

Population demography and spatial distribution of the mantis shrimp *Squilla biformis* (Stomatopoda, Squillidae) from Pacific Costa Rica

Patricio Hernáez^{1,2,3,*}, Tayler McLellan Clarke¹, Catalina Benavides-Varela^{1,4},
Fresia Villalobos-Rojas¹, Jaime Nívia-Ruiz¹, Ingo S. Wehrtmann^{1,4}

¹Unit for Fishery Research and Aquaculture (UNIP) of the Research Center for Marine Science and Limnology (CIMAR), University of Costa Rica, Costa Rica

²Ocean Museum (Museo del Mar), University Arturo Prat, Casilla 121 Iquique, Chile

³Laboratory of Bioecology and Crustacean Systematics, Department of Biology, FFCLRP, University of Sao Paulo, Posgraduate Program Av. Bandeirantes 3900, 14040-901, Ribeirão Preto, São Paulo, Brazil

⁴School of Biology, University of Costa Rica, 2060 San José, Costa Rica

ABSTRACT: The mantis shrimp *Squilla biformis* is the most conspicuous and abundant stomatopod captured during benthic trawling operations off the Pacific coast of Costa Rica. Due to its abundance, this species is considered a potential fisheries resource for the region. Nevertheless, its life history is practically unknown. The present study describes the population demography, spatial distribution and behaviour of *S. biformis* from Pacific Costa Rica. The population was principally composed of individuals between 20 and 32 mm carapace length (CL), forming 2 age groups. Individuals of 35 to 45 mm CL and >45 mm CL were poorly represented. We assume that larger individuals are more frequent at greater depths (probably on the continental slope), thus out of the reach of the fishing vessels used in our study. Males outnumbered females, as observed in other stomatopods. Visual evidence of their behaviour demonstrates that the adults in this species possess a benthic and pelagic life style. Largest numbers of individuals (50% of the total) were found between 240 to 260 m, the same bathymetric range that was historically occupied by commercial shrimps. This shift may be related to intense fishing activities. We observed a synchronized moulting of females and males during less luminous (third and fourth) lunar phases. The evolutionary development of a group moulting system could confer advantages to *S. biformis* in comparison to other stomatopods whose moulting process is individual and asynchronous.

KEY WORDS: Population biology · Moulting cycle · Behaviour · Central America · Shrimp fishery

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INTRODUCTION

The order Stomatopoda is comprised of the so-called mantis shrimps, which occupy many marine habitats in shallow and deep waters. They are divided into 2 groups based on the morphology and function of their raptorial appendage (Caldwell & Dingle 1976, Ah Yong 2001): 'smashers' live in pre-existing cavities within hard substrates that are limited in abundance. In contrast, 'spearers' live in self-excavated burrows made of sand or mud that are not limited in abundance. 'Spear-

ers' kill and feed on soft-bodied prey and are considered to be less aggressive than 'smashers' (Caldwell & Dingle 1975). They have been less studied because of their deeper, murkier habitats and their non-agonistic behaviour (see review in Wortham-Neal 2002).

'Spearers' are fished commercially in many parts of the world, principally in the Mediterranean (e.g. *Squilla mantis* Linnaeus, 1758: Abelló & Martin 1993), Japan (*Oratosquilla oratoria* de Haan, 1844: Kubo et al. 1958), India (*O. nepa* Latreille, 1828: James & Thirumilu 1993) and Australia (*O. stephensoni* Manning,

1978; Dell & Sumpton 1999). In contrast to the above-mentioned countries, and despite their abundance on the continental shelf of many countries of the region (see Hendrickx & Salgado-Barragán 1994, Hendrickx 1995, Wehrtmann & Echeverría-Sáenz 2007), stomatopods from the Pacific coast of America are completely neglected as a local fishery resource (Hendrickx & Salgado-Barragán 1989),

With 8 species, *Squilla* is one of the most specious stomatopod genera off the Pacific coast of America (Hendrickx 1995). During the last 3 decades, *Squilla* and other stomatopods have been studied intensively, especially off the west coast of Mexico (ecology and population demography: Hendrickx & Salgado-Barragán 1989, Hendrickx 1995, Hendrickx & Sánchez-Vargas 2005; spatial distribution: Hendrickx 1984, Hendrickx & Salgado-Barragán 1994, Hendrickx 1995). In contrast, our knowledge regarding the ecology of *Squilla* off Central America is far from complete.

The available information on representatives of this group off Central America focuses on taxonomy (Manning 1972, Manning & Reaka 1979), geographic distribution (Schmitt 1940, Reaka & Manning 1980, Dittel 1991, Vargas & Cortés 1997), ecology (Schmitt 1940, Reaka & Manning 1980, 1981), and population biology (Dittel 1991). In addition, a recent study on the crustacean fauna associated with the deep-water shrimp fishery provides general annotations on the abundance of stomatopods off the Pacific coast of Costa Rica (Wehrtmann & Echeverría-Sáenz 2007); these authors refer to the mantis shrimp *Squilla biformis* Bigelow, 1891 as the most common by-catch species. However, published data on population demography and spatial distribution of *S. biformis* or any other of the 8 species of *Squilla* reported for the American Central Pacific (Hendrickx 1995) are not available.

Squilla biformis occurs along the Pacific coast from the Gulf of California, Mexico to Huacho, Peru (Chirichigno et al. 1982, Hendrickx & Salgado-Barragán 1989, Hendrickx & Salgado-Barragán 1991). The species inhabits muddy and sandy bottoms in the meso-littoral zone at depths between 25 and 518 m (Hendrickx & Sánchez-Vargas 2005); however, *S. biformis* in Central America can be found mainly from 200 to 300 m (Wehrtmann & Echeverría-Sáenz 2007). In order to understand the prominent role of this stomatopod in deep-water systems and its importance as by-catch in the commercial shrimp fishery along the Pacific coast of Costa Rica (Wehrtmann & Nielsen-Muñoz 2009), it is necessary to obtain adequate information about its population demography. Additionally, we present data on spatial distribution, the relationship between the moulting cycle of *S. biformis* and lunar phases, and video observations of the behaviour of this species.

Such information may provide valuable insights into the ecology of this mantis shrimp and its role in the multispecies deep-water fishery along the Pacific coast of Central America.

MATERIALS AND METHODS

Stomatopod sampling. Fieldwork was conducted along the Pacific coast of Costa Rica. Population demography was analyzed by collecting monthly samples (September 2007 to September 2008) of mantis shrimps, mainly from the central zone of the Pacific Costa Rican coast (Fig. 1A). Spatial distribution and abundance were analyzed by examining the material collected during 2 research cruises in August 2008 (rainy season) and May 2009 (dry season) along the entire Pacific coast (Fig. 1B; Table 1). All samples were collected from commercial shrimp trawlers (22.5 m in length, 270 hp) equipped with 2 standard epibenthic nets (20.5 m long; mouth opening of 5.35×0.85 m; mesh size 4.5 cm; cod-end mesh size 3.0 cm); sampling duration was 20 min at a speed of 2.0 knots (~ 3.7 km h⁻¹). Initial and final positions were recorded with a GPS, and fishing depth by an echo-sounder. The ships 'Onuva' and 'Sultana', owned by The Rainbow Jewels, were equipped especially for scientific purposes as part of a joint project with this company undertaken by the University of Costa Rica since 2003. Sampling depth varied from 140 to 350 m, covering the depth range of *Squilla biformis* previously reported by Wehrtmann & Echeverría-Sáenz (2007). Bottom temperature and salinity were recorded with a CTD-SBE25. Stomatopods were separated from the catch, and a sample was stored in ice water and subsequently frozen in the laboratory of the Unit for Fishery Research and Aquaculture (UNIP) of the Research Center for Marine Science and Limnology (CIMAR), University of Costa Rica, Costa Rica.

Population demography. Specimens were sexed according to the criteria described in the literature (e.g. Bigelow 1894, Griffiths & Blaine 1988, Dittel 1991, Wortham-Neal 2002), and measured (CL, carapace length: from the anterior to the posterior margins of the carapace without rostrum; ± 0.1 mm).

The CL was considered as an independent variable; adjustment of each regression was analyzed by least squares method (Sokal & Rohlf 1995). This procedure was applied to males and females. Specimens of each category were grouped into 1 mm size classes; subsequently data were plotted as monthly length-frequency histograms to analyze the shrimp population structure. The normal component of each sample was separated using the Battacharya method included in FISAT software (Gayanilo et al. 1996). This analysis,

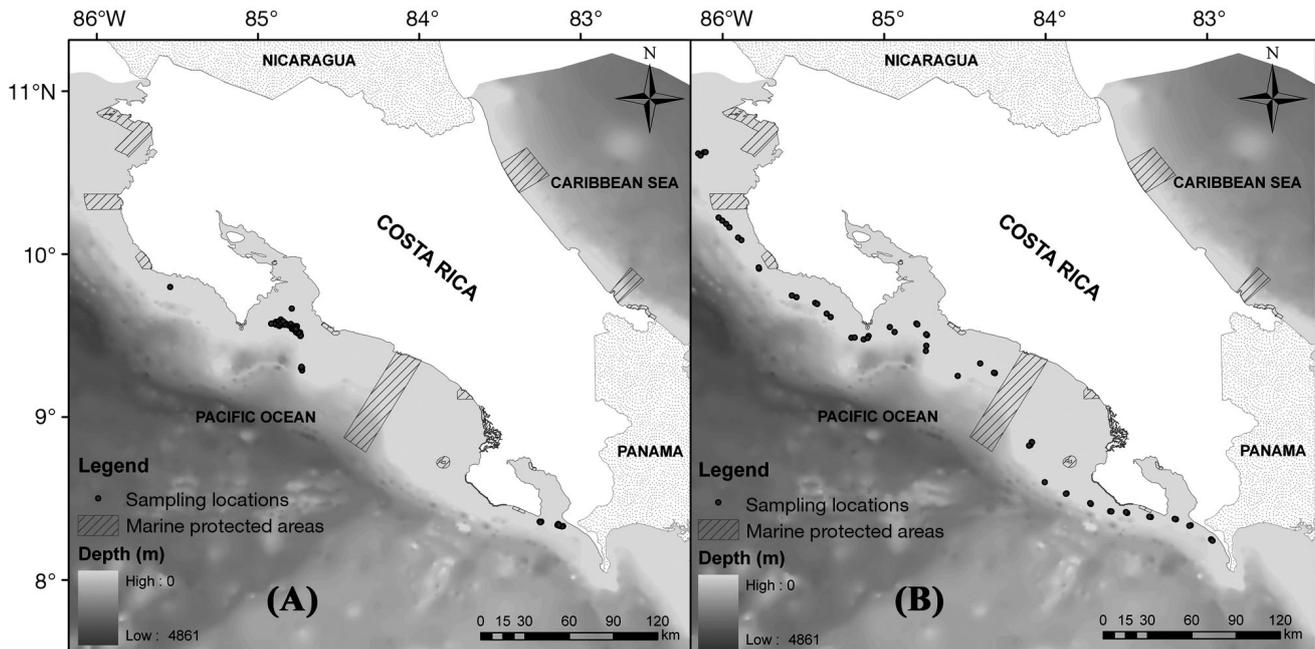


Fig. 1. Sampling sites along the Pacific coast of Costa Rica. *Squilla biformis* specimens were collected in the frame of (A) a monthly sampling programme (September 2007 to September 2008) and (B) 2 research cruises (August 2008, May 2009)

based on the identification of each cohort's mean, allowed separation of each modal component (see Gayanilo et al. 1996).

Knowledge of stomatopod larvae, both taxonomically and ecologically, is limited. Of the ~350 known stomatopod species, only ~10% can be identified at their larval stages (Diaz & Manning 1998). The information reported in some species of the *Squilla* genus indicates some kind of planktonic larval development (Morgan & Provenzano 1979, Diaz 1998). Assuming that *S. biformis* has a larval planktonic development like other congeners (Morgan & Provenzano 1979, Diaz 1998) and is benthic during juvenile and adult phases, we describe recruitment as the proportion of small individuals (≤ 21 mm CL) using the 5th percentile method, a measure that is less prone to bias than that of the single smallest individual (Rivadeneira et al. 2010). This value was obtained from overall size frequency distributions. Monthly variations in sex ratios were analyzed applying χ^2 tests (1:1; $p < 0.05$, Sokal & Rohlf 1995).

The percentage of moulting males and females during each month was calculated as the ratio 'number of soft individuals:total number of individuals'. Moulting peaks of freshly moulted (soft) individuals were considered to be those months where $>40\%$ of the population was undergoing ecdysis. A correlation test (Zar 1996) was applied to examine the possible synchronicity between male and female moulting patterns. The lunar phases (i.e. full moon, first quarter,

new moon, and third quarter) were determined for each sample. The percentage of moulting individuals during each month was compared to the lunar phase in which they were collected, and also to temperature and depth.

Spatial distribution, abundance and behaviour. The spatial distribution of *Squilla biformis* was estimated through an explicit geographic correlation between the data obtained from the sampling sites. For each sampling location we estimated the mean, minimum and maximum body sizes (CL) according to sex, as well as the sex ratio. The minimum and maximum sizes were also estimated using the percentile method (5th and the 95th). The sex ratio (M:F) was determined and compared to a theoretical 1:1 ratio using the χ^2 test (Sokal & Rohlf 1995). A Spearman correlation test was used to analyze the relationship between mantis shrimp CL and sex, and the spatial distribution across the study area (Zar 1996).

In order to calculate the biomass, we used the swept area method (see Alverson & Pereyra 1969). Using abundance (number of individuals) as a measure of biomass (B), this is assumed to be a linear function of the population density (D , measured in weight or number of individuals per area unit, also known as 'catch per unit area' or CPUA) over the population's global distribution area (A). It is assumed that the coefficient of proportionality is equal to the catchability coefficient (q , Ricker 1975, see also Ralston & Tagami 1992, Roa & Bahamonde 1993 for specific applications). This relationship is represented as:

$$B \equiv A \times D \quad (1)$$

$$D \equiv \frac{C}{AB} \quad (2)$$

$$AB \equiv APA \times DR \quad (3)$$

where C represents the catch registered during each haul, the swept area (AB) is the product of the net's wing span (APA) and the covered distance (DR, in geographic coordinates). The covered distance (DR) of the area swept by the trawl on each haul was calculated using initial and final positions recorded by the GPS and Pythagoras' theorem corrected for latitudinal position (Sparre et al. 1989):

$$DR = 60 \times \sqrt{\left\{ (X_i - X_j)^2 + (Y_i - Y_j)^2 \times \cos \left[\frac{\left(\frac{X_i + X_j}{2} \right) \times \pi}{180} \right] \right\}^2} \quad (4)$$

where X_i and X_j are the initial and final latitudes of the tow; Y_i and Y_j correspond to the tow's initial and final longitudes. In the absence of specific information, it

was assumed that $q = 1$. This value means that all individuals within the path swept by the trawl (and no others) were caught by the trawl. This assumption can be supported by the fact that no herding effect, which causes the capture of individuals from outside the swept area ($q > 1$), has been described for benthic crustaceans (Roa et al. 1995).

In order to document the behaviour of *Squilla biformis* in its habitat, we analyzed video tapes from 12 deployments off the central zone of the Pacific Costa Rican coast taken with a submarine belonging to DeepSee/Undersea Hunter Group (<http://www.underseahunter.com/uh.htm>). These videos were recorded off Herradura (09° 15' 13" N, 84° 26' 57" W) at between 300 and 320 m depth. All deployments were carried out between 08:00 and 12:00 h, and each tape recorded observations lasting ~10 min. Each tape was viewed twice by one of us (P.H.) and 2 behaviour categories were used: (1) 'stationary' (shrimp standing relatively still) and (2) 'locomotory' (shrimp moving), each further broken into the following subcategories: (1a) resting on the sediment or (1b) inside the burrows; (2a) swimming, (2b) hunting, and (2c) walking.

Table 1. *Squilla biformis*. Latitudinal position of sampling sites, sampling depth and catch per unit area (CPUA, kg ha⁻¹) during 2 cruises along the Pacific coast of Costa Rica in August 2008 and May 2009. * = biomass peak in each period

— August 2008 (Rainy season) —			— May 2009 (Dry season) —		
Latitude N	Depth (m)	CPUA	Latitude N	Depth (m)	CPUA
8°13'30"	347	4.63	8°13'02"	293	202.45
8°18'46"	256	11.68	8°18'34"	247	6188.27*
8°20'60"	155	0	8°21'11"	155	11.80
8°21'58"	256	820.79	8°22'04"	238	701.50
8°23'31"	347	69.22	8°23'52"	302	157.54
8°24'11"	256	36.24	8°24'08"	238	494.93
8°27'00"	155	11.54	8°27'17"	146	0.44
8°30'54"	256	6.83	8°30'49"	247	0
8°35'07"	347	6.06	8°48'35"	256	3690.60
8°48'51"	256	0.30	8°49'50"	183	287.47
8°49'58"	183	104.04	9°15'38"	260	18.69
9°14'29"	155	2.97	9°19'05"	165	413.70
9°15'26"	274	83.52	9°25'43"	329	0
9°23'47"	347	1200.35	9°28'39"	219	31.78
9°28'11"	256	57.31	9°28'52"	347	5785.89
9°28'50"	347	3235.99*	9°29'55"	256	672.15
9°29'39"	256	15.89	9°30'50"	347	80.34
9°33'56"	155	0	9°32'41"	247	251.52
9°37'45"	165	0	9°33'35"	161	205.31
9°41'42"	256	92.94	9°36'27"	146	1.06
9°44'30"	247	43.19	9°41'20"	247	12.59
9°54'25"	165	36.48	9°43'50"	219	1.78
10°05'56"	256	2465.24	9°54'53"	146	2.17
10°10'60"	183	221.14	10°04'60"	247	90.05
10°13'21"	256	1761.98	10°09'40"	192	11.04
10°36'58"	183	133.81	10°12'11"	247	15.13
10°37'25"	155	5.81	10°36'14"	146	283.57
			10°37'29"	146	1473.21

RESULTS

Population demography

A total of 1863 individuals were analyzed in monthly samples (September 2007 to September 2008) of which 56.8% were males and 43.2% females. Males were statistically (t -test, $p < 0.01$) larger than females (27.4 ± 6.30 mm CL and 25.0 ± 5.51 mm CL, respectively). The majority of individuals (~80%) were in the range of 22.0 to 29.0 mm CL. We detected large specimens (between 47 and 61 mm CL; ~4% of the total) in a sample collected in November 2007 in the northern zone of the Pacific Costa Rican coast (9° 52' N, 85° 38' W) at 292 m depth (Fig. 2). The cohort analysis confirmed the general presence of 2 cohorts throughout the year, with the exception of November and October 2007 where 5 and 3 cohorts were found, respectively, and February and March where only 1 cohort was found (Fig. 2).

The monthly mean body size fluctuated between 22.5 mm CL (September 2008) and 29.9 mm (March 2008). Monthly evolution of body sizes was significantly correlated to the percent-

age of recruited individuals each month (Spearman, $R = -0.62$, $p < 0.05$) (Fig. 3). The monthly entry of small individuals (≤ 21 mm CL) into the benthic population was generally below 6% throughout the year; the only exception was September 2008, when the percentage of recruits was 32% (26 recruits) (Fig. 3). During almost half of the study period, the sex ratio differed significantly from 1:1 (Fig. 2). With the exception of September 2007 and 2008, and February 2008, males were sig-

nificantly more numerous than females (Fig. 2). The bottom temperature varied between 11.7°C (September 2007) and 13.9°C (July 2008) with no statistically significant differences among months (ANOVA, $p < 0.05$). The same pattern was observed for salinity, which was relatively stable during the study period. Temperature and salinity during the dry season were slightly lower (12.81°C, 34.84 psu) than during the wet season (13.05°C, 34.85 psu).

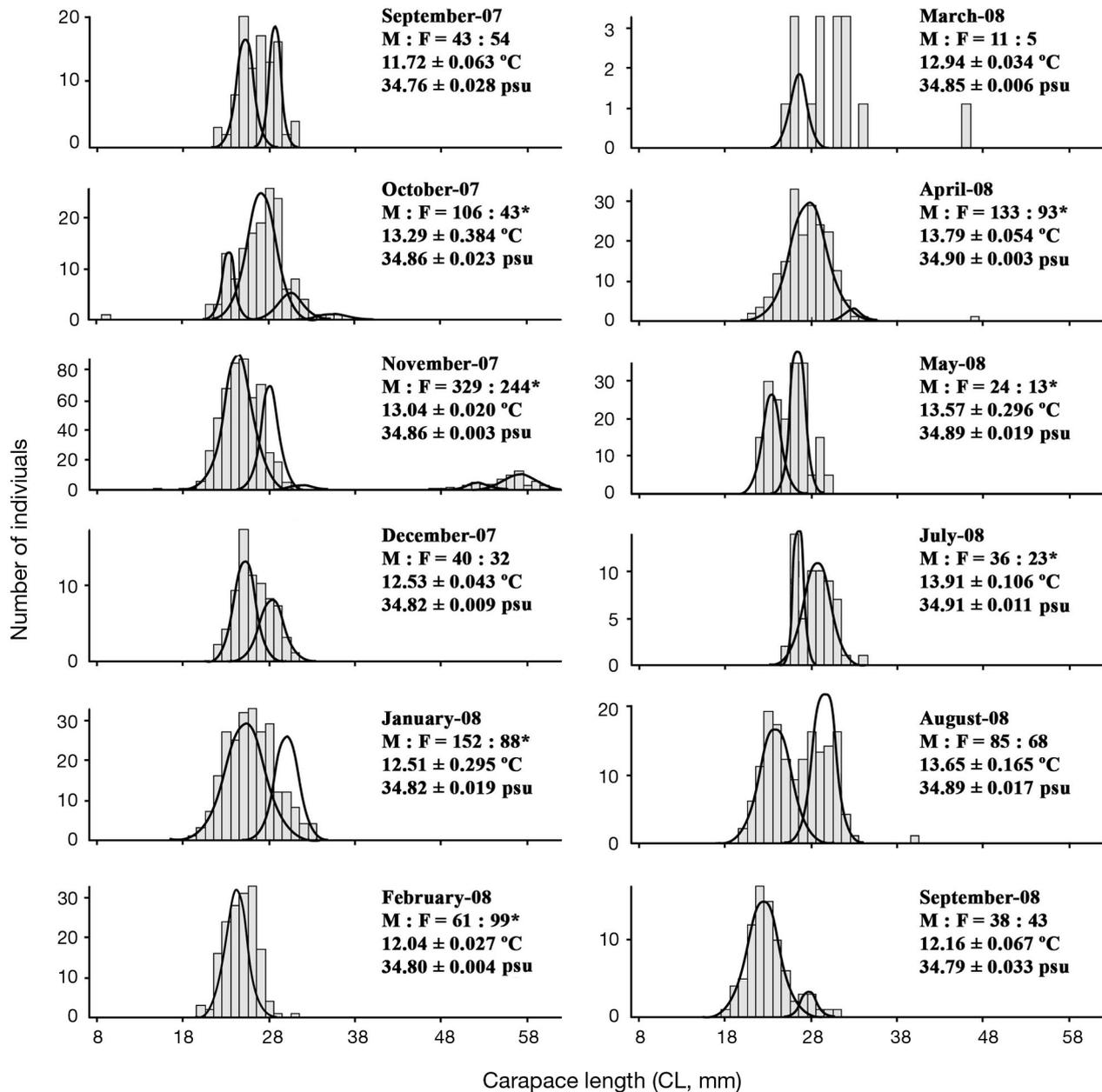


Fig. 2. *Squilla biformis*. Monthly (September 2007 to September 2008) size frequency distribution from Pacific Costa Rica. Monthly cohorts are represented by normal distribution curves. The legend shows the sex ratio (M:F), mean bottom water temperature (°C), and mean salinity (psu) for each month. * = ratio significantly different ($p < 0.05$; χ^2 test) from 1:1. No sample was taken in June 2008

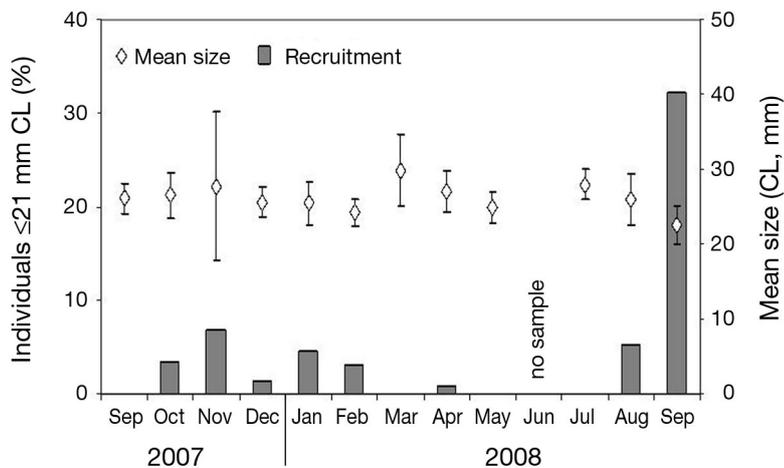


Fig. 3. *Squilla biformis*. Size distribution (mean \pm SD) and percentage of individuals ≤ 21 mm CL (recruiting individuals; $n = 97$) from the Pacific coast of Costa Rica during the study period (September 2007–September 2008)

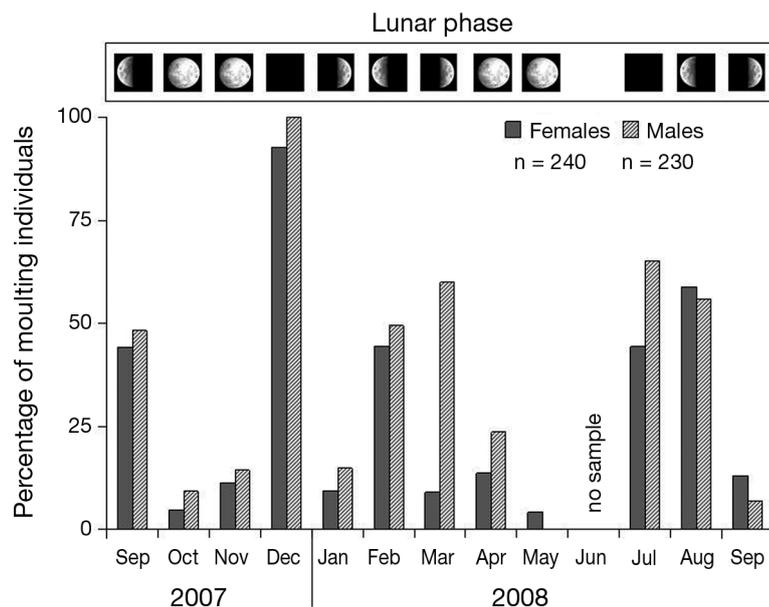


Fig. 4. *Squilla biformis*. Monthly (September 2007–September 2008) percentage of freshly moulted (soft) individuals found in samples collected along the Pacific coast of Costa Rica, with the corresponding lunar phases

Moulting of females and males showed a synchronous pattern with 5 synchronized moulting peaks during the sampling period: in September and December the mean body sizes were 26.0 ± 0.36 and 25.6 ± 0.29 mm CL, while in February this value was 24.4 ± 0.28 mm CL and in July and August 2008 the mean body sizes were 27.8 ± 0.43 and 26.4 ± 0.26 mm CL; a further peak in March 2008 (26.5 ± 0.95) was constituted exclusively by males (Fig. 4). A statistical analysis showed similar mean sizes (CL) of individuals that

moulted in December, September and August (ANOVA, $p > 0.05$). On the other hand, there was no statistically significant correlation (Pearson, $p > 0.05$) between the percentage of recently-moulted individuals and temperature or salinity. However, except in March 2008, we observed a strong correlation between the moulting peaks of *Squilla biformis* and the third and fourth lunar phases (Fig. 4).

Spatial distribution, abundance and behaviour

A total of 1778 individuals (890 males, 888 females) was collected during 2 research cruises (August 2008: $n = 616$ ind., May 2009: $n = 1162$ ind.). *Squilla biformis* was present in 87% of all trawls ($n = 55$) and the spatial aggregation pattern revealed a continuous distribution (Fig. 5). Vertical distribution ranged from 146 to 347 m depth, and the largest numbers of individuals were found between 240 to 260 m (50%) and from 340 to 360 m depth (14%) (Fig. 6). The size of individuals collected in August (2008) and May (2009) varied between 16.4 and 43.3 mm CL. The mean body size (CL) tended to decrease significantly with depth (August 2008: $R = -0.56$, $p < 0.05$, $n = 11$; May 2009: $R = -0.68$, $p < 0.05$, $n = 11$) (Fig. 7).

The mean body size (CL) per sampling station was not correlated with latitude (Fig. 7). However, when using all individual measurements of all sampling locations, body size decreased significantly with increasing latitude (Spearman, females: $R = -0.56$, $p < 0.05$, $n = 318$; males: $R = -0.26$, $p < 0.05$, $n = 298$). The sex ratio remained balanced (1:1) in half of all sampled stations (χ^2 test, $p > 0.05$) and did not reveal a latitudinal trend. However, at some stations, males significantly outnumbered females and vice versa. Although it was possible to find unbalanced sex ratios in all depths (χ^2 test, $p < 0.05$), the overall sex ratio was not related with depth.

In several sampling sites, CUPA reached >1000 kg ha^{-1} , with maximum values recorded in the central (August 2008) and southern regions (May 2009) of the study area (Table 1). Total biomass was higher in the dry season in May 2009 than in the rainy season in August 2008.

During August 2008, a total of 10 428 kg was obtained, while in May 2009 a total of 21 054 kg was captured.

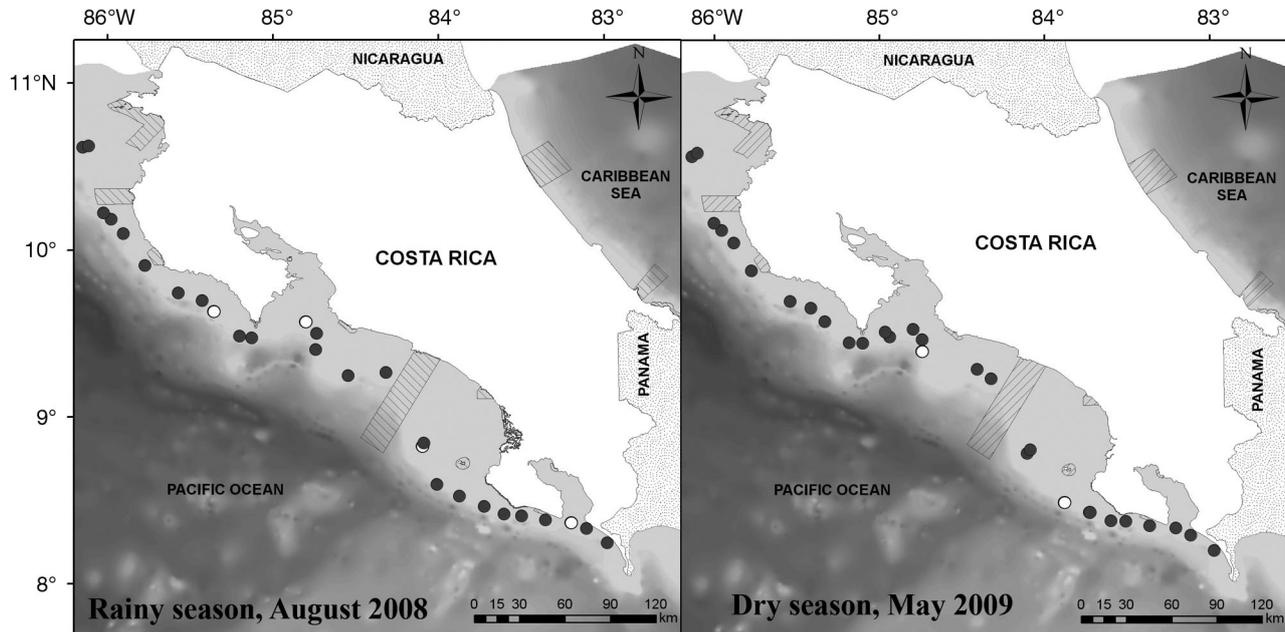


Fig. 5. *Squilla biformis*. Presence (●) and absence (○) during cruises along the Pacific coast of Costa Rica in August 2008 and May 2009

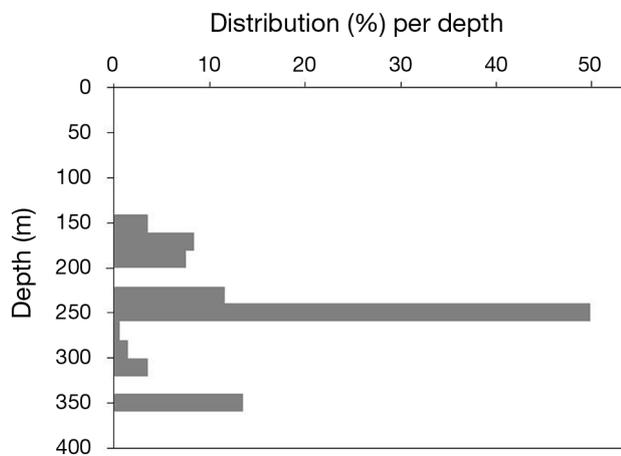


Fig. 6. *Squilla biformis*. Depth distribution of specimens collected during August 2008 and May 2009 along the Pacific coast of Costa Rica, showing presence (%) of the individuals ($n = 1778$) per depth. Samples were obtained exclusively between 140 and 350 m

Likewise, the maximum density value registered during the rainy season (3235 kg ha^{-1}) was considerably lower than the maximum density observed during the dry season (6188 kg ha^{-1}). Generally the C_{PUA} was higher in samples taken during the cruise in May 2009 (Table 1).

The video tapes revealed that *Squilla biformis* occurred on the bottom as well as between 10 and 15 m above the sea bed. The specimens displayed diverse behaviours (Fig. 8). Many individuals were observed resting or walking on the sediment (benthic lifestyle),

but a similar proportion was observed swimming in the water column (pelagic lifestyle). The most commonly observed behaviour was resting on the sediment, followed by swimming (Fig. 9).

DISCUSSION

Population demography, spatial distribution and behaviour of *Squilla biformis*

Information on stomatopods from the Central American Pacific is scarce. Most of our knowledge refers to the results published by Dittel (1991), who partially analyzed the population demography of 4 species of shallow water stomatopods inhabiting the Gulf of Nicoya, Costa Rica.

In general, the *Squilla biformis* 35 to 45 mm CL size class was practically absent during our study period, corresponding to 0.1 and 0.6% of the individuals collected during the monthly sampling program and the 2 scientific cruises, respectively. A similar situation occurred with individuals >45 mm CL (3.5%), which were only found in the monthly catches. According to Hendrickx (1995), *Squilla biformis* is frequently found at the limit between the continental shelf and slope. Accordingly, we assume that larger individuals are more frequent at greater depths (probably on the continental slope), thus out of the reach of the fishing vessels used in our study. Another possible explanation for the scarcity of larger individuals in our bottom trawls is

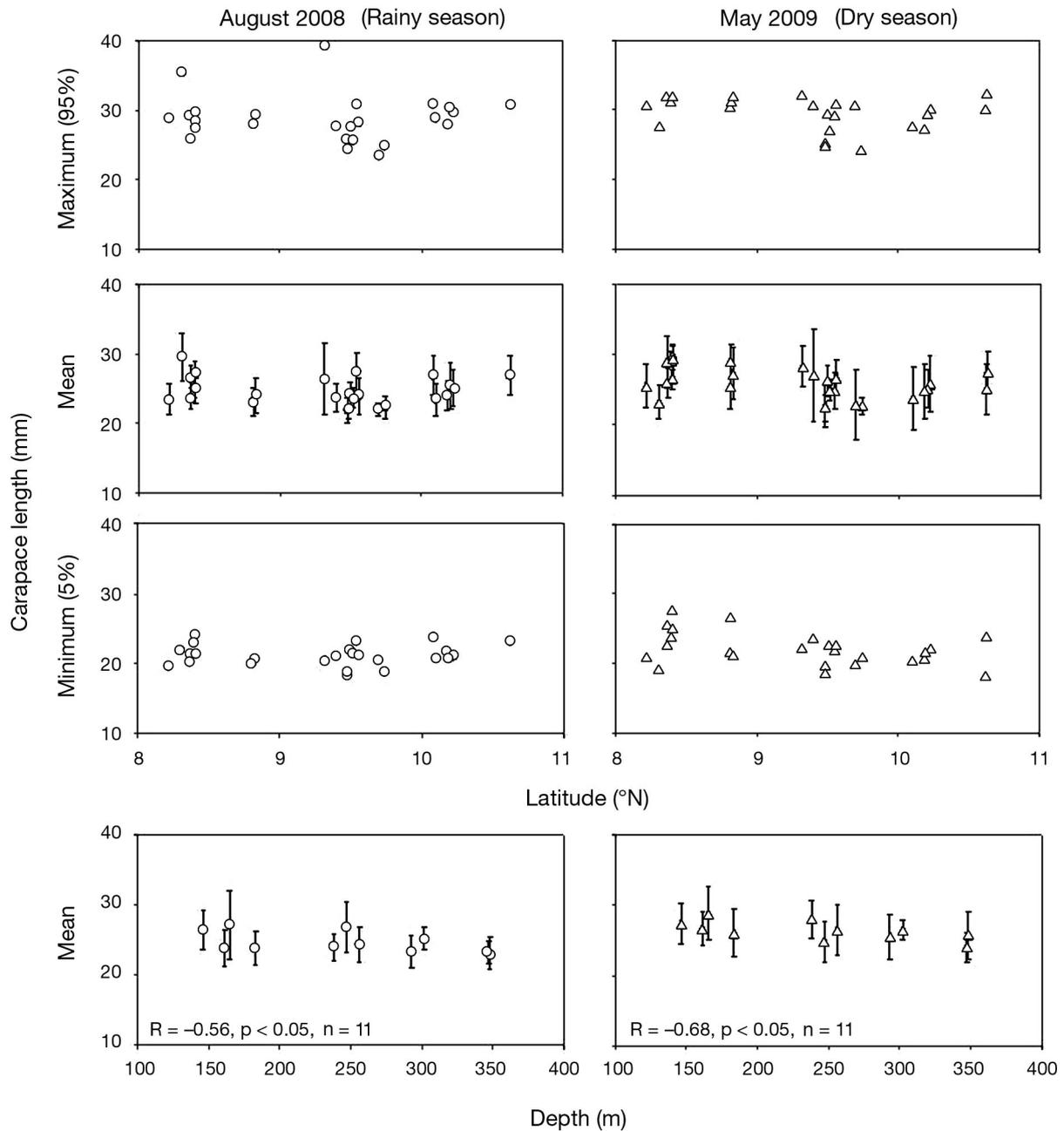


Fig. 7. *Squilla biformis*. Size (CL) of specimens in samples collected in August 2008 and May 2009 along the Pacific coast of Costa Rica, according to latitude and depth. Error bars: \pm SD

that these specimens may be common in the water column; however, we cannot substantiate this assumption, because the video images examined by us did not allow us to measure the size of observed individuals.

Some surveys conducted off the Mexican coast (Hendrickx 1984, Hendrickx & Salgado-Barragán 1994, Hendrickx & Sánchez-Vargas 2005), and along the Pacific coast of America (Hendrickx & Salgado-Barragán 1991) showed that *Squilla biformis* is fre-

quently found between 61 and 118 m, and more frequently below 100 m (Hendrickx & Sánchez-Vargas 2005). However the total range of vertical distribution in *S. biformis* is between 25 to 518 m (Schmitt 1940, Brusca 1980), and all the studies mentioned above sampled to a maximum depth of only 150 m. Our sampling reached a greater depth and thus provides a broader picture of the vertical distribution of the entire population. The individuals between 20 and 35 mm CL

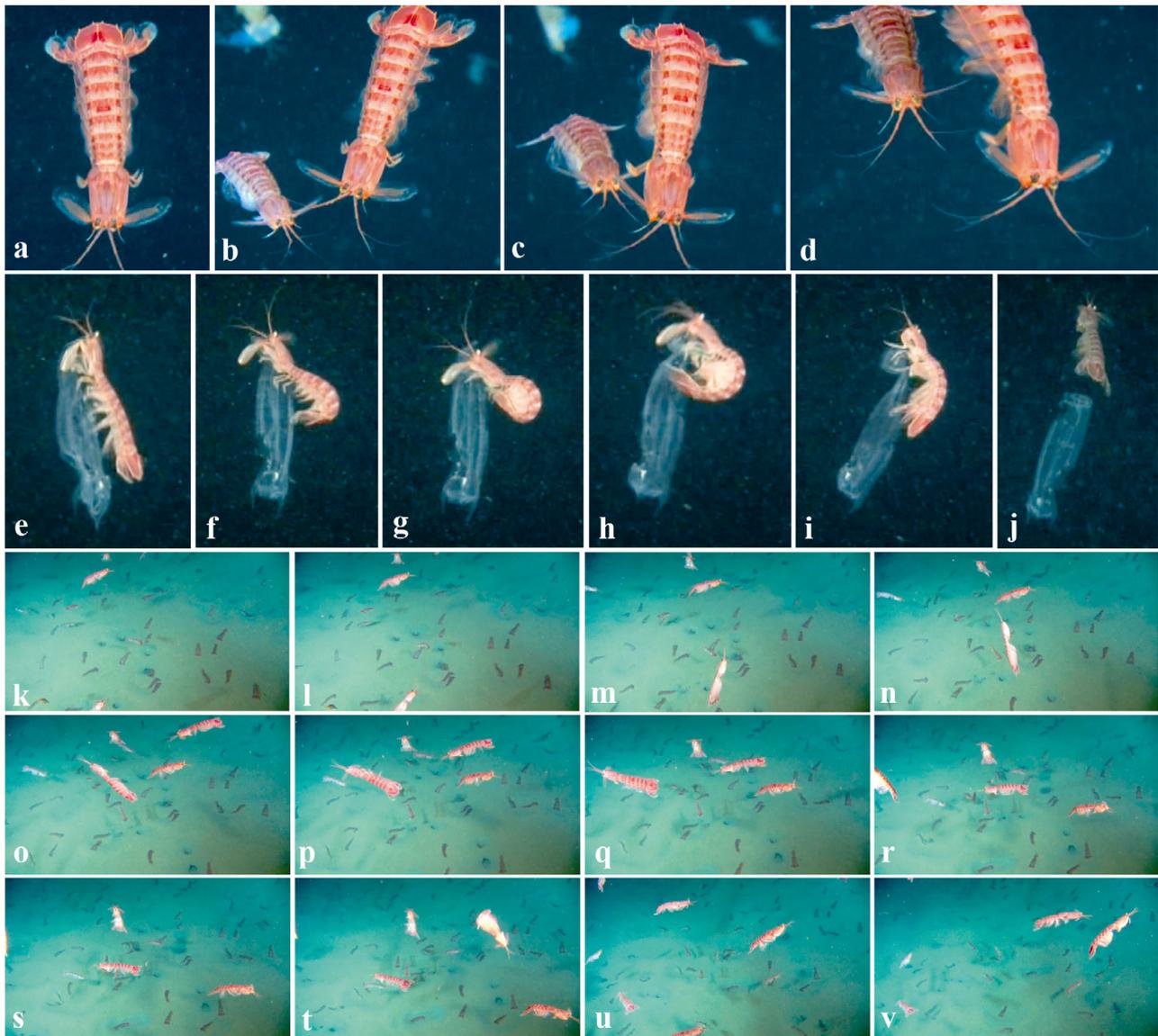


Fig. 8. *Squilla biformis*. Images obtained from a video taken by the Deep-See/Undersea Hunter Group (between 300 and 320 m depth) at the Pacific coast of Costa Rica (off Herradura: 09° 25' N, 84° 45' W). The frames show close-ups of swimming specimens (a to d), a gelatinous structure being manipulated by one of mantis shrimp (e to j), and specimens on bottom displaying diverse behaviours (k to v)

(95% of the total caught) were represented at all depths from 140 to 350 m; however, they were especially abundant (50%) between 240 and 260 m.

In Mexico, *Squilla biformis* occurs on muddy bottoms (silt and clay) between 61 to 117 m, where dissolved oxygen levels are very low (0.37 to 0.55 ml l⁻¹) (Hendrickx 1984). Vertical distribution and migration of marine invertebrates are often restricted by the oxygen minimum zone (OMZ), which extends vertically from about 50 to 1200 m in the eastern Pacific, with considerable variations depending on location, currents and other factors (Fernández-Álamo & Färber-

Lorda 2006). The thickness of the OMZ varies from 600 to 200 m in the south Pacific and from 1100 to 400 m in the north Pacific. In Central America, specifically in Costa Rica, the upper boundary of the OMZ is located at 40 to 60 m (Fiedler & Talley 2006), a depth below which 95% of *S. biformis* were found. Many organisms are adapted to these oxygen-deficient zones (Longhurst 1967, Mullins et al. 1985) and use it as a refuge or feeding zone (Wishner et al. 1995). It is speculated that *S. biformis* is adapted to these low oxygen conditions, and that observed swimming behaviour is a strategy that may be associated with the search for food or with

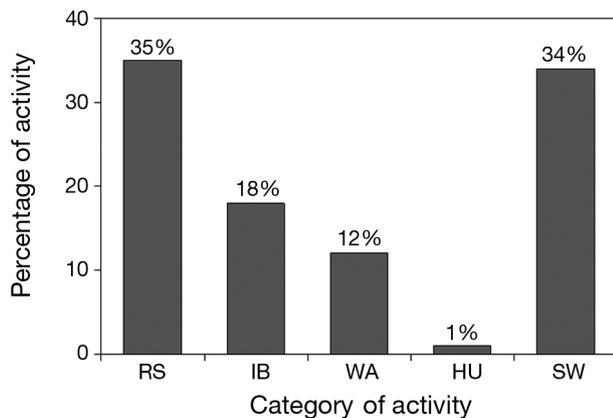


Fig. 9. *Squilla biformis*. Percentage of total activities spent on stationary (RS: resting on the sediment, IB: inside of the burrows) and locomotory behaviour (WA: walking, HU: hunting, SW: swimming) observed during 12 camera deployments conducted at various locations along the central Pacific coast of Costa Rica (n = 4032 ind.)

gaining access to the layer above the oxygen minimum zone. Additional studies are required to corroborate this hypothesis.

Recruits (≤ 21 mm CL) were present from August 2007 to February 2008 and in April 2008. This recruitment pattern could reflect an extensive reproductive period, a common feature of organisms living in deep-water environments (see Sastry 1983). According to Orton (1920), such a pattern may be related to the relative temperature stability that allows continuous reproduction in many deep-water invertebrates. Since the bottom temperatures in our study area did not vary by more than 2.5°C and the salinity remained practically constant, we assume that *Squilla biformis* has an extensive reproductive period similar to those reported for other deep-water decapod species (see Omori 1974, Wenner 1978, Company & Sardà 1997).

During this study, males outnumbered females, confirming previous observations for *Squilla biformis* and other squillid mantis shrimps, including *S. hancocki* Schmitt, 1940, *S. mantoidea* Bigelow, 1893 and *S. pamamensis* Bigelow, 1891 off the Mexican coast (Hendrickx & Sánchez-Vargas 2005). According to Griffiths & Blaine (1988), females prefer the safety of their burrows, especially when carrying eggs. In contrast, males can be found more often outside the burrows, thus making them more vulnerable to bottom trawling. However, bias in the sex ratio is very common in decapods (Wenner 1972), and has also been attributed to latitudinal (Defeo & Cardoso 2002, Rivadeneira et al. 2010) and temporal variations (Wenner 1972, Bas et al. 2005). Although our data does not allow any robust conclusion about the observed predominance of males, we cannot exclude the possibility that females migrate

(temporarily) out of our study area or into the water column, causing the observed bias. This interpretation is supported by the study of Hamano et al. (1987), who described a similar migration pattern for *Oratosquilla oratoria*.

Squilla biformis is one of the most abundant species associated with deep-water shrimp fishery along the Pacific coast of Costa Rica where this species represents 25% of the catches carried out between 301 and 350 m depth (Wehrtmann & Echeverría-Sáenz 2007). Its incidental capture has increased considerably in the past years, contrasting with the concomitant decrease in catches of the commercially exploited deep-water shrimp species *Solenocera agassizii* Faxon, 1893 and *Heterocarpus vicarius* Faxon, 1893 (Wehrtmann & Nielsen-Muñoz 2009). Our results indicate that *S. biformis* is particularly abundant on bottoms deeper than 240 m, a depth level traditionally occupied by *H. vicarius* (Wehrtmann & Echeverría-Sáenz 2007). This apparent shift may be related to intense fishing activities and the reduction (or disappearance) of *H. vicarius* stocks, creating a vacancy, which is now increasingly occupied by *S. biformis* populations. This tendency has also been observed in El Salvador (A. Olivares, unpubl. data), thus indicating that a significant change might be occurring in the marine ecosystem structure off Central America.

Ecdysis process in *Squilla biformis* and its relationship to the lunar cycle

Our results indicate a possible association between the moulting process in *Squilla biformis* and the lunar cycle (Fig. 4), as has been reported by other authors in different stomatopod species (Reaka 1976, Christy & Salmon 1991). The presence of a high percentage of moulting individuals of both sexes during the third and fourth lunar phases is clear evidence of well-defined circalunar and synchronic rhythm in *S. biformis*.

The moult in both sexes of *Squilla biformis* occurred principally during the less luminous lunar phases (3rd and 4th phases) and apparently on the bottom. Moonlight plays a significant role in the vision of deep-water organisms, because it may penetrate much deeper than daylight (Denton 1990). The level of bright moonlight is about 3×10^{-6} of that of sunlight, which means that on bright moonlit nights its contribution to submarine light at about 400 m is close to that found in full sunlight at about 800 m (Sathyendranath & Platt 1990). The highly specialized visual system of stomatopods (see Marshall et al. 1999, Cronin et al. 2006) may allow them to detect small changes in the moonlight intensity, which in turn may trigger the moulting cycle. In our study, a close correlation between moult frequency in *S. biformis* and lu-

nar phases is apparent, as was demonstrated by Reaka (1976) in stomatopods from shallow waters.

Moult synchrony is a common trait in crustaceans (e.g. euphausiid shrimps) that form large aggregations of individuals (Buchholz 1985, Morris 1985). One hypothesis explains this synchronous behaviour as being related to fluctuations in food availability, which control the moulting cycle of the population (Buchholz 1991). Our data do not allow any conclusion about the possible relation between food fluctuations and the moulting cycle; however, the presence of simultaneously moulting individuals of *S. biformis* needs further attention.

In contrast to solitary mantis shrimps ('smashers'), 'speakers' like *Squilla biformis* form large aggregations of individuals and are less aggressive than 'smashers' (Caldwell & Dingle 1975). This proposition is confirmed by our visual evidence of the main activities performed by *S. biformis* (see Fig. 8), which did not provide evidence of agonistic interactions. We assume that, like their other activities, the moulting cycle of *S. biformis* has developed in a way that avoids agonistic interactions. The sociable behaviour of *S. biformis* might reflect the evolution of a social moulting system that is advantageous in comparison with the individual and asynchronous moulting processes found in other stomatopods (see Reaka 1976).

Acknowledgements. The present study was partially financed by Ristic AG (Oberferrieden, Germany), and the Universidad de Costa Rica (projects V.I. 111-A4-508; V.I. 808-A9-536, and V.I. 808-A9-537). Additional funds came from the Consejo Superior Universitario Centroamericano (CSUCA), University of Kassel, and the Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) in the frame of the project Programa Universidad—Empresa para un Desarrollo Sostenible (PUEDES). Special thanks to Deep-See/Undersea Hunter Group (in the person of Shmulik Blum) for providing the images analyzed in this study; we appreciate that Jorge Cortés (Universidad de Costa Rica) informed us about the existence of these video tapes. We are thankful to the captains and crews of the shrimp trawlers 'Onuva' and 'Sultana' as well as to René Diers, The Rainbow Jewels. Last not least, we are more than grateful to all the students and assistants (especially Edgar Villegas and Juliana Herrera) who collaborated enthusiastically during the fieldwork. The Centro de Investigación en Ciencias del Mar y Limnología (CIMAR) and Escuela de Biología, Universidad de Costa Rica, provided working facilities to carry out this study, which is greatly appreciated. Finally, the constructive comments of 4 anonymous referees were greatly appreciated and helped to improve the quality of the manuscript.

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