

Northernmost occurrence and geographic distribution of *Scyllarides astori* Holthuis, 1960 (Scyllaridae) in the Eastern Tropical Pacific

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ABSTRACT

The Galapagos slipper lobster (*Scyllarides astori* Holthuis, 1960) is a species extensively distributed on rocky and coral reefs, sand, and mud in the Eastern Tropical Pacific Ocean, within the Gulf of California, Galapagos Archipelago, mainland Ecuador, and Isla de Cocos. Its presence has been reported in the southern region of the Baja California peninsula (Los Cabos). Here we report the presence of *S. astori* in the Baja California peninsula from Natividad Island, Guadalupe Island, and Socorro Island, Revillagigedo Archipelago. The Guadalupe Island record extends the distribution of this species 1,055 km north of its known limit. We developed a potential distribution model, and the results revealed a high probability of occurrence in different regions of the Eastern Tropical Pacific, such as the Baja California coast, Gulf of California, Colombia, and Ecuador.

KEYWORDS

Baja California, biogeography, distribution, Galapagos slipper lobster, new record

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INTRODUCTION

The slipper lobsters (Scyllaridae) are widespread in shallow temperate and tropical seas (Booth *et al.*, 2005). They can be distinguished from other lobster families in the infraorder Achelata by their wide and flat antennal peduncle segments, and by an antennal flagellum with a single broad and flat segment without noticeable articulations (Holthuis, 1991; Hearn, 2006). Scyllaridae includes 20 genera distributed in four subfamilies (Arctidinae, Ibacinae, Scyllarinae, and Theninae) with 82 named species (Holthuis, 1991; 2002). The genus *Scyllarides* Gill, 1898 includes 14 species worldwide, and only one species is registered from the Eastern Tropical Pacific (ETP): *Scyllarides astori* Holthuis, 1960 (Johnson, 1975; Hendrickx, 1995; WoRMS, 2020).

Scyllarides astori has a maximum reported total length of 37.8 cm and lives in shallow tropical and subtropical areas, generally at 0–40 m depth, but with reports of a depth of 90 m (Spanier and Lavalli, 2006). The species is usually associated with rocky reefs, coral reefs, mud, mud-sand and sand habitats (Holthuis, 1985; Hearn, 2006). The Galapagos slipper lobster is omnivorous with a varied diet of mollusk species, but the white sea urchin *Tripneustes depressus* A. Agassiz, 1863 is its preferred prey (Lavalli and Spanier, 2007).

The Galapagos slipper lobster is not listed in an appendix of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), but is considered as “Data Deficient” in the Red List of the International Union for Conservation of Nature (Butler *et al.*, 2011). The population of this lobster in the Galapagos Islands (Ecuador) has been exploited commercially for more than 20 years (Hearn *et al.*,

2007). On the other hand, although there is no formal *S. astori* fishery in Mexico, the Galapagos slipper lobster catch is reported as incidental in lobster traps or gill nets (DOF, 2018).

The geographic distribution of Galapagos slipper lobster spans the ETP, with reports from the Gulf of California, Central Mexican Pacific, Galapagos Archipelago, Clipperton Island, mainland Ecuador, and Cocos Island (Holthuis and Loesch, 1967; Holthuis, 1991; Hendrickx, 1995; Béarez and Hendrickx, 2006; Butler *et al.*, 2011; Azofeifa-Solano *et al.*, 2016; Carbajal-López *et al.*, 2017). Studies and databases of the ETP marine fauna consider *S. astori* as absent in the central and northern Baja California Pacific coast (Fischer *et al.*, 1995; Azofeifa-Solano *et al.*, 2016), and report the species from the southernmost area of the Baja California Pacific coast, with distribution limits at 22.883°N and 109.916°W (Los Cabos). The objective of this paper is (1) to report a new georeferenced record of *S. astori* that substantially expands its known geographic range in the Pacific Baja California coast, which represents its northernmost occurrence in the ETP, and (2) to present a map revealing the potential geographic distribution area of the species based on updated information.

MATERIAL AND METHODS

Lobster fishers captured two specimens of *S. astori* with lobster traps at a depth of 60 m, one at Loma Linda, four kilometers southeast of Natividad Island, in January 2018 (27.81848°N 115.14938°W); and the second one at Guadalupe Island, in April 2020 (28.88237°N 118.26523°W) (Fig. 1). A third



Figure 1. Adult specimens of *Scyllarides astori*, taken at Guadalupe Island (a), Natividad Island (b) and Socorro Island (c) (photographs taken by Javier González, Ramon Martínez/Elba López and Arturo Bocos).

record was obtained during underwater monitoring at Revillagigedo National Park, in February 2019 at Roca Oneal — Socorro Island — (18.8327°N 111.0580°W), at 25 m deep and 24 °C (Fig. 1). The identification of *S. astori* specimens was determined with the use of field guides (Holthuis, 1991).

We obtained historical georeferenced distribution records of the species in the ETP from the Ocean Biogeographic Information System (www.iobis.org), the Global Biogeographic Information Facility (GBIF, 2020), the Mexican Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (<http://enciclovida.mx/especies/64875-scyllarides-astori>), scientific literature (Hearn *et al.*, 2007; Azofeifa-Solano *et al.*, 2016; Carbajal-López *et al.*, 2017), and field data from a major monitoring program (PANGAS, 2011; Comunidad y Biodiversidad, 2018; ECO monitoring program) of rocky and coral reefs in Mexico (Revillagigedo Archipelago, Gulf of California, and Baja California Pacific coast), Nicaragua and Panama (ECO monitoring program). The reefs were

surveyed using belt transects (60 m²) to register macro-invertebrates (mollusks, crustaceans, and echinoderms). All the occurrence records were revised in order to discard repeated data and remove those with wrong coordinates. Georeferenced distribution records of larvae were discarded as we focused only on adult specimens, comprising a total of 20 records (Fig. 2a).

We used the maximum entropy software MaxEnt version 3.4.1 (Phillips *et al.*, 2017) to develop an ecological niche model of *S. astori* on the basis of occurrence records and on yearly average, annual range, maximum and minimum values of a series of oceanographic factors (see below). The marine superficial data layers were downloaded from Bio-ORACLE software with a 5 arcmin spatial resolution (Tyberghein *et al.*, 2012; Assis *et al.*, 2017) in order to obtain present oceanographic conditions (monthly averages from 2000–2014), covering the historical reported distribution of *S. astori*. The oceanographic variables were selected based on the biological

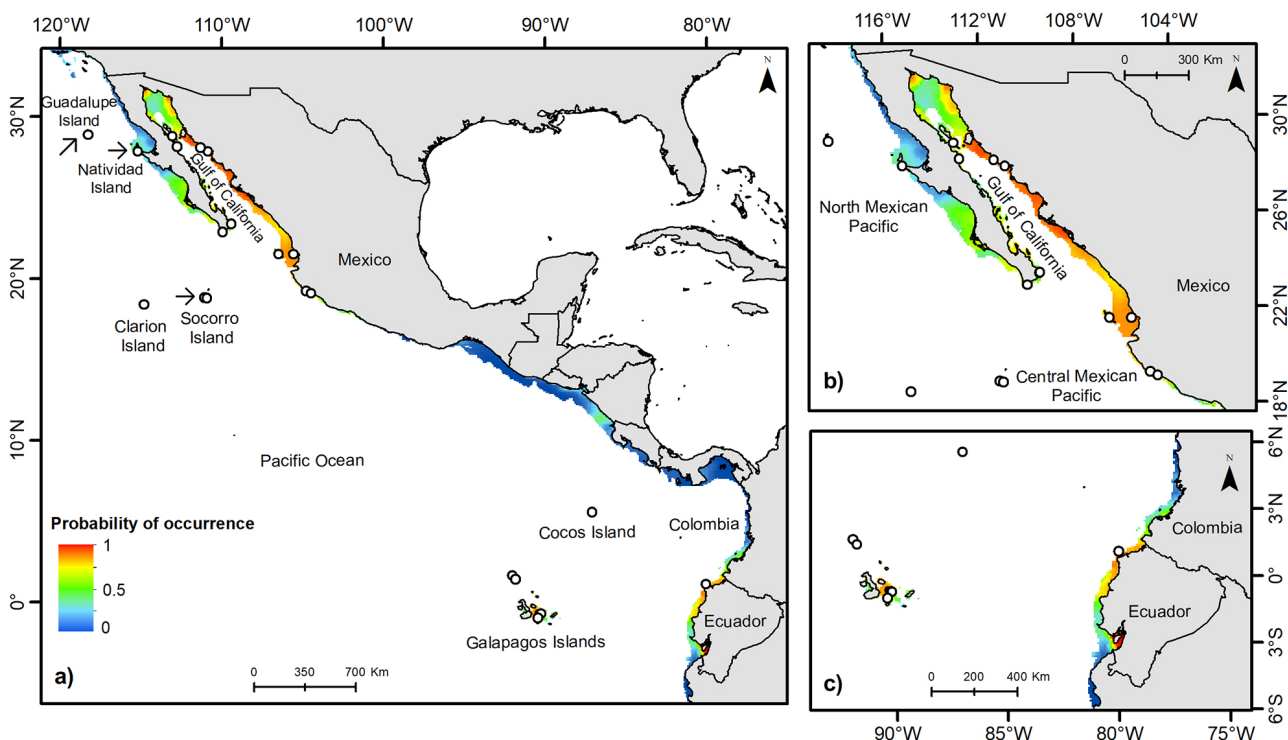


Figure 2. Georeferenced occurrences of *Scyllarides astori* in the Eastern Tropical Pacific (white dots) and potential distribution areas resulting from the MaxEnt model. Colors show the probability of occurrence of the species, where blue colors indicate a low probability of occurrence, and green, yellow, and red colors show a high probability of occurrence. Arrows indicate the location of the new georeferenced occurrence described in the text (Guadalupe Island, Natividad Island, and Socorro Island). The resulting potential distribution areas are shown in the complete geographic distribution range of *S. astori* (a), as well as in those areas with a high probability of occurrence (northern and Central Mexican Pacific (b), and Colombia, Ecuador and Galapagos Islands (c).

relevance for the species (Tab. 1) and following the recommendations made by Peterson *et al.* (2011). Variables included phosphates, nitrates, dissolved molecular oxygen, primary productivity, salinity, current velocity and temperature (for more details see Tyberghein *et al.*, 2012; Assis *et al.*, 2017). Bathymetry were obtained from the Global Bathymetric Chart of the Oceans (www.gebco.net) using ArcGIS 10.2.2, extracting only depth values between 0–200 m; we overlapped this layer with the resulting model prediction distribution. For modeling purposes, in MaxEnt we used a maximum iteration value of 1000 and the logistic output to evaluate the probability of

occurrence of the species in each pixel with a scale from 0 to 1, where 0 represents unsuitable and 1 represents very suitable. Peterson *et al.* (2011) proposed that values of 0.5 and higher represent the presence of the species at that pixel. Occurrence of *S. astori* (from field and historic records) were randomly partitioned into 70 % as training data to create the predictive model, and the remaining 30 % to test and assess the accuracy of the model (Peterson *et al.*, 2011; Feng *et al.*, 2019). Model accuracy was determined with the area under the curve (AUC) of the threshold independent receiver operating characteristic analysis (ROC) (Merow *et al.*, 2013).

Table 1. Environmental variables used to develop the potential distribution model. Not applied (NA) and no records (NR)

Variable	Max	Min	Mean	Range	Maximum average value in the latitudinal range	Minimum average value in the latitudinal range
Phosphates (mol.m ⁻³)	x	x	x	x	NR	NR
Nitrates (mol.m ⁻³)	x	x	x	x	NR	NR
Dissolved molecular oxygen (mol.m ⁻³)	x	x	x	x	NR	NR
Primary productivity (g.m ⁻³ .day ⁻¹)	x	x	x	x	NR	NR
Salinity (PSS)	NA		x	NA	NR	NR
Current velocity (m ⁻¹)	NA		x	NA	NR	NR
Temperature (°C)	x	x	x	x	x	x

RESULTS

During the lobster fishing season 2018 and 2020 two specimens of *S. astori* were captured in lobster traps in Natividad Island and Guadalupe Island, respectively, 765 km and 1,055 km north of the northernmost geographic range limit known within the Pacific coast, which is 22.883°N 109.916°W (Los Cabos). This range extension corresponds to an area with colder/temperate water (27°N and 28°N; Fig. 2a) compared to the Gulf of California and Central Mexican Pacific. During the fieldwork, we recorded the presence of *S. astori* only at two sites: (1) in the northern part of the Gulf of California (density 0.006 ind/100 m²) and (2) in Socorro Island, where the individuals were detected outside the monitoring transects. We did not encounter any specimens of *S. astori* during the marine monitoring programs conducted in Baja California Pacific (2,768 visual censuses), southern Gulf of California (353 censuses), central Gulf of California (2,256 censuses), Nicaragua (280 censuses), nor Panama (720 censuses) (Tab. 2).

The potential distribution model presented a high predictive value (AUC = 0.98), and the variables with the highest contribution to the model were maximum nitrates (25 %), minimum temperature (18 %), and maximum primary productivity (15 %). The species showed preference for subtropical (Galapagos, Gulf of California, and Baja California) and tropical areas (Ecuador, Colombia, and Central Mexican Pacific). Considering the new records, the results of the model suggested that the northernmost areas of the potential presence of *S. astori* might be along the west coast of Baja California, between San Juanico (26°N) and Los Cabos (22°N).

The model presented a high probability of occurrence on previously reported areas such as the Gulf of California (Mexico), Cocos Island (Costa Rica), and Galapagos Islands (Ecuador) (Fig. 2a). New potential distribution areas (probability of occurrence over 0.5) are displayed; north Mexican Pacific (Baja California Pacific coast; Fig. 2b), Central Mexican Pacific (including Socorro Island; Fig. 2b), and mainland coast of Ecuador and Colombia (Fig. 2c).

Table 2. Macroinvertebrate censuses carried out by country, region and site

Country	Region	Site	Number of belt transect (monitoring years)
Mexico	Baja California Pacific	Natividad Island	1,364 (15 years)
		El Rosario	972 (9 years)
		Magdalena Bay	432 (5 years)
	South Gulf of California	Cabo Pulmo	353 (6 years)
		Corredor (La Paz – Cerralvo)	114 (2 years)
	Central Gulf of California	Loreto	1,512 (15 years)
		San Pedro Nolasco Island	630 (5 years)
		Midriff Islands region	559 (3 years)
	North Gulf of California	San Pedro Martir Island	1,296 (15 years)
		Revillagigedo	225 (4 years)
			280 (2 years)
Nicaragua			720 (4 years)
Panama			

DISCUSSION

There are no scientific reports of *S. astori* from the Baja California Pacific coast (Butler *et al.*, 2011). According to Soberón and Peterson (2005), the distribution of a species is determined mainly by three factors: (1) abiotic conditions (climate and physical environment), (2) biotic interactions among species, and (3) accessible areas according to the dispersion limits of the species from where they originally evolved. The distribution of lobster-like species is influenced by their lifecycles and dispersive planktonic larval stage (Sandifer, 1975). The duration of the larval stage is one of the key factors that determine dispersal patterns and population connectivity (Shanks *et al.*, 2003; Palero *et al.*, 2008; Ayata *et al.*, 2010). The larval ecology (especially number of larval stages and their duration) of *S. astori* is poorly known (Johnson and Knight, 1975), but larvae could be transported thousands of kilometers away from their parental stock by ocean currents (Béarez and Hendrickx, 2006), to areas with similar biological and physicochemical conditions within the ecoregion (Tropical East Pacific; Spalding *et al.*, 2007) or biogeochemical provinces

(central American coastal and North Pacific equatorial countercurrent; Reygondeau *et al.*, 2013). The genus *Scyllarides* has a relatively long larval phase, with seven to nine planktonic stages, comprising a duration of six months of planktonic life (Atkinson and Boustead, 1982; Ito and Lucas, 1990; Kittaka *et al.*, 1997). These characteristics provide larvae of *S. astori* the potential to cover thousands of kilometers before finally settling out of the water column and metamorphosing into juveniles. Nevertheless, the distribution of larvae and the recruitment to adult populations do not depend solely on currents, since specific physical and biological characteristics enable their settlement (habitat, food availability, temperature, and salinity; Booth *et al.*, 2005).

The distribution of *S. astori* is related to subtropical waters. Hearn (2006) and Hearn *et al.* (2007) mentioned that there is limited knowledge of *S. astori* distribution throughout the ETP, presenting records only from the Galapagos Islands and the Gulf of California. These two sites represent the highest number of data used for this model (Fig. 1a), but there is a wide occurrence gap in tropical waters (Hearn *et al.*, 2007). Nonetheless, the distribution model

showed the presence of the species in tropical areas such as Ecuador, Colombia, and the Central Mexican Pacific, contradicting that it is a characteristic species for subtropical waters (Hearn, 2006; Béarez and Hendrickx, 2006). The expansion in the distribution of *S. astori* to warmer waters was documented recently by Azofeifa-Solano *et al.* (2016) and Carbajal-López *et al.* (2017) for Cocos Island (Costa Rica) and Central Mexican Pacific, respectively.

Here we present the first record of *S. astori* in adult stage in three islands in the Eastern Pacific Ocean: Guadalupe, Natividad, and Socorro (Fig. 2a). These three new records could be due to the connectivity between banks, sea mountains, archipelagos, islands, and islets present in the ETP (Lessios and Baums, 2016) because water masses and circulation in the ETP enhances larval dispersal in a northwestern direction during the reproductive season of the Galapagos slipper lobster (Hearn *et al.*, 2007; Portela *et al.*, 2016; Fiedler and Lavin, 2017). In the summer (July to September), the current speed in front of Baja California is around 0.52 knots in a northwesterly direction, and in the north equatorial current it is between 0.20–0.24 knots (Wyrtki, 1965). It may take 80 days (with an average speed of 0.2 knots) for a *S. astori* larvae to cover the distance of about 600 km from Central Mexican Pacific Marias Islands to Revillagigedo Archipelago; ~130 days from Revillagigedo Archipelago and Maria Islands to Natividad or Guadalupe Islands (more than 1,000 km), and ~20 days between Baja California to Natividad or Guadalupe Islands (less than 200 km).

Another possible explanation for the records of *S. astori* to new sites is the variation in marine currents, temperature, and phytoplankton availability (food for lobster larvae) due to mesoscale changes such as ENSO (El Niño Southern Oscillation) events (García-Morales *et al.*, 2017; Farach-Espinoza *et al.*, 2021). The lobsters found at Natividad and Guadalupe Islands were 20 and 30 cm in length, respectively. Using the lobster growth model (Hearn, 2006), we estimated that their ages were between six and eight years old, suggesting that their larval settlements in those islands occurred in 2012. In that same year, a warming event occurred in the eastern Equatorial Pacific during spring, moving westwards to the central Equatorial Pacific during summer (Su *et al.*, 2014). This anomaly

in the Pacific Ocean could have supported the arrival of the larvae in Natividad and Guadalupe islands.

The presence of adult specimens of *S. astori* in the central Baja California peninsula, Gulf of California, Central Mexican Pacific, Colombia, and Ecuador (Fig. 2) suggests that the species can be found in cooler temperate-subtropical and warm-tropical waters. The distribution model of the lobster, however, revealed a preference of *S. astori* for subtropical waters (Fig. 2), and this does not correspond to abundances found in monitoring programs in the Mexican Pacific and cooler waters of the Gulf of California.

In Galapagos Islands, the species has been reported in different regions (Hearn *et al.*, 2007), with abundance values between 0.06 and 1.00 ind/100 m² in the central-south region, west and Bolivar channel (Edgar *et al.*, 2002). This situation allows the development of an important fishery in the region (Hearn *et al.*, 2007). The Galapagos slipper lobster is very rare in the northern Mexican Pacific region, and even though some fishers mention that they have captured it (pers. comm., Camilo Cazares Cota and Leopoldo Encinas in the central Gulf of California; Miguel Bracamontes in Pacific of Baja California), the development of a fishery is not sustainable because of its low abundance. These conditions (low presence and low abundance) have also been registered in marine monitoring programs carried out in the Pacific coast of Baja California, central and southern Gulf of California, Panama, and Nicaragua (Tab. 2). In the northern Gulf of California we found a density of 0.006 ind/100 m² (Tab. 2). In the remaining monitored sites from the ETP the species was not recorded.

The fact, however, that it was not detected in the surveys does not mean that the species is absent in other ETP areas as predicted by the model. Underwater surveys may have two biases when recording species: (1) the observational field method used in our surveys (area, time, and depth) does not pay attention to cryptic species that hide under rocks or crevices, or at depths greater than 20 m; and (2) daytime surveys are not adequate for the detection of nocturnal species such as lobsters (Spanier and Lavalli, 1998).

The presence of *S. astori* in areas of its putative range in the ETP adds to an already large body of research, which evidences that many species have been

recorded for the first time in areas that were colder in the past (Hernández-Veslaco *et al.*, 2016; Lonhart *et al.*, 2019). These authors repeatedly cite the possible effect of global climate change to explain the new records, and the occasional warm water and current change along the Eastern Pacific coast. Robinson (2016) and Xiu *et al.* (2018) documented a clear warming tendency of the California Current during the last five years, resulting in the occurrence of shifting between northern and southernmost species. This effect has been observed not only in the Pacific (Hernández-Velasco *et al.*, 2016; Lonhart *et al.*, 2019). Several studies have identified lobster species expanding their distribution ranges (Dall'Occo *et al.*, 2007; Lakshmi and Thirumilu, 2007; Azofeifa-Solano *et al.*, 2016).

Little is known about the biology and ecology of *S. astori* and we encourage expanding the studies of this species to learn more about these aspects. Also, increasing monitoring and sampling of this species could help to better understand its distributional patterns and preferences, having a higher accuracy for future species distribution models of the species could help to avoid small sample size as a limitation (Barry and Elith, 2006).

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