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First record of the genus *Paracaristius* (Perciformes: Caristiidae) from the Pacific of Central America, with comments on their association with the siphonophore *Praya reticulata* (Siphonophorae: Prayidae)

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Manefish are not very common and there are few observations of associations with other organisms. An adult of the manefish Paracaristius maderensis *and a juvenile of* Paracaristius *sp. are reported for the first time for the Pacific coast of Central America. The adult specimen (215 mm standard length) was captured off Panama, at a depth of 1000 m. The juvenile specimen (17.5 mm standard length) was recorded on video, in association with the siphonophore* Praya reticulata *at Isla del Coco National Park, Costa Rica, at a depth of 100 m. A brief description of specimens supporting this record as well as comparative morphometric data and distributional information are provided. The fish–siphonophore association is illustrated.*

Keywords: new records, eastern Pacific, manefish, siphonophores, symbiosis, Costa Rica, Isla del Coco

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INTRODUCTION

The family Caristiidae, commonly known as manefish or veilfins, includes four genera (*Caristius* Gill & Smith, 1905; *Neocaristius* Stevenson & Kenaley, 2011; *Paracaristius* Trunov, Kukuev & Parin, 2006; and *Platyberyx* Zugmayer, 1911) and nineteen recognized species (Trunov *et al.*, 2006; Stevenson & Kenaley, 2011, 2013; Kukuev *et al.*, 2012, 2013; Eschmeyer & Fong, 2014). These fish are characterized by having relatively short heads, steep snouts, large eyes, deep and strongly compressed bodies, very long and high dorsal fins, greatly elongated pelvic fins (Trunov *et al.*, 2006; Benfield *et al.*, 2009; Stevenson & Kenaley, 2011, 2013; Kukuev *et al.*, 2012, 2013), and for maintaining symbiotic relationships with siphonophores (Janssen *et al.*, 1989; Lindsay *et al.*, 2001; Nelson, 2006; Benfield *et al.*, 2009).

Manefish are found throughout the oceans of the world, but appear to be relatively uncommon (Trunov *et al.*, 2006; Benfield *et al.*, 2009; Stevenson & Kenaley, 2011, 2013; Kukuev *et al.*, 2012, 2013). Larvae are epipelagic and juveniles occur from the epipelagic to the mesopelagic (Moser, 1996; Beltrán-León & Ríos, 2000; Benfield *et al.*, 2009; Jiménez-Rosenberg *et al.*, 2010); while adults are mesopelagic and bathypelagic, occurring at depths ranging from 100 to 2000 m, but usually between 300 and 800 m (Benfield *et al.*, 2009; Stevenson & Kenaley, 2011, 2013).

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In the eastern Pacific region four species of manefish have been formerly recorded: *Caristius macropus* (Bellotti, 1903) from the Bering Sea, and the west coast of Canada down to California; *Paracaristius maderensis* (Maul, 1949), from the California Current region and the Colombian coasts; *Paracaristius nudarcus* Stevenson & Kenaley, 2011 from off California and the Central Eastern Pacific; and *Platyberyx andriashevi* (Kukuev *et al.*, 2012), a single record from off California, San Pedro Basin (Moser, 1996; Beltrán-León & Ríos, 2000; Trunov *et al.*, 2006; Stevenson & Kenaley, 2011, 2013). Notably, most records of *Paracaristius maderensis* in eastern Pacific waters are on the basis of juvenile specimens (Moser, 1996; Beltrán-León & Ríos, 2000; Jiménez-Rosenberg *et al.*, 2010), and only two adult specimens have been previously recorded from this region (see Trunov *et al.*, 2006 for detailed localities).

In this paper the manefish family Caristiidae is reported for the first time on the Pacific coast of Central America on the basis of two specimens: an adult specimen of *Paracaristius maderensis* (215 mm standard length (SL)), captured on 15 June 1973 using a 3 m Isaacs-Kidd midwater trawl, at 103 km, 192.7° from Punta Burica, Panama (7°07′20.64″N 83°04′22.80″W), at a depth of 950–1000 m; and a juvenile specimen of *Paracaristius* sp. (17.5 mm SL), captured on video with the DeepSee submersible on 18 August 2013, at the Piedra Drop diving site on Isla del Coco National Park, Costa Rica (5°34′39.3″N 87°03′32.34″W), at a depth of 100 m. A brief description of these specimens as well as comparative morphometric data and distributional information are presented. Additionally, we document the association of

Paracaristius sp. with the siphonophore *Praya reticulata* (Bigelow, 1911), also captured on video with the DeepSee submersible. A brief description of the siphonophore and comparative distributional information are also provided.

MATERIALS AND METHODS

The adult specimen of *Paracaristius maderensis* was deposited at the Fish Collection of the Museo de Zoología, Universidad de Costa Rica (UCR-Velero-IV 19073). Counts and measurements (Table 1) were taken on the left side of the specimen and follow those in Hubbs & Lagler (1958). Measurements were made using a caliper to the nearest 1 mm. Comparative information was obtained from Trunov *et al.* (2006), Stevenson & Kenaley (2011, 2013) and Kukuev *et al.* (2012, 2013).

The juvenile specimen of *Paracaristius* sp. and the siphonophore were recorded on video, taken with a high-definition digital camera mounted on the DeepSee submersible (see Cortés & Blum, 2008 for details). Video was recorded on mini-DV tapes and then digitized to a QuickTime format. Image grabs for examination were obtained in the laboratory using the iMovie and the FinalCut software (Apple Inc.).

The descriptions in Moser (1996), Beltrán-Léon & Ríos (2000), Jiménez-Rosenberg *et al.* (2010) and Stevenson & Kenaley (2011, 2013) were used to identify the juvenile specimen of *Paracaristius* sp. The siphonophore was identified and compared with the descriptions by Pugh (1999) and Mapstone (2009); terminology of the gastrovascular canals, which are an important taxonomic feature, follows that given in Haddock *et al.* (2005) with modifications by Mapstone (2009).

Table 1. Morphometric and meristic data of *Paracaristius maderensis* from Panama (UCR-Velero-IV 19073) and comparative material (data from Stevenson & Kenaley, 2011): morphometric data expressed as percentages of standard length (SL), except when indicated as percentages of head length (HL).

Characters	This study	Stevenson & Kenaley (2011)
Morphometric		
Standard length (mm)	215	180–247
Body depth	54.0	49.6–57.6
Head length	34.1	29–34.3
Predorsal length	23.3	15.9–24.5
Prepectoral length	39.2	31.7–40.4
Prepelvic length	31.4	27.8–46.2
Pectoral-fin base	6.9	6.7–7.6
Preanal length	57.7	59–69.6
Dorsal-fin base	71.6	66–75.3
Anal-fin base	35.8	33.7–38
Peduncle length	12.6	11.4–14.5
Peduncle depth	14.1	14.9–16
Upper jaw length (% HL)	46.7	44.4–52.2
Lower jaw length (% HL)	39.6	39.5–49.2
Bony orbit width (% HL)	38.4	37–43.8
Preorbit length (% HL)	19.9	5.6–21.3
Meristic		
Dorsal-fin rays	29	29–31
Anal-fin rays	19	18–19
Pectoral-fin rays	17	16–18
Upper jaw teeth	87	34–85
Lower jaw teeth	61	20–72
Gill rakers	22	22–23

RESULTS

SYSTEMATICS

Order PERCIFORMES
Family CARISTIIDAE
Genus *Paracaristius* Trunov, Kukuev & Parin, 2006
(Figures 1 & 2)

DESCRIPTION

The adult specimen (*Paracaristius maderensis*; Figure 1) had a rectangular body, brown in colour; head laterally compressed, deep, and relatively short, with the anterior profile rounded; snout extremely compact; mouth relatively large, upper jaw with the posterior margin extending nearly to mid-orbit; dentary and premaxillary teeth in 2–3 indistinct rows along most of dentary and premaxilla, diminishing to a single row only near posterior terminus of dentition; vomerine teeth absent; pharyngobranchial teeth long and needle-like, approximately of the same length as rakers of first gill arch; eye relatively large; suborbital space relatively broad, completely covered with scales; fingerlike papillae absent along dorsal margin of hyoid arch and at articulation of interhyal and posterior ceratohyal; scales on body irregular in size, not arranged in distinct rows; lateral line absent; predorsal distance relatively short, dorsal-fin originating posterior to dorsal end of preopercle; and pectoral, pelvic, and anal fins elongate, delicate and black. Additional morphometric and meristic data of specimen and comparative information are given in Table 1.

The juvenile specimen of *Paracaristius* sp. (Figure 2) had a teardrop-shaped body, with its maximum depth about 59% of

Fig. 1. *Paracaristius maderensis*, adult specimen, 215 mm standard length (UCR-Velero-IV 19073), caught off Panama. Scale bar: 20 mm.

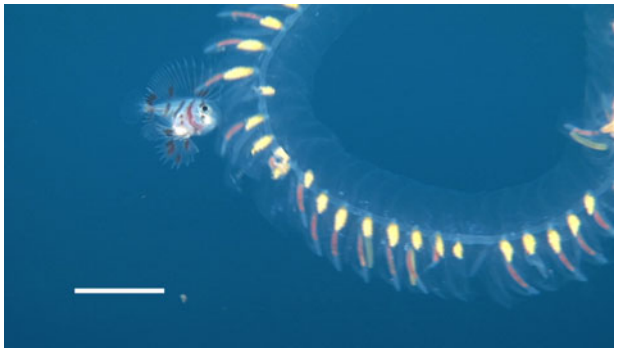

Fig. 2. *Paracaristius* sp., juvenile specimen, 17.5 mm standard length, and siphosome of *Praya reticulata*, photographed off Isla del Coco National Park, Costa Rica, at a depth of 100 m. Scale bar: 20 mm.

Table 2. Comparison of some meristic characters (dorsal and anal fin counts) and position of the dorsal fin origin relative to the eye of adults and juveniles of the four species of Caristiidae known to occur in the eastern Pacific region. Stage: A, adult; J, juvenile. D, dorsal fin rays. afr, anal fin rays; d, e, position of the origin of the dorsal fin relative to the eye; *, juvenile description not available.

Species	Stage	D	afr	d, e	Reference
Caristius macropus	A	32–36	21-26	Posterior	Stevenson & Kenaley, 2013
	J	34	22	Posterior	Okamoto *et al.*, 2010
Paracaristius maderensis	A	29–31	18-19	Posterior	Stevenson & Kenaley, 2011
	A	29	19	Posterior	This study
	J	29	17	Posterior	Beltrán-León & Ríos, 2000
	J	26–31	15-20	Above	Moser, 1996
*Paracaristius nudarcus**	A	27–31	17-20	Above	Stevenson & Kenaley, 2011
Paracaristius sp.	J	26	17	Above	This study
*Platyberyx andriashevi**	A	31–35	20-22	Above	Stevenson & Kenaley, 2013

the SL; silvery-white coloured, with six vertical black bands: (1) crossing the eye, (2) in the upper region of the gill opening, (3) in the lower horizontal half of the body near the pectoral fin, (4) above the origin of the anal fin to the dorsal fin base, (5) located up to the posterior half of the anal fin and (6) a thicker band than the others located in the caudal peduncle; and a relatively large head, about 42% of SL; transparent fan-like fins (pelvic and dorsal fins with several black blotches); dorsal relatively long, its base 77% of SL; and anal fin relatively short, its base 26% of SL. According to Moser (1996), this specimen matches well with the description of *Paracaristius maderensis*; however, it is important to note that the early stage of the recently described *Paracaristius nudarcus*, also present in the region, has not yet been adequately described; thus, our identification remains at the generic level. Some comparative morphological data from adults and juveniles of all eastern Pacific manefish species are given in Table 2.

SYSTEMATICS

Order SIPHONOPHORAE
Family PRAYIDAE
Genus *Praya* Quoy & Gaimard, 1834
Praya reticulata (Bigelow, 1911)
(Figures 2 & 3)

DESCRIPTION

Colony up to 100 cm in length (Figure 2), with definitive nectophores with a baso-ventral extension below the ostium of the nectosac (Figure 3), radial canals of nectosac with many anastomoses which form a reticulated pattern; ascending surface diverticulum with many short lateral branches; and somatocyst consisting of a single median ascending branch only. The bracts, although not visible in the video, are described by Pugh (1999) and Mapstone (2009) as having a long upper canal curving in the direction of hydroecial lobe, and the anterior hydroecial canal is also long and curves distally. This species can be distinguished from its other eastern Pacific congener *Praya dubia* Quoy & Gaimard (1834) in having several short lateral branches that rise from the ascending surface diverticulum (vs two subdividing lateral branches in *P. dubia*) and several anastomosing radial canals of the nectosac (vs bifurcating canals in *P. dubia*) (Pugh, 1999; Mapstone, 2009).

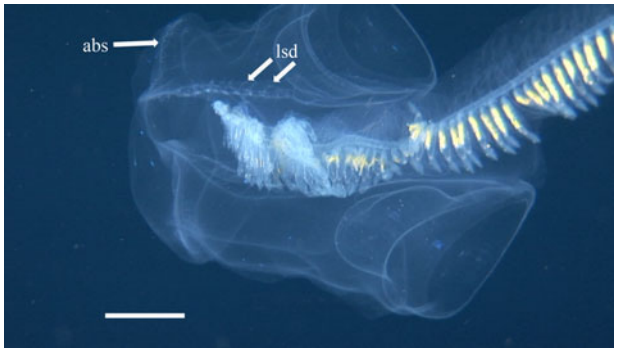

Fig. 3. *Praya reticulata*, detail of the definitive nectophores. Abs, ascending branch of somatocyst; lsd, lateral surface diverticulum. Scale bar: 20 mm.

FISH SIPHONOPHORE ASSOCIATION

The observations of the fish–siphonophore association were made during a DeepSee submersible immersion at the Piedra Drop diving site, on 18 August of 2010, between 15:20 and 15:24 h, at a depth of 100 m (bottom depth = 315 m). The manefish was observed swimming freely very close to *Praya reticulata* while the colony was moving. During that time no predation events or other specific interactions were recorded.

Horizontal and vertical displacements of the fish and the siphonophore were observed. The fish, always in close contact with the gastrozoids showed at all times the pelvic fins in a broadly expanded or parachute-like position, making only slight movements. Most of the time, the fish was observed swimming, in a normal position (horizontal), with the anterior region directed to the oral end of the gastrozoids, and using only pectoral and pelvic fins' flapping movements. Vertical sinusoidal movements of the caudal fin were also observed while the fish showed a nearly vertical head down position in both vertical and horizontal displacements; these displacements were performed in order to follow the serpentine movements of the siphonosome. No specific interaction between a single zooid and the fish was recorded.

DISCUSSION

In general terms, observations of associations between fish and siphonophores are rare (Purcell & Arai, 2001), and details about these associations are relatively well known in only a few cases, e.g. *Caranx malabaricus* (Bloch & Schneider, 1801) with

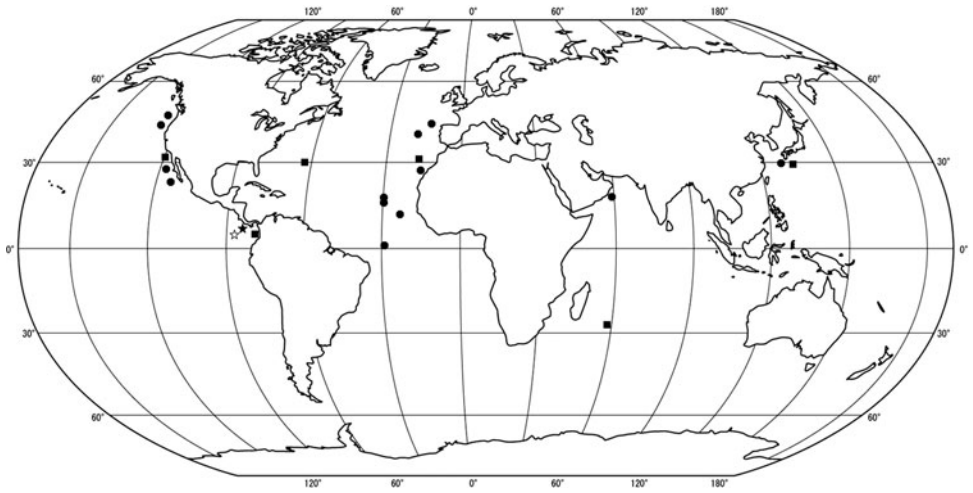

Fig. 4. Distribution of *Paracaristius maderensis* (squares) and *Praya reticulata* (circles) (Alvariño, 1971; Shih *et al.*, 1971; Trunov, 2006; Mapstone, 2009; Stevenson & Kenaley, 2011); stars indicate the present records (closed star, adult *P. maderensis*; open star, *Paracaristius* sp. and *P. reticulata*).

Porpita porpita (Noble, 1963) and *Nomeus gronovii* (Gmelin, 1789) with *Physalia physalis* (Arai, 1988). In the few cases reported, adult fish are known to feed on the siphonophores (Jenkins, 1983; Purcell & Arai, 2001), whereas juvenile fish shelter among their tentacles, steal prey and/or eat part or the whole animal (Biggs, 1976; Purcell & Arai, 2001). In caristiid fish all these scenarios appear to be feasible (e.g. *Caristius* sp. has been observed stealing food and eating parts of the cystonect siphonophore *Bathyphysa conifera* (Janssen *et al.*, 1989); unidentified caristiid juveniles have been observed associated with the siphosome of an unidentified *Praya* species (Lindsay *et al.*, 2001); and adult specimens of *Paracaristius* sp. have been observed in close proximity of damaged siphonophores of the family Apolemiidae, suggesting that the damage observed in the colony might have been produced by these fish (Benfield *et al.*, 2009)).

Until now a specific association between *Paracaristius* and *Praya reticulata* has not been properly described in the literature. Our observations, preliminary and very limited in space and time, suggest that the presence of the *Paracaristius* sp. juvenile does not disturb to *Praya reticulata*, and that the fish uses the siphonophore as a shelter. These results are consistent with what has been observed in other caristiid species (see above). Based on our observations we cannot conclude that the fish feeds on the siphonophore; however, given the evidence (e.g. Janssen *et al.*, 1989), this hypothesis cannot be rejected.

In this sense, the morphology of the fish (Figure 2) could indicate that the prey it eats is probably stolen from the siphonophore (as reported by Janssen *et al.*, 1989 in *Caristius* sp.); given that these fish are not shaped like a typical pelagic predator, but have a tear drop shaped body and fan-like fins, characteristics of fish that manoeuvre around objects. Benfield *et al.* (2009) suggested that the parachute-like position exhibited by the fish during the time that was observed provides greater stability when swimming in close proximity to siphonophores. Ting & Yang (2008) suggested that the vertical sinusoidal movement of the caudal fin also exhibited by the fish, termed caudal fin-wave propagation, is adaptive in providing stabilization during head-down postures, as we also noted. All these factors could explain why the fish was observed swimming very close to *Praya reticulata* while the colony was moving.

Adult *Paracaristius maderensis*, of circumtropical distribution (Figure 4), are found at depths of 100 to 2000 m (Trunov *et al.*, 2006; Stevenson & Kenaley, 2011; Froese & Pauly, 2014). Juveniles have been collected at depths between 44 and 285 m on the Pacific coast of Colombia (Beltrán-León & Ríos, 2000), and have been captured on video at depths between 496 and 829 m in the northern Gulf of Mexico (Benfield *et al.*, 2009). In the eastern Pacific region, this species has been previously recorded in the California Current region (Moser, 1996; Jiménez-Rosenberg *et al.*, 2010), and off the Colombian central coast (Beltrán-León & Ríos, 2000) (Figure 4). Other species in the genus have similar horizontal and vertical distribution patterns (see Trunov *et al.*, 2006 and Stevenson & Kenaley, 2011 for details). *Praya reticulata*, also of circumglobal distribution (Figure 4), is found at depths of 50 to 4380 m (Alvariño, 1971; Shih *et al.*, 1971; Mapstone, 2009). In the eastern Pacific region this species has been previously recorded in the Subartic Province (Stepanjants, 1967), in the California Current region, where it seems to be more common than *Praya dubia* (Bigelow, 1931; Alvariño, 1971, 1991; Shih *et al.*, 1971; Mills, 1981; Mapstone, 2009), in equatorial waters (Alvariño, 1971), and in the southern portion of the eastern Pacific, including the Subantartic Province (Totton, 1965). The overlap in the horizontal and vertical distribution of *Paracaristius* species and *Praya reticulata* suggests that this association may be common in epi- and mesopelagic waters worldwide. Although the encounter reported here is a short-term observation, and the specific identification of the manefish is provisional, this study increases the information of the siphonophore association and *in situ* behaviour of this unusual group of fish.

The discovery of these specimens in Costa Rican and Panamanian waters, particularly this new record of *Paracaristius maderensis*, increases the knowledge about our marine fauna and provides evidence of a broader distributional pattern for these species in the eastern Pacific region.

Supplementary material and methods

The supplementary material referred to in this article can be found online at journals.cambridge.org/mbdcup.

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