females carrying eggs in *M. gracilipes, M mexicana, M. obesa* and *M. refulgens* measured 13.1 mm, 3.6 mm, 16.4 mm, and 4.3 mm CL, respectively.

Discussion

Species diversity

The analyses of the extensive material retrieved from deepwater areas along the Pacific coast of Costa Rica revealed the presence of six squat lobster species. So far, a total of 12 species of the family Galatheidae, representing three genera (*Munida, Munidopsis, Pleuroncodes*) have been reported from Pacific Costa Rica (Vargas and Wehrtmann, 2009). Here we present the first record of *Munida mexicana* for Costa Rica (from the collection of the Museo de Zoología); thus, this species was not included in the compilation prepared by Vargas and Wehrtmann (2009). The distribution of *M. mexicana* ranges from Mexico to Panama and Galapagos (Hendrickx, 2000). Therefore, the presence of this species in Costa Rica corroborates the above-mentioned geographic distribution of this squat lobster species.

Summarizing the available information (our field and collection data plus published information), the Costa Rican deepwater zone of the Pacific harbors 13 species (Table II). However, the examination of material not yet incorporated in the collection of the Museo de Zoología revealed the presence of two additional species, *Pleuroncodes planipes* Stimpson, 1860 and most probably *Munidopsis alvisca* Williams, 1988 (E. Macpherson, *pers. obs.*). Therefore, it can be assumed that the deepwater fauna of Pacific Costa Rica is comprised at least by 15 galatheid species. Macpherson *et al.* (2010) mentioned a total of 28 deep-sea squat lobster species (< 2000 m) for the Mesoamerican Province (Mexico – Central America). Thus, species diversity of galatheids in Costa Rican deepwater zones is surprisingly high, representing 54% of all species so far reported to occur in the Mesoamerican Province.

The identification of *P. monodon* needs further attention. Material collected during our field campaigns did not match exactly the original description of *P. monodon,* but neither that of *P. planipes* (see Hendrickx, 1995). In fact, the specimens examined showed a certain mixture of morphological characteristics of both species (E. Macpherson, *pers. obs.*). Preliminary molecular-genetic analyses of a few specimens from our collected material revealed that we are dealing with *P. monodon* (E. Macpherson, unpubl. data). This finding corroborates the identification of this species by Bianchi (1991), who mentioned *P. monodon* as an abundant species off the coast of Nicaragua. Moreover, Longhurst and Seibert (1971) indicated that they obtained material of *P. monodon* from El Salvador and Costa Rica. It is speculated that Central America is a transition zone for these two species (see Hendrickx and Harvey, 1999), which need to be substantiated by future field and laboratory analyses.

Bathymetric and spatial distribution

For most galatheid species analyzed by us, the depth range encountered coincided with the values published in the literature (Table II). However, there are two exceptions: our data expand the known bathymetric distribution of *M. gracilipes,* since we recorded the species in both shallower and deeper water than previously reported. In accordance with these findings, Wehrtmann and Echeverría-Sáenz (2007) mentioned *M. gracilipes* to be common between 220 and 300 m. In the case of *M. obesa,* the minimum depth reported in literature was 117 m; however, we recorded the species from substantially shallower depths (Table II). More collections from shallow waters are needed to confirm the presence of this species in depths less than 100 m.

From the 13 squat lobster species currently recorded from Pacific Costa Rica, almost half of all species (46%) occur in depths > 2000 m (Table II). The predominance of species in greater depths is not surprising, considering that 7 of the 13 galatheid species from Pacific Costa Rica belong to the genus *Munidopsis,* and species of this genus typically inhabit waters deeper than 900 m, including abyssal plains (Macpherson, 2007; Macpherson *et al.,* 2010).

The spatial distribution of the squat lobsters collected during the present study indicates that

three species (*M. gracilipes, M. obesa* and *P. monodon*) can be found along most parts of the Pacific coast of Costa Rica (Fig. 2). In contrast, the occurrence of *Munida refulgens* is restricted to the central-northern part of the coast (Fig. 2). This result may be related to the fact that *M. refulgens* is a common species in shallow water, and our sampling campaigns were orientated toward deeper water. However, such an argument does not explain the presence of this squat lobster species in the central-northern zone, where samples were taken from depths well below 100 m. Therefore, additional collections in the southern part of the Pacific coast of Costa Rica are recommended to obtain a more detailed picture on the spatial and bathymetric distribution of *M. refulgens* in Costa Rica. Considering the few specimens examined of both *M. mexicana* and *M. hamata,* it seems premature to discuss their spatial distribution along Pacific Costa Rica.

Demographic patterns

The mean maximum body size of deepwater squat lobsters (< 2000 m depth) from the Eastern Pacific is highest in the northern region (Canada, Alaska), diminishes subsequently toward lower latitudes, reaching its lowest value in Colombia, and then increases steadily toward the southern provinces (Macpherson *et al.,* 2010). According to these authors, the mean maximum body size for squat lobsters in the Mesoamerican Province is 14.7 mm CL. Our corresponding data indicate a substantially higher mean value (24.0 mm CL) for the six species examined by us (Table I). Even if we exclude the largest of our species (*P. monodon*), the average mean value is 20.8 mm CL, which is still considerably higher than the value presented by Macpherson *et al.* (2010). However, this comparison includes only six of the 13 species from Pacific Costa Rica (Table I). Additional material of the other species is necessary to complete a data set concerning the body size of deepwater galatheids from Costa Rica.

The material examined by us revealed the presence of ovigerous females in four squat lobster species, while no egg-bearing females were encountered in *M. hamata* and *P. monodon.* The absence of reproducing females in *P. monodon* was surprising, especially when considering the large number of individuals collected during the two PUEDES-campaigns. According to Palma and Arana (1997), reproduction in *P. monodon* from Chile occurs once a year, principally between May and October, and these months coincide temporally with the two oceanographic campaigns in the present study (May and August). It is assumed that latitudinal differences between reproductive timing of both populations (Chile and Costa Rica) may explain the complete absence of ovigerous females in our material. Such intraspecific variation of life history traits along a latitudinal gradient has been documented for a variety of other decapod species (*e.g.,* Jones and Simons, 1983; Henmi, 1993; Lardies and Castilla, 2001; Defeo and Cardoso, 2002; Castilho *et al.,* 2007).

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