MARINE IMPACTS IN THE ANTHROPOCENE

HERMIT CRABS ASSOCIATED TO THE SHRIMP BOTTOM-TRAWL FISHERY ALONG THE PACIFIC COAST OF COSTA RICA, CENTRAL AMERICA

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ABSTRACT. Studies of the bycatch associated to the shrimp trawling fishery in the Pacific coast of Costa Rica do not assess small organisms (< 10 cm TL) and non-dominant species (< 0.1% of total catch). There is a void in assessing the maintenance of the ecology and ecosystem on which the fishery depends. Furthermore, the Constitutional Court of Costa Rica prohibited the renewal of existing and the issuing of new shrimp bottom-trawl licenses, indicating the necessity of more scientific information on the impacts of this fishery. We present the results of a 23-month study of the shrimp bottom-trawl fishery, performed between 50 and 350 m deep in the Pacific coast of Costa Rica. A total of 109 hermit crabs were collected (six species and two families). *Paguristes* cf. *holmesi* was the most common species. Zone II presented the highest species richness and abundance. Most specimens (81.8%) were caught in shallower waters (50-149 m). More than 45% of the trawls presented hermit crabs. It is imperative to further assess the trawling effects on non-commercial benthic fauna and changes on predator-prey relationships, before issuing new shrimp licenses.

Key words: Bycatch, benthos, non-dominant species, deep waters, biodiversity.

INTRODUCTION

Trawling –the dragging of nets across the seabed– can be dated back to 1376, when concerns and complaints were raised by fishermen about the use of beam trawling (‘a new destructive and wasteful fishing habit’) in England (Roberts 2007). Since then, the introduction of steamed vessels and otter trawls has evolved in the adaptation of trawl fishing technology of many species (Gillett 2008). Furthermore, technological development, market demands and overexploitation of shallow water fishing grounds have led the fishing fleet to progressively explore into deeper waters causing the deep water ecosystems to face great threats (Roberts 2002; Morato et al. 2006; Ramírez-Llodra et al. 2011; Norse et al. 2012).

Shrimp fisheries have used many types of gears (beach seines, lift nets, cast nets, tramps, etc.), but the otter trawl is currently the most important commercial gear worldwide (Gillett 2008). In recent decades, the concern over the bycatch of the shrimp trawling fisheries has increased significantly (Dumont and D’Incao 2011; Queirolo et al. 2011; Meltzer et al. 2012; Arana et al. 2013; Villalobos-Rojas et al. 2017; Clarke et al. 2018), and the discard rates of these fisheries has increased significantly (Kelleher 2005; Arana et al. 2013). Moreover, information voids on the biology of both target and non-target species preclude any solid conclusions about the impacts of these fisheries (Bensch et al. 2008; Polidoro et al. 2008; Soykan et al. 2008). Deep water fisheries in Latin America focus mainly on benthic and demersal invertebrates (Arana et al. 2009; Wehrtmann et al. 2012). Detailed information on the composition of shrimp bottom-trawl fisheries' catch in the region is limited to the Chilean nylon shrimp fishery (*Heterocarpus reedi* Bahamonde, 1955), and the northern nylon shrimp (*Heterocarpus vicarius* Faxon, 1893) and kolibri shrimp (*Solenocera agassizii* Faxon, 1893) in Central America and Colombia (Chile: Queirolo et al. 2011; Arana et al. 2013, Colombia: Puentes et al. 2007, Costa Rica: Wehrtmann and Echeverría-Sáenz 2007; Arana et al. 2013; Villalobos-Rojas et al. 2017). Nevertheless, little attention has been paid to hermit crabs caught as bycatch in these fisheries. Puentes et al. (2007) reported *Xylopagurus cancellarius* Walton, 1950, as part of the bycatch of the trawling fishery from the Colombian Pacific, while Wehrtmann and Echeverría-Sáenz (2007) mentioned two species of hermit crabs from shrimp trawls along the Costa Rican Pacific: *Paguristes bakeri* Holmes, 1900 and *Petrochirus californiensis* Bouvier, 1895.

The Costa Rican Pacific waters support a high biodiversity of hermit crabs, comprising currently four families and 34 species (Vargas and Wehrtmann 2009), with 19 of these species reported from waters deeper than 50 m (Vargas and Wehrtmann 2009). Hermit crab taxonomy is presently under review, and a large number of new species have been recently described while others have been re-described for the Eastern Tropical Pacific (Ayón-Parente and Madrid-Vera 2009; Ayón-Parente and Hendrickx 2012a, 2012b, 2013; Ayón-Parente and Wehrtmann 2019). Shrimp bottom-trawl fisheries, thus, represent an excellent opportunity to access biological material from deep waters (> 50 m), especially in countries like Costa Rica, which do not have research vessels. The collected information allows expanding the description of the hermit crab diversity and distribution patterns along the Costa Rican Pacific continental shelf (Wehrtmann and Nielsen-Muñoz 2009; Wehrtmann et al. 2012; Ayón-Parente and Wehrtmann 2019).

In 2013, the constitutional court of Costa Rica prohibited both the renewal of existing and the issuing of new shrimp bottom-trawl licenses, indicating the necessity of more scientific information on the impacts of this fishery (Sentencia No 2013-10540 2013). In order to assess the possible impacts of shrimp trawling on the ecosystem, it is imperative to gather information on the diversity and ecological patterns of deep water species, including the hermit crabs. Therefore, the results of this study provide information necessary for the development of management approaches aimed to secure the sustainability of these deep water resources.

MATERIALS AND METHODS

Specimens were collected during a 23-month period (March 2010-February 2012) along the Costa Rican Pacific continental shelf. The sampling was carried out as part of a project to study the fisheries of commercially important deep-water shrimps (*H. vicarius* and *S. agassizii*). Samples were obtained using commercial shrimp trawlers (22.5 m long, 270 HP) equipped with two standard epibenthic nets (20.5 m length, mouth opening 5.35 width × 0.85 m height, mesh size 4.5 cm, cod-end mesh size 3.0 cm), at a speed of 2.0 knots (~ 3.7 $km \cdot h^{-1}$). The specimens were collected in the framework of scientific sampling programs along the entire Pacific coast of Costa Rica with samples collected between 50 and 300 m, with a total of 179 samples (44.75 h) (Figure 1). The study area was divided into three geographic zones based on oceanographic conditions to analyze the geographic distribution of hermit crabs captured by the shrimp bottom-trawl fishery: Zone I, influenced by a seasonal upwelling in the northern Pacific coast; Zone II, Golfo de Nicoya estuarine system, Central Pacific and Térraba-Sierpe estuarine system; and Zone III, mouth of Golfo Dulce, a tropical fjord with anoxic conditions (Nielsen-Muñoz and Quesada-Alpízar 2006; Cortés and Wehrtmann 2009) (Figure 1). The bathymetric distribution was divided into four depth ranges: 50-99 m, 100-149 m; 150-199 m, and 200-350 m. The collected hermit crabs were stored on board at 0 °C and subsequently transported to the laboratory. All specimens were identified to species level using the available literature (Ball and Haig 1974; McLaughlin 1981a, 1981b, 1982; Lemaitre 1989; Hendrickx 1995; Lemaitre and McLaughlin 1996; Hendrickx and Harvey 1999; Ayón-Parente 2009; Ayón-Parente and Hendrickx 2010; McLaughlin et al. 2010), preserved in 70% ethanol and deposited in the collection of the Museo de Zoología of the Universidad de Costa Rica (MZUCR).

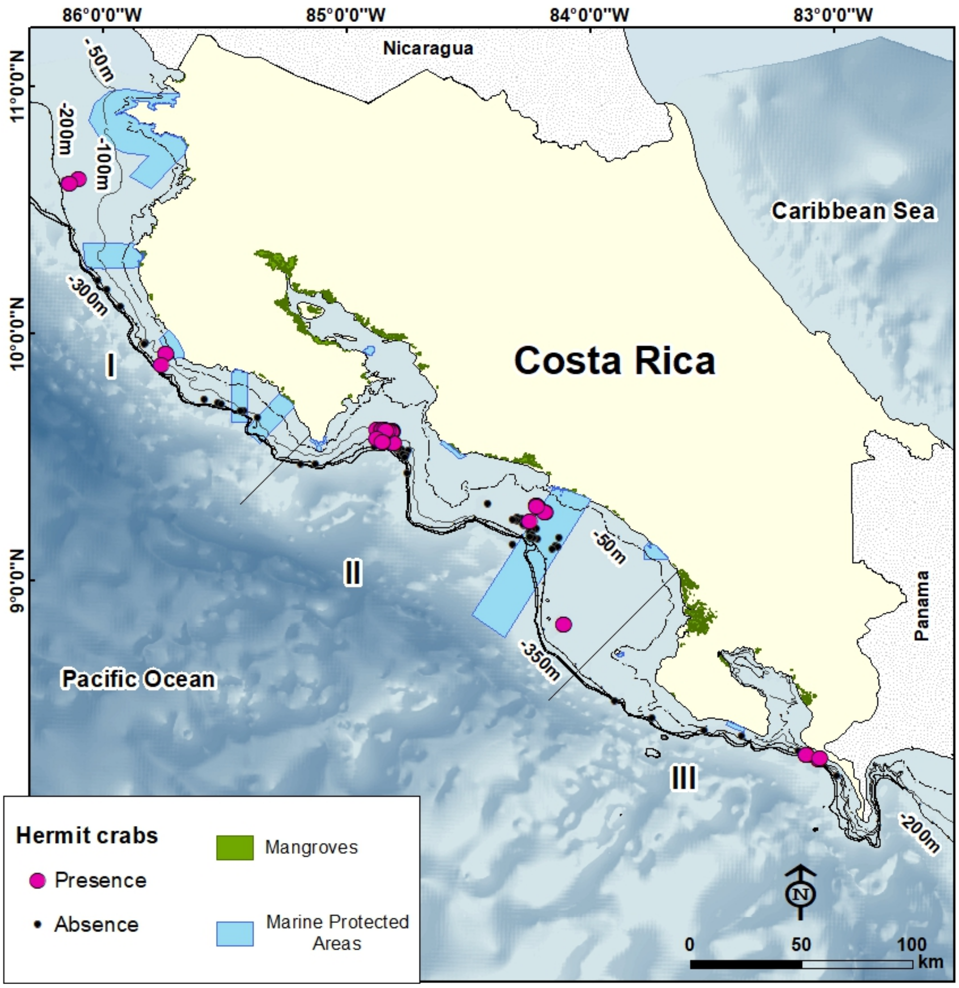

Figure 1. Pacific coast of Costa Rica, Central America, divided into the three zones used in the analyses. The sampling stations indicate the presence (pink circle) or absence (small black circle) of hermit crabs in the bycatch.

Species composition

To compile a species list of hermit crabs we examined both the living specimens collected during our surveys (2010-2012) as well as additionally specimens collected at the same fishing grounds and depths during other shrimp bottom-trawl surveys carried out between 2008 and 2012 with the same methodology. A species accumulation curve was calculated to assess the completeness of the sampling methods used to record the hermit crabs inhabiting the surveyed area (2010-2012), using the 'vegan' library (Oksanen et al. 2016) in the R statistical package v3.1.3.

Morphometric measurements

The cephalothorax length (CL), abdomen length (AL) and total length (TL = CL + AL) of hermit crabs were measured using a caliper (± 0.05 mm) (Figure 2). Additionally, each specimen was weighted (± 0.001 g) and sexed using the location of gonopores at the base of the third (females) or fifth (males) pereiopods (Hendrickx 1995; Hendrickx and Harvey 1999). Photographs of at least one specimen per species were taken with a Canon EOS7D camera equipped with macro lens Canon EF 100 mm and lens Canon MP-E 65 mm. A Chi-square goodness of fit test

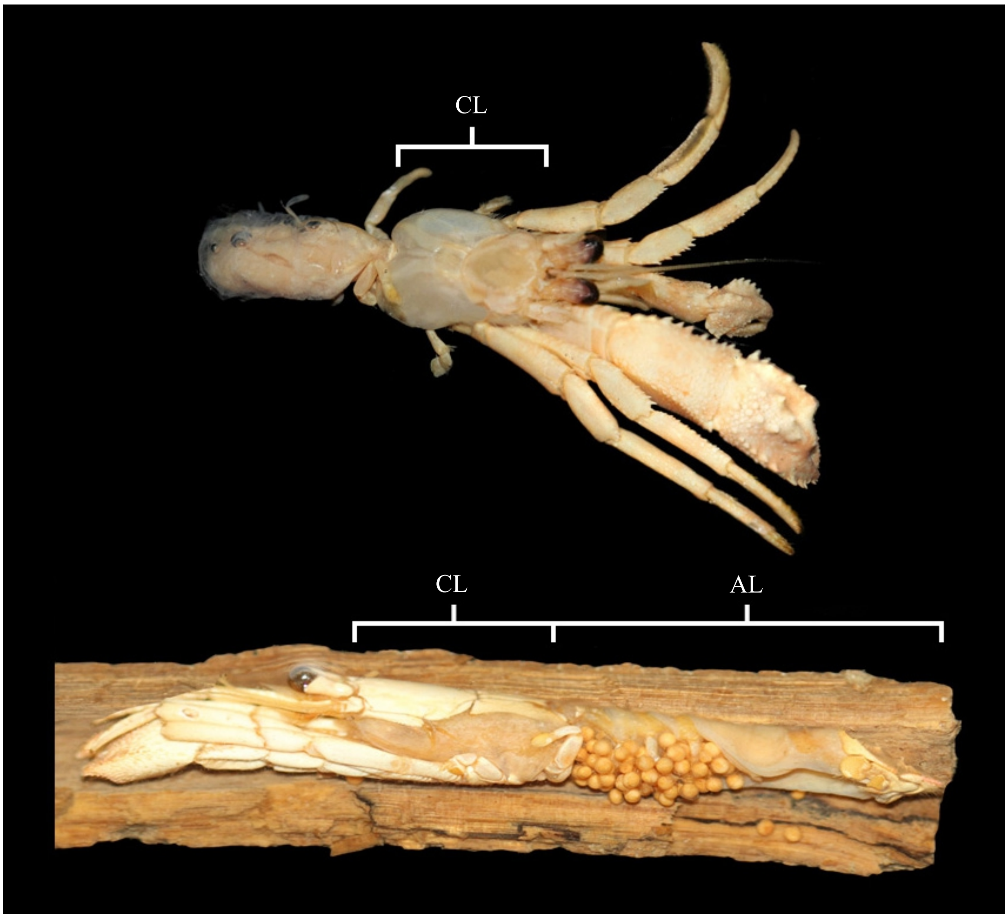

Figure 2. Measurements recorded for hermit crabs collected along the Pacific coast of Costa Rica. CL: carapace length, AL: abdomen length.

was conducted to detect species with sex ratios, which were different from the expected 1:1 ratio (Zar 1999; Hernáez et al. 2012; Villalobos-Rojas and Wehrtmann 2018).

Species geographic and bathymetric distribution

We used a Generalized Linear Model (GLM) with binomial distribution to identify environmental variables influencing the presence/absence of hermit crabs. Seven independent variables were considered for the analysis: (1) geographic zones (I, II, III), (2) depth level (50-99 m, 100-149 m, 150-199 m and > 200 m), (3) seasonality (rainy, transition and dry season; according to Amador et al. 2006), (4) Oceanic Niño Index (ONI categories: cold, normal and warm; NWSCPC 2019), (5) marine bottom substrate (bathyal soft-bottoms, infralittoral hard-bottom and sublittoral lithoclastic mud) as provided by TNC (2008) (6) shortest distance to the closest protected area and mangrove area and (7) sea bottom slope. The shortest distance to the closest protected area and mangrove area were obtained with spatial data from ITCR (2014) and the tool 'Near' of the Analysis toolbox, while sea slope bottom data were obtained using the Digital Elevation Model (DEM) for the Eastern Tropical Pacific (TNC 2008) and the tool 'Slope' of the 3D Analyst toolbox. Slope values for each record were extracted using the tool 'Extract multivalues to points' from Spatial Analyst toolbox. The GIS and all toolboxes used are part of ArcGIS10.4 (ESRI 2019).

Statistical analyses were performed using the 'coin' package (Hothorn et al. 2006) in R v3.1.3. A Tukey *post-hoc* test was applied to determine differences considering the categorical environmental variables that were significant in the binomial-GLM using the 'multcomp' package (Hothorn et al. 2008).

RESULTS

Species composition

A total of 109 specimens were collected, comprising six species, five genera and two families (Table 1; Figure 3). The most common species was *Paguristes* cf. *holmesi* Glassell, 1937 (n = 63), followed by *Areopaguristes praedator* (Glassell, 1937) and *Tomopagurus merimaculosus* (Glassell, 1937) with 15 specimens each (Table 1). *Dardanus nudus* Ayón-Parente and Hendrickx, 2009 and *D. stimpsoni* Ayón Parente and Hendrickx, 2009 were collected only during the additional surveys (between 2008 and 2012) (Table 1). Both *D. nudus* and *D. stimpsoni* are new reports for Costa Rica. Figure 4 shows the species accumulation curve with a relatively low slope and Figure 5 presents the locality of all hermit crabs analyzed.

Morphometric measurements

Table 2 summarizes morphometric measurements obtained from the 109 specimens collected. The largest specimen belonged to *D. stimpsoni* with 83.0 mm TL (29.4 mm CL), whereas in average *D. nudus* presented the largest length (62.6 ± 12.7 mm TL). The smallest specimen was represented by *P.* cf. *holmesi* with a total length of 11.7 mm (8.4 mm CL), whereas in average *A. praedator* comprised the smallest specimens (25.3 ± 5.2 mm TL) (Table 2).

Species geographic and bathymetric distribution

A total of 189 shrimp bottom-trawl surveys were carried out between 2010 and 2012 (Table 3). The Zone II presented the highest sampling effort (32.75 h), with the highest species richness (four) and abundance (n = 60). In all zones, more

Table 1. Species list, number of collected specimens (n), geographic distribution and depth range (m) reported in literature compared to the depth range for the hermit crabs collected as bycatch in the shrimp bottom-trawl fishery along the Costa Rican Pacific (2008-2012).

Species	n	Geographic distribution	Previously reported depth range (m)	Study depth range (m)
Diogenidae				
Areopaguristes praedator (Glassell 1937)	15	Gulf of California to Costa Rica[6]	6-155[6]	93.5-158.9
*Dardanus nudus** Ayón Parente and Hendrickx (2009)	4	Gulf of California-Panamic Region[4]	16-55[4]	41.1-56.1
*Dardanus stimpsoni**, †, ‡ Ayón Parente and Hendrickx (2009)	10	Gulf of California[4, †]	2-144[4]	187‡
Paguristes cf. *holmesi**, †, ‡ Glassell 1937	63	Gulf of California[5, †]	60-150[5]	84.1-187‡
Paguridae				
Tomopagurus merimaculosus (Glassell 1937)	15	Gulf of California to Colombia[2, 3]	35-183[2, 3]	67.3-187
Xylopagurus cancellarius‡ Walton 1950	2	Costa Rica and Colombia[1, 2, 3]	73[1, 2, 3]	93.5‡
Total specimens	109			

*New report for Costa Rica.
†Geographic distribution extension.
‡Depth range extension.
[1]Lemaitre (1995).
[2]Vargas and Cortés (2004).
[3]Vargas and Wehrtmann (2009).
[4]Ayón-Parente and Hendrickx (2009).
[5]Ayón-Parente and Hendrickx (2010).
[6]Ayón-Parente et al. (2015).

than 45% of the trawls presented at least one species of hermit crab. Only *Paguristes* cf. *holmesi* was collected in all three sampling areas.

Most of the specimens (81.8%) were caught in the first two depth levels (50-99 m and 100-149 m). The 50-99 m depth level had the highest sampling effort (15.3 h), the highest percentage of samples with hermit crabs (90.2%), the highest species richness (four), and the highest abundance (n = 55). On the other hand, the 150-199 m depth level had the second highest sampling effort (12.8 h), but less than 40% of the samples contained hermit crabs. The 100-149 and > 200 m depth levels had similar sampling efforts (7.8 h and 9 h); nevertheless, hermit crabs were absent at the deepest level. *Tomopagurus meri-*

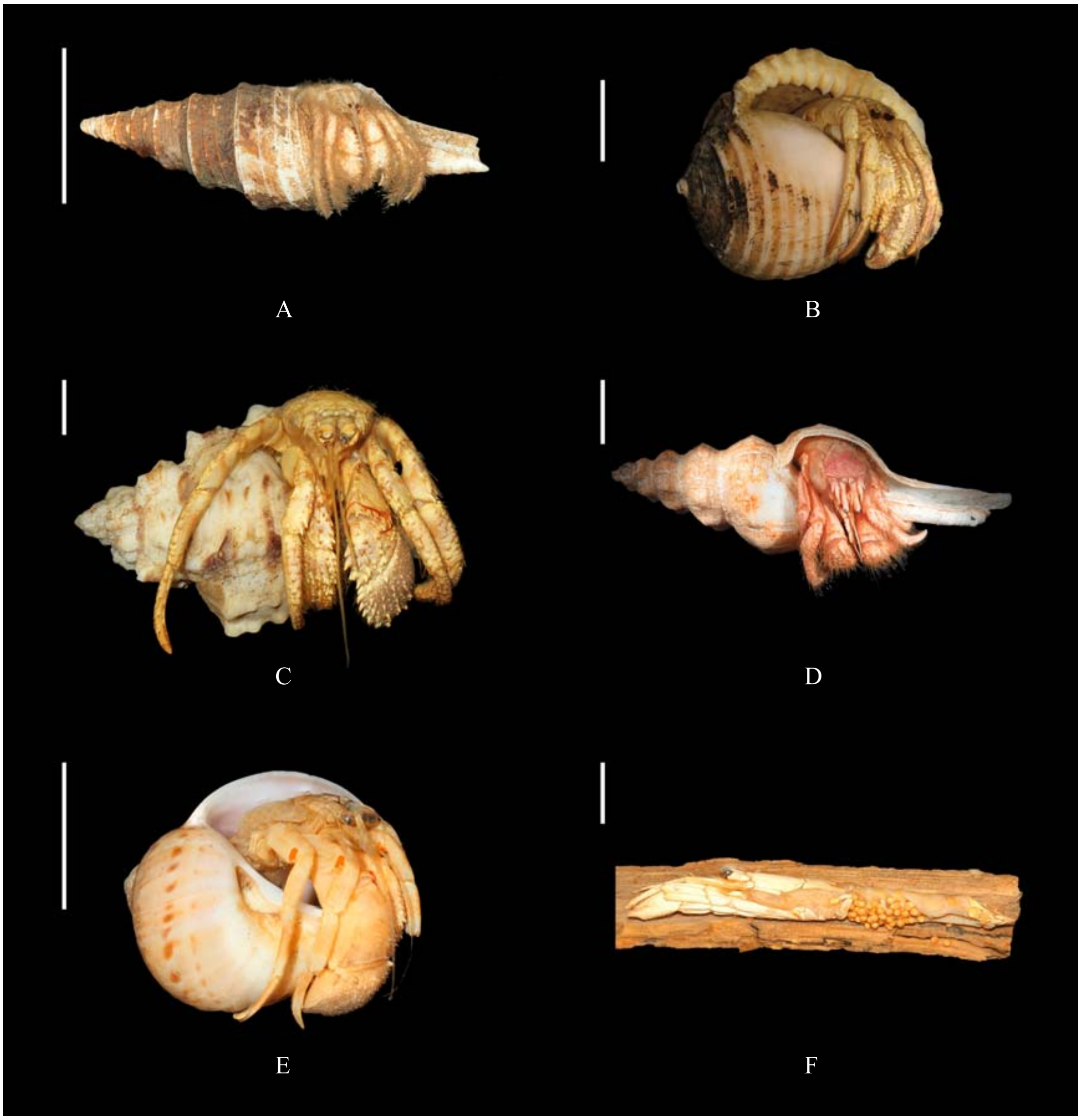

Figure 3. Hermit crabs collected as bycatch in the shrimp bottom-trawl fishery along the Costa Rican Pacific. Diogenidae. A) *Areopaguristes praedator*, 9.95 mm CL (MZUCR 3594-1). B) *Dardanus nudus*, 25.0 mm CL (MZUCR 3537). C) *Dardanus stimpsoni*, 20.5 mm CL (MZUCR 3595-1). D) *Paguristes* cf. *holmesi*, 19.0 mm CL (MZUCR 3593-1). Paguridae. E) *Tomopagurus merimaculosus*, 10.0 mm CL (MZUCR 3595-2). F) *Xylopagurus cancellarius*, 20.3 mm CL (MZUCR 3596-1). Scale bars = 10 mm.

maculosus presented the widest depth distribution range (67-187 m), whereas *Xylopagurus cancellarius* occurred only at 93.5 m depth (Table 1).

The results from the binomial-GLM selected five variables that significantly influenced ($p < 0.05$) the presence of hermit crabs: (1) depth level, (2) ONI categories, (3) marine bottom substrate (4) sea bottom slope, and (5) geographic coordinates. The GLM (hermit crab presence ~ depth + ONI + marine bottom substrate + sea bottom slope

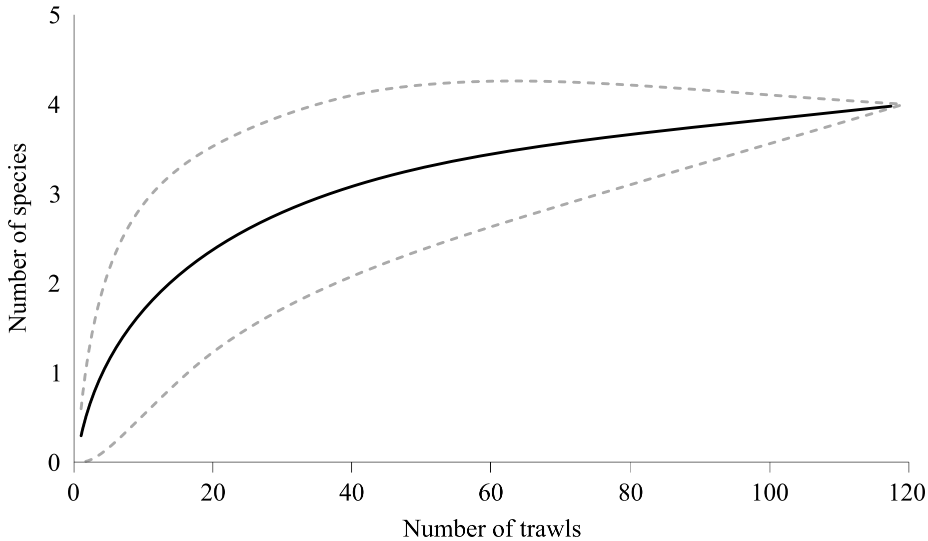

Figure 4. Number of hermit crab species accumulated by number of shrimp bottom-trawls carried out between 2010 and 2012 along the Pacific coast of Costa Rica, Central America.

+ geographic coordinates) explained 72.4% of the observed variance. Additionally, the Tukey *post-hoc* test revealed significant differences between the factors of the categorical variables according to the probability of presence of hermit crabs: depth level (50-99 m > 100-149 m, 150-199 m and > 200 m, $p < 0.01$), marine bottom substrate (lithoclastic mud > bathyal soft-bottoms; $p < 0.01$) and ONI categories (cold > normal). Although no significant differences were detected between the geographic zones (I, II and III), a significant tendency to find more hermit crabs in higher longitudes was determined ($p > 0.05$) Table 4.

DISCUSSION

The hermit crab fauna from the Costa Rican Pacific is currently comprised by 34 species; including the two new records obtained by the present study (*Dardanus nudus* and *D. stimpsoni*: 1 sp. of Coenobitidae, 14 spp. of Diogenidae, 17 spp. of Paguridae and 2 spp. of Parapaguridae). Nineteen of these species are distributed deeper than 50 m: 7 spp. of Diogenidae, 10 spp. of Paguridae, and 2 spp. of Parapaguridae (Vargas and Cortés 2004, Vargas and Wehrtmann 2009). The six species found in our study represent 31.6% of hermit crabs fauna reported at these depths.

Published information on the hermit crabs associated to the Costa Rican shrimp bottom-trawl fisheries is scarce. Campos (1986) reported 'crustaceans in gastropod shells' representing 0.0006% of total capture of shrimp trawls between 27 m and 238 m deep, but no species identification was provided. Wehrtmann and Echeverría-Sáenz (2007) reported *Paguristes bakeri* as rare (< 15% of hauls) and *Petrochirus californiensis* as occasional (15% of hauls) fauna in the northern nylon shrimp (*Heterocarpus vicarius*) fisheries of Costa Rica, collected at 273 m and 293 m deep, respectively. Therefore, there are a total of seven hermit crab species associated to the Costa Rican shrimp fisheries since the *P. bakeri* found by Wehrtmann and Echeverría-Sáenz (2007) is probably *P. holmesi* found and identified in our study.

All six species found in our study were previously documented for the Panamic Region

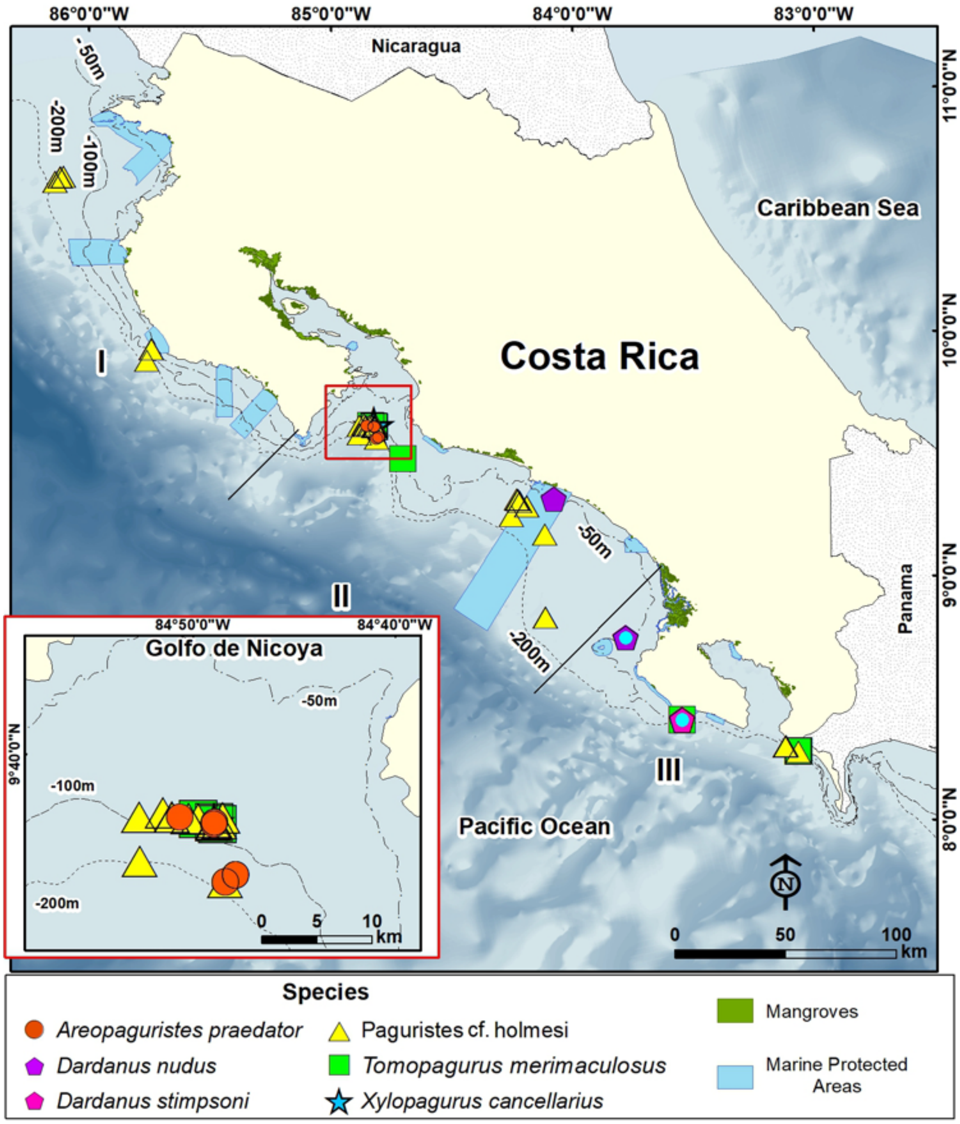

Figure 5. Presence of hermit crab species associated to the shrimp bottom-trawl fishery from 2010 to 2012 along the Pacific coast of Costa Rica, Central America. The close-up shows the distribution of hermit crab species collected in the entrance of the Golfo de Nicoya.

(Ayón-Parente and Hendrickx 2010). Nevertheless, here we present the first report of two hermit crab species: *Dardanus nudus* and *Dardanus stimpsoni* for the Costa Rican Pacific. Our records expand the depth range for *D. stimpsoni* down to 187 m (both were previously reported at 144 m) (Ayón-Parente and Hendrickx 2010). Three of the other collected species have been previously reported: *Areopaguristes praedator*, *Tomopagurus merimaculosus*, and *Xylopagurus cancellarius* (see Lemaitre 1995; Vargas and Cortés 2004; Vargas and Wehrtmann 2009; Ayón-Parente et al. 2010, 2015). Nevertheless, our data extend the depth range for *X. cancellarius* from 73.1 m deep (Vargas and Wehrtmann 2009) down to 93.5 m.

Table 2. Measurements and sex ratio of hermit crabs collected as bycatch in the shrimp bottom-trawl fishery along the Costa Rican Pacific (2008-2012). SD: standard deviation, n: number of specimens analyzed, F: females, M: males.

			Carapace length (mm)		Total length (mm)		Weight (g)	
Species	n	Sex ratio (F/M)	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Diogenidae								
Areopaguristes praedator (Glassell 1937)	15	0.9	8.13 ± 1.6	5.6-10.5	25.3 ± 5.2	15.45-32.1	0.43 ± 0.3	0.1-0.9
Dardanus nudus Ayón-Parente and Hendrickx (2009)	4	0.0	20.9 ± 4.0	16.0-25.6	62.6 ± 12.7	48.7-79.2	8.4 ± 4.8	4.69-15.1
Dardanus stimpsoni Ayón-Parente Hendrickx (2009)	10	0.6	16.1 ± 5.6	9.8-29.4	47.6 ± 14.6	29.8-83.0	4.0 ± 4.8	0.4-16.7
Paguristes cf. holmesi Glassell 1937	63	0.4*	15.3 ± 3.8	8.4-25.6	43.6 ± 12.6	11.7-75.7	3.19 ± 2.5	0.2-11.8
Paguridae								
Tomopagurus merimaculosus (Glassell 1937)	15	0.3*	13.6 ± 2.4	9.65-18.55	36.8 ± 6.7	12.15-50.2	2.3 ± 1.3	0.9-55.9
Xylopagurus cancellarius Walton 1950	2	1.0	17.3 ± 4.2	14.3-20.3	52.7 ± 19.1	39.2-66.2	3.0 ± 2.7	1.1-4.9
Total specimens	109							

The specimens of *Paguristes* cf. *holmesi* were identified as *confer* because its taxonomy is still under revision in the Eastern Tropical Pacific (M. Ayón-Parente, pers. comm). This species was previously synonymized with *Paguristes bakeri* Holmes, 1900 (Haig and Hopkins 1970). Afterwards, Moran and Dittel (1993) reported specimens of *P. holmesi* from material collected in Costa Rica. Nevertheless, Hendrickx and Harvey (1996) indicated that the material mentioned by Moran and Dittel (1993) could not be located in the Los Angeles County Museum of Natural History where it was allegedly deposited. Recently, Ayón-Parente (2009) examined additional material from the Mexican Pacific and found enough morphological differences for them to be considered as a separate species. Consequently, it is possible that the species identified as *Paguristes bakeri* by Wehrtmann and Echeve-rría-Sáenz (2007) is *Paguristes* cf. *holmesi*. Therefore, our study reports five additional species associated to shrimp bottom-trawl fisheries to the previous study (Wehrtmann and Echeverría-Sáenz 2007).

Regarding the geographic distribution of the species, results indicated a tendency to find more hermit crabs in higher longitudes. For example, although Zones I and III had similar sampling efforts, higher abundance was found in Zone I.

Table 3. Number of species, number of individuals, percentage of samples with hermit crab, and total number of samples by geographical area and depth range associated with shrimp bottom-trawl fisheries along the Costa Rican Pacific (2010-2012).

	Geographic area			Depth range (m)			
Species	I	II	III	50-99	100-149	150-199	> 200
Diogenidae							
Areopaguristes praedator	-	15	-	8	5	2	-
Paguristes cf. *holmesi*	9	40	10	39	6	14	-
Paguridae							
Tomopagurus merimaculosus	9	3	-	6	6	-	-
Xylopagurus cancellarius	-	2	-	2	-	-	-
Number of specimens	18	60	10	55	17	16	0
Number of species	2	4	1	4	3	2	0
Samples with hermit crabs (%)	69.2	45.8	45.5	90.2	54.8	31.4	0
Number of samples	26	131	22	61	31	51	36
Sampling effort (h)	6.5	32.75	5.5	15.3	7.8	12.8	9

Nevertheless, additional studies with a higher sampling effort are required to confirm this tendency.

Our results suggest that the probability of finding hermit crabs is higher at shallower waters (50-99 m) and decreases towards deeper waters (> 200 m). A similar pattern was observed for hermit crabs of the family Diogenidae in the Eastern Pacific, where the species richness was highest at shallower waters (Ayón-Parente and Hendrickx 2010). Our results follow the general distribution pattern of marine benthic invertebrates (Sanders 1963). Therefore, shrimp fisheries carried out in shallower waters (< 100 m) will have a greater impact on the hermit crab community than deep-water shrimp fisheries. In Costa Rica, the shallow-water shrimp fishery has focused on seven Penaeidae species (*Litopenaeus vannamei*, *L. stylirostris*, *L. occidentalis*, *Xiphopenaeus riveti*, *Trachypenaeus byrdii*, *Farfantepenaeus brevirostris*, and *F. californiensis*) and was carried out between 5 and 120 m deep (Álvarez and Salazar 2010). In the case of the trawling shrimp fisheries will be reinstalled in Costa Rica, the monitoring program should include identifying hermit crab species.

The probability of finding hermit crabs off the Costa Rican Pacific is higher during cold Oceanic Niño Index (ONI) than during normal ONI conditions Hermit crabs are affected in different ways by temperature changes (Briffa et al. 2013; Gilland 2017). For example, Gilland (2017) suggested that changes in temperature levels affect the ability of tide pool hermit crabs to occupy high quality shells that will protect them from predators and desiccation, as well as decrease growth rate and increase energy usage. To our knowledge there are no studies associating deep water hermit crabs with temperature, however, our results suggest that temperature could be affecting their distribution, which might be important considering the different climate change scenarios (Gorman et al. 2018).

In our study, hermit crabs were caught on soft bottom sediments (lithoclastic mud and bathyal

Table 4. Generalized Linear Model for the presence of hermit crabs associated with shrimp bottom-trawl fisheries along the Costa Rican Pacific (2010-2012).

Coefficients	Estimate	Standard error	z	Pr(>|z|)
(Intercept)	296.3248	857.9968	0.345	0.729818
Depth 100	2.8904	0.7457	-3.878	0.000225*
Depth 150	-2.8904	0.7349	-4.439	0.000252*
Depth 200	-20.847	2467.13	-0.008	0.992546
Depth 250	-20.847	3400.71	-0.006	0.994615
Depth 300	-20.847	5377	-0.004	0.996911
Latitude	-68.0098	51.0083	-1.33	0.1824
Longitude	12.6376	6.5037	1.943	0.049*
Latitude × Longitude	-0.8824	0.6107	-1.445	0.1485
ONI cold category	-1.61E+00	7.62E-01	-2.113	0.0346*
ONI normal category	-1.34E-01	8.76E-01	-0.152	0.8789
Sea bottom slope	-1.56E+00	3.99E-01	-3.921	0.0000884*
Marine bottom substrate	1.5444	0.6524	2.367	0.0179*

*p < 0.05.
GLM (hermit crab presence ~ depth + ONI + marine bottom substrate + sea bottom slope + geographic coordinates, family = binomial, link = logit).
Null deviance: 121.901 on 112 degrees of freedom.
Residual deviance: 33.679 on 85 degrees of freedom.
AIC: 89.679.

soft-bottoms), due to the characteristics of commercial shrimp trawling. Most hermit crabs were captured in trawls taken on the lithoclastic mud bottom, which were covered by fine grain to very fine sediments (SINAC 2008). Sediment particle size (Stanski et al. 2016) and sediment organic-matter content (Fransozo et al. 1998; Frameschi et al. 2014; Stanski et al. 2016) has been correlated to the abundance species of hermit crabs.

Impact of shrimp trawling fisheries

Few studies assessing the fauna associated to bottom-trawl shrimp fisheries have considered its impacts on small and non-dominant species (< 0.1% of total catch) (Branco et al. 2015; Villalobos-Rojas et al. 2017). In fact, hermit crabs have been rarely identified when monitoring the bycatch present in shrimp bottom-trawl fisheries (Branco et al. 2015; Gimenez-Hurtado et al. 2016). Non-dominant species, however, can have important ecological functions in the community. For example, hermit crabs have been reported as important allogenic ecosystem engineers in marine habitats and to have a large number of symbiotic relationships (Gutierrez and McDermott 2004; Pretterebner et al. 2012).

The impact of shrimp trawling on hermit crabs has been poorly studied (Ramsay et al. 1996; Groenewold and Fonds 2000; Stanski et al. 2016). Ramsay et al. (1996) suggested that some scavenging hermit crabs could migrate to recently trawled areas to feed on the damaged or disturbed fauna affected by trawling. Although trawling can lead to these shortcuts in trophic relationships and enhance secondary production, the direct importance of the additional food resource for populations of scavengers is considered to be relatively small (Groenewold and Fonds 2000).

Trawling is known to impact the structure and functioning of benthic ecosystems (Alverson et al. 1994; Collie et al. 2000; Hinz et al. 2009; Hiddink et al. 2017). The pressure of constant extraction can damage the maintenance of populations as it impacts recruitment, reproduction and growth of specimens (Stanski et al. 2016). The constant trawling impact on non-commercial species can change the predator-prey relationships due to the loss of biological diversity, disturbance or elimination of local species and can jeopardize the balance of the marine ecosystem (Stanski et al. 2016). Taking into account that surveys had a ~ 20 min duration and that commercial trawls last between 2 and 6 h (Álvarez and Salazar 2010; Marín-Alpízar et al. 2019) an increase in the abundance of hermit crabs in these nets is expected due to mesh plugging and reduction of selectivity (Stanski et al. 2016). According to Marín-Alpízar et al. (2019) trawls for fisheries focused on *Solenocera agassizii* and *Farfantepenaeus brevirostris* should have a maximum duration of two hours so that the mesh will not become obstructed and increasing the bycatch. Nevertheless, these authors did not provide information on non-dominant species or small invertebrates present in these two fisheries. Therefore, the possible impact of the suggested two-hour trawls still needs to be investigated.

In order to attain a sustainable and democratic fishery it is indispensable to consider the sustainability of exploited fish stocks, the maintenance of the ecosystem on which the fishery depends, and an effective and responsible management of the fishery (Pacheco-Urpí et al. 2012; Baigún 2013). Due to the decision taken by the Constitutional Court of Costa Rica (Sentencia No 2013-10540 2013), studies have aimed to assess the fishery and reduce the abundance of the bycatch associated to shrimp trawling fishery at the Pacific coast of Costa Rica (AJDIP/336-2018 2018; AJDIP/498-2018 2018, Marín-Alpízar et al. 2019). The majority of the results in these studies has not been officially published and do not assess small organisms (< 10 cm TL) such as gastropods, bivalves and hermit crabs. Therefore, there is a clear gap of information assessing the maintenance of the ecology and ecosystem on which the fishery depends. Considering that more than 45% of the survey trawls contained hermit crabs, it is imperative to assess the trawling effects on both non-commercial benthic fauna and changes on predator-prey relationships, before insinuating the possibility of obtaining a sustainable fishery. In case that the trawling shrimp fisheries will be reinstalled in Costa Rica, monitoring programs need to be installed to accompany these fisheries, and special attention should be given to the shallow-water fishery bycatch (< 100 m), which should include the identification of hermit crab species and other small invertebrates (< 10 cm TL).

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