Journal of the Marine Biological Association of the United Kingdom, 2018, 98(6), 1219–1226.
doi:10.1017/S0025315417000558

New records of gelatinous zooplankton from an oceanic island in the Eastern Tropical Pacific

MARCO CORRALES-UGALDE[1,2], ANDRÉS J. QUESADA[3], BEATRIZ NARANJO-ELIZONDO[1,4] AND JORGE CORTÉS[1,4]

[1]Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Ciudad de la Investigación, Universidad de Costa Rica, San Pedro, 11501-2060 San José, Costa Rica, [2]Oregon Institute of Marine Biology, University of Oregon, Eugene, OR 97403, USA, [3]Salish Sea Research Center, Northwest Indian College, 2522 Kwina Road, Bellingham, WA 98226, USA, [4]Escuela de Biología, Universidad de Costa Rica, San Pedro, 11501-2060 San José, Costa Rica

Gelatinous zooplankton are an abundant and diverse group of animals in the pelagic environment. However, knowledge of species diversity and spatial distributions, as well as their ecological role, is scarce. We present information of epi- and mesopelagic gelatinous zooplankton recorded by the 'DeepSee' submersible between 2006 and 2012 at Isla del Coco (Cocos Island), Costa Rica, an oceanic island in the Eastern Tropical Pacific. Two species of scyphomedusae, three species of hydromedusae, two genera of siphonophores, and two species of ctenophores were observed in the videos, at depths between 50 and 400 m. None of these species had been previously recorded in the waters around the island. Furthermore, except for the jellyfish Pelagia noctiluca *and a siphonophore in the genus* Praya*, all are new records for Costa Rican waters. This study also includes the first record of the cnidarians* Modeeria rotunda, Solmissus *sp.,* Halitrephes maasi *and* Apolemia *spp., and the ctenophore* Thalassocalyce inconstans *in the Eastern Tropical Pacific. We show that surveys in regions with little information about gelatinous zooplankton may broaden our knowledge of their natural history and may result in new records of gelatinous species.*

Keywords: Hydrozoa, Scyphozoa, Ctenophora, new records, marine biodiversity, submersible, Isla del Coco, Cocos Island, Costa Rica

Submitted 2 June 2016; accepted 21 March 2017; first published online 2 May 2017

INTRODUCTION

The abundance and diversity of gelatinous zooplankton became evident when biologists began to dive in the open ocean (Hamner *et al.*, 1975; Madin & Harbison, 1978). In recent years, direct observations from submersibles have shown that these organisms are extremely abundant at depths of 200–400 m, where presumably they play an important role in pelagic processes (Angel, 2003; Robison, 2004). Although knowledge of their ecological role in the oceans is scarce, they are considered important consumers of basal producers, both as grazers of phytoplankton and predators of fish larvae and other gelatinous zooplankton (Lucas *et al.*, 2014). Because they also act as hydroclimatic indicators (Richardson, 2008), knowledge of species distribution is crucial to have well defined baseline information.

Isla del Coco (also known as Cocos Island) is located in the Eastern Tropical Pacific (ETP), a distinct epipelagic province where striking changes in species composition occur between the epi- and mesopelagic zones (Longhurst, 2001; Spalding *et al.*, 2012). This island has been a site of intense scientific study due to its rich marine biodiversity, yet some animal groups, such as gelatinous zooplankton, remain poorly studied both locally at Isla del Coco (Cortés, 2012) and regionally in the ETP (Costello *et al.*, 2010; Cortés *et al.*, 2017).

The 'DeepSee' submersible has explored the island to depths of 450 m since 2006 (Cortés & Blum, 2008) and has taken video footage of the local pelagic and benthic ecosystems. Here we present genera and species of cnidarians and ctenophores that have been opportunistically recorded around Isla del Coco National Park, along with images, species descriptions, and spatial and temporal distributions of these organisms.

Corresponding author:
M. Corrales-Ugalde
Email: mcugalde88@gmail.com

MATERIALS AND METHODS

Images of gelatinous zooplankton were captured from videos taken with the 'DeepSee' submersible (Cortés & Blum, 2008) at several locations around Isla del Coco National Park (Figure 1). During some immersions, when a gelatinous organism was observed, the camera was turned on and recorded the animal for ~ 1 min. Videos were recorded with an AVI format on mini-DV tapes by a high definition Sony HDX7 camera (frame size: 1920 × 1080 pixels) and then transcoded with a 4:2:2 low codec to a .mov format. Image grabs were made in the laboratory using Imovie and FinalCut software (Apple Inc.). The videos were recorded on dives made from 2006 to 2012. Videos were recorded every year, but the depth varied, with 100 and 300 m usually being targeted.

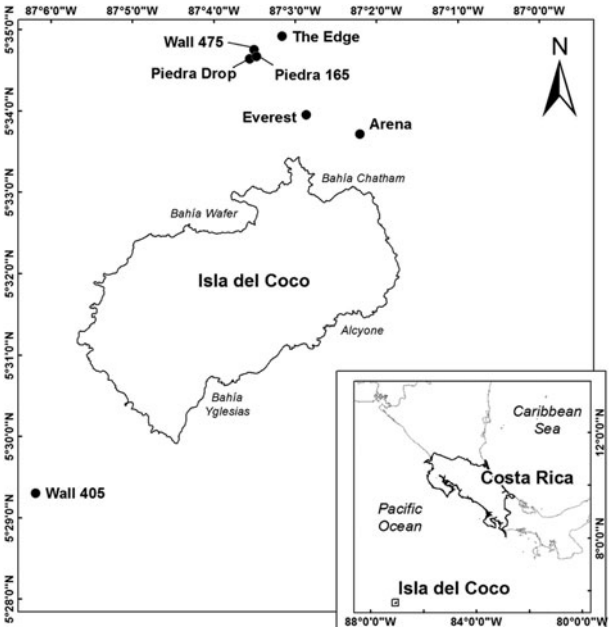

Fig. 1. 'DeepSee' dive sites around Isla del Coco National Park, Costa Rica.

The descriptions of the observed organisms were supplemented with information from Kramp (1961), Segura-Puertas (1984), Suárez & Gasca (1991), Wrobel & Mills (1998), Bouillon (1999), Mianzan (1999), Mianzan & Cornelius (1999), Pugh (1999) and Lindsay *et al.* (2015). Our identifications were verified by experts on these groups: Dhugal Lindsay, Casey W. Dunn, Rebeca Gasca, Jun Nishikawa, Laurence P. Madin, Phil R. Pugh, Jennifer E. Purcell and Karina Rodríguez-Sáenz. Images of the species are included along with a brief description, distribution data at Isla del Coco National Park (e.g. location, depth, date, time of day), previous reports in the Eastern Tropical Pacific, and comments on their known distribution.

RESULTS

Nine species of medusae, ctenophores and siphonophores were observed at Isla del Coco National Park (Table 1), none of which had been previously recorded in this island. All of these species, except *Pelagia noctiluca* (Forsskål, 1775) and the genus *Praya* are new records for Costa Rican waters. This study includes the first record of the species *Modeeria rotunda* (Quoy & Gaimard, 1827), *Solmissus* sp., *Halitrephes maasi* Bigelow, 1909, *Apolemia* spp. and *Thalassocalyce inconstans* Madin & Harbison, 1978, in the Eastern Tropical Pacific.

Due to the limitations of video resolution and the orientation of some organisms when they were recorded, only the genus could be determined for *Solmissus* sp., *Praya* sp., *Apolemia* spp. and *Hormpihora* sp. Also, because the 'DeepSee' is used mostly for tourism, this study does not include precise information of each observation made such as depth, temperature and salinity. Approximate depths for each observation were included only when the organism was observed near the sea floor (the maximum dive depths were recorded in the submersible log). Otherwise, a range is given based on the maximum dive depth, amount of light present,

Table 1. Species recorded in the videos taken by the 'DeepSee' submersible at Isla del Coco.

Species	Sites	Depth (m)	'DeepSee' video log
Cnidaria-Schypozoa			
Pelagia noctiluca (Forsskål, 1775)	Arena (05°33.732′N 87°02.232′W)	200	581
	Wall 0475 (05°34.753′N 87°03.504′W)	80	426, 583
Phacellophora camtschatica Brandt, 1835	Everest (5°33.950′N 87°02.862′W)	50–300	1072, 1099, 1209
	Piedra 165 (05°34.670′N 87°03.473′W)	300	278
	Piedra Drop (5°34.640′N 87°03.557′W)	310	420, 1029, 1062, 1096, 1101,
	Wall 0475 (05°34.753′N 87°03.504′W)	300, 315, 330, 320, 302	1209, 454, 479, 526, 527, 540, 542, 957, 959, 972, 979
Cnidaria-Hydrozoa			
Modeeria rotunda (Quoy & Gaimard, 1827)	Piedra 165 (05°34.670′N 87°03.473′W)	200	953
	Wall 0475 (05°34.753′N 87°03.504′W)		1030
Solmissus sp.	Piedra Drop (5°34.640′N 87°03.557′W)	150–300	1148
	Wall 0475 (05°34.753′N 87°03.504′W)		900
Halitrephes maasi Bigelow, 1909	Piedra 165 (05°34.670′N 87°03.473′W)	100–300	1244
	Piedra Drop (5°34.640′N 87°03.557′W)		1248
Praya sp.	Everest (5°33.950′N 87°02.862′W)	0–400	559
	The Edge (05°34.920′N 87°03.161′W)		280
	Piedra Drop (5°34.640′N 87°03.557′W)		1146, 1165
	Wall 0475 (05°34.753′N 87°03.504′W)		452, 453, 560
Apolemia spp.	Piedra Drop (5°34.640′N 87°03.557′W)	300–400	1231, 1236
	Wall 0475 (05°34.753′N 87°03.504′W)		497, 981
Ctenophora			
Hormiphora sp.	Wall 0475 (05°34.753′N 87°03.504′W)	300	452
Thalassocalyce inconstans Madin & Harbinson, 1978	Piedra 165 (05°34.670′N 87°03.473′W)	200–326	523, 1244
	Wall 0475 (05°34.753′N 87°03.504′W)		949

background terrain, and where one of us (JC) and others have observed them.

SYSTEMATICS

Phylum CNIDARIA Verrill, 1865
Class SCYPHOZOA Goette, 1887
Order SEMAEOSTOMEAE Agassiz, 1862
Family PELAGIIDAE Gegenbaur, 1856
Genus *Pelagia* Perón & Lesueur, 1810
Pelagia noctiluca (Forsskål, 1775)
(N = 7)
(Figure 2A–C)

RECORDED MATERIAL

Arena: 05°33.732′N 87°02.232′W, and Wall 0475: 05°34.753′N 87°03.504′W. One individual observed on 19 January 2008 at a depth of 200 m at Arena, and six individuals on 12 May 2007 at Wall 0475 at a depth of 80 m (Figure 2C).

DESCRIPTION AND DISTRIBUTION

Bell covered with numerous stinging warts. Eight marginal tentacles alternating with 7–8 rhopalia and 16 marginal lappets. Mouth arms also with numerous nematocyst warts and crenulated margins. Gonads well developed. The individuals observed had a golden brown colouration.

Pelagia noctiluca is a common epipelagic oceanic species found mostly in warm seas, from the coast of Mexico to Chile (Larson, 1990; Wrobel & Mills, 1998). This species is one of the most abundant in certain areas of the ETP, such as the shelf area off central Mexico during summer (Segura-Puertas *et al.*, 2010). In Costa Rica, it has been found in the Gulf of Nicoya and the Gulf of Papagayo (Rodríguez-Sáenz & Segura-Puertas, 2009).

Class SCYPHOZOA Goette, 1887
Order SEMAEOSTOMEAE Agassiz, 1862
Family ULMARIIDAE Haeckel, 1879–80
Genus *Phacellophora* Brandt, 1835
Phacellophora camtschatica Brandt, 1835
(N = 4)
(Figure 2D–F)

RECORDED MATERIAL

Wall 0475: 05°34.753′N 87°03.504′W; Everest: 5°33.950′N 87°02.862′W, Piedra Drop: 5°34.640′N 87°03.557′W; and Piedra 165: 05°34.670′N 87°03.473′W. Observed from April to November at a depth range between 50–300 m. A single individual observed each time.

DESCRIPTION AND DISTRIBUTION

Bell with orange colouration. Marginal lappets 15–16, broad and curved, outer margin divided into sub-lappets. Rhopalia: 16 in deep clefts. Oral arms long, about twice the size of the bell diameter, also with orange colouration. Radial canals broad, 4–5 in each lappet, typically wider than the gaps between them. Present in all of the Eastern Pacific (Larson, 1990), with a scattered distribution globally (Wrobel & Mills, 1998).

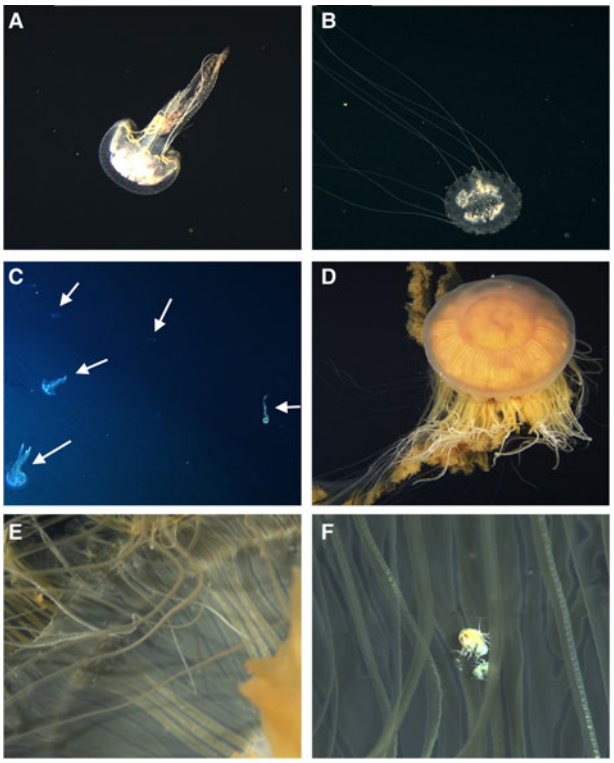

Fig. 2. Scyphomedusae recorded at Isla del Coco National Park. A–C: *Pelagia noctiluca*, (A) lateral view, (B) oral plane, (C) aggregation of *P. noctiluca* close to the bottom at the site 'Wall 0475'. D–F: *Phacellophora camtschatica*, (D) whole animal, (E) close-up of the radial canals, (F) hyperiid amphipods on subumbrellar cavity.

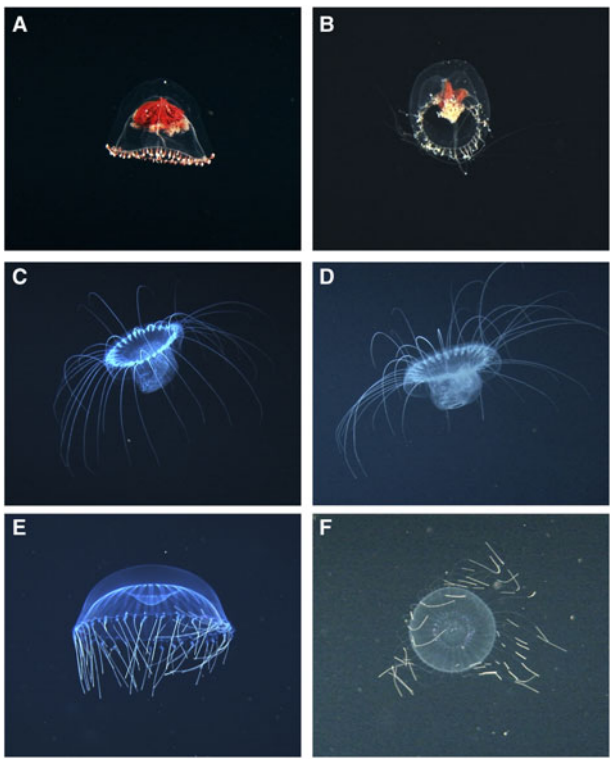

Fig. 3. Hydromedusae recorded at Isla del Coco National Park. A–B: *Modeeria rotunda*, (A) lateral view, (B) aboral plane, tentacles extended. C–D: *Solmissus* sp., (C) lateral view, (D) oral plane with gastrovascular cavity expanded, possibly due to prey capture. E–F: *Halitrephes maasi*, (E) lateral view with tentacles retracted, (F) aboral plane, tentacles extended.

Class HYDROZOA Owen, 1843
Order LEPTOTHECATA Cornelius, 1992
Family TIARANNIDAE Russell, 1940
Genus *Modeeria* Forbes, 1848
Modeeria rotunda (Quoy & Gaimard, 1827)
(N = 2)
(Figure 3A, B)

RECORDED MATERIAL
Piedra Drop: 5°34.640′N 87°03.557′W; Wall 0475: 05°34.753′N 87°03.504′W. One individual observed each time on 10 February 2010 at Piedra Drop and on 16 October 2009 at Wall 0475; at an approximate depth of 200 m in both cases.

DESCRIPTION AND DISTRIBUTION
Disc hemispherical, mesoglea thick, apex rounded, manubrium short, broad, cruciform. One individual with 25 tentacles (Figure 3A) and the other with 44 (Figure 3B). Mouth with four large, slightly crenulated lips. Gonads well developed and attached to the 4 radial canals. *Mooderia rotunda* is found in the North Atlantic, Mediterranean, Pacific and Antarctic oceans (Wrobel & Mills, 1998). This species has been collected in the San Clemente Basin off San Diego, California (Wrobel & Mills, 1998), but there are no previous records from the ETP.

Class HYDROZOA Owen, 1843
Order NARCOMEDUSAE Haeckel, 1879–80
Family CUNINIDAE Bigelow, 1913
Genus *Solmissus* Haeckel, 1879–80
(N = 2)
(Figure 3C, D)

RECORDED MATERIAL
Wall 0475: 05°34.753′N 87°03.504′W; and Piedra Drop: 5°34.640′N 87°03.557′W. One individual observed each time in June 2009 and July 2010 at an approximate depth of 150 and 300 m, respectively.

DESCRIPTION AND DISTRIBUTION
Bell flat. Mouth consists of a simple opening in the centre. Stomach pouches and lappets as numerous as tentacles, with a well-defined conical insertion base. One individual with 30 tentacles (Figure 3C, D) and the other with 27 (Supplementary material). Found previously in all warm and temperate seas, from the surface to abyssal depths (Kramp, 1961). There is no previous record of this genus in the ETP.

Class HYDROZOA Owen, 1843
Order TRACHYMEDUSAE Haeckel, 1866
Family HALICREATIDAE Fewkes, 1886
Genus *Halitrephes* Bigelow, 1909
Halitrephes maasi Bigelow, 1909
(N = 2)
(Figure 3E, F)

RECORDED MATERIAL
Piedra 165: 05°34.670′N 87°03.473′W; and Piedra Drop: 5°34.640′N 87°03.557′W. One individual observed at each site in December 2010 at an approximate depth of 300 and 100 m, respectively.

DESCRIPTION AND DISTRIBUTION
Bell thick, disc-shaped. One individual with 28 non-branching radial canals and 54 marginal tentacles (Figure 3E), another with 27 non-branching radial canals and 49 marginal tentacles (Figure 3F). All tentacles arranged in a single series, with a flexible proximal portion and a stiff spine-like distal portion. *Halitrephes maasi* is a deep-water species, probably cosmopolitan in warm and temperate regions (Wrobel & Mills, 1998). There are no previous records of this species in the ETP.

Class HYDROZOA Owen, 1843
Order SIPHONOPHORAE Eschscholtz, 1829
Family PRAYIDAE Quoy & Gaimard in de Blainville, 1834
Genus *Praya* Quoy & Gaimard, 1833
(N = 4)
(Figure 4A, B)

RECORDED MATERIAL
Wall 0475: 05°34.753′N 87°03.504′W; Everest: 5°33.950′N 87°02.862′W; Piedra Drop: 5°34.640′N 87°03.557′W; and The Edge: 05°34.920′N 87°03.161′W. A single colony was recorded each time. Nectophores were visible on all colonies. Species observed from July to December in 2006, 2007, 2010 at variable depths (0–400 m).

DESCRIPTION AND DISTRIBUTION
Two large cylindrical nectophores, with a baso-ventral extension below the ostium of the nectosac. Recorded for the Northern Pacific, Atlantic, Antarctic and Indian Oceans

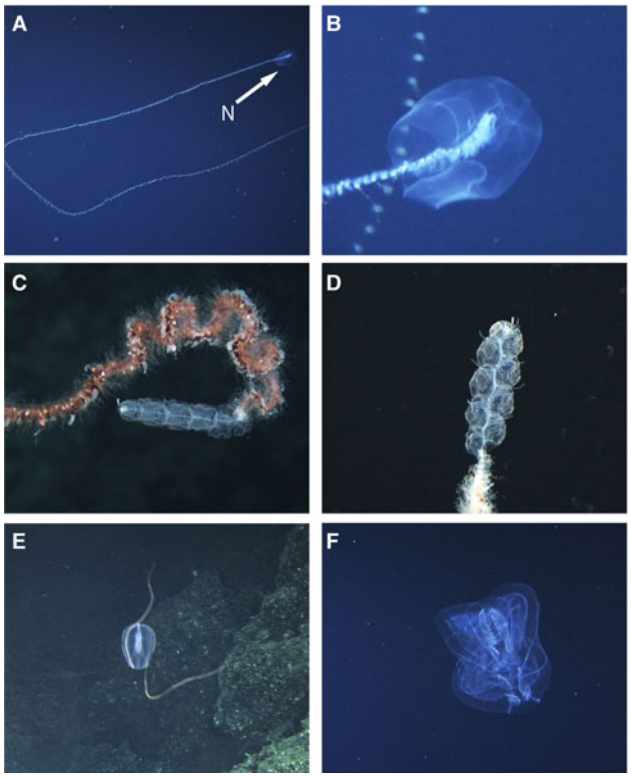

Fig. 4. Siphonophores and ctenophores recorded at Isla del Coco National Park. A–B: *Praya* sp., (A) whole colony, N: nectophore, (B) detail of the nectophores. C–D: *Apolemia* spp., (C) specimen without palpons and clear nectophores, (D) specimen with palpons and opaque spots on the nectophores, (E) *Hormiphora* sp. with tentacles extended. (F) aboral plane of *Thalassocalyce inconstans.*

(Mapstone, 2009). Alvariño (1971) reports the species *Praya reticulata* (Bigelow, 1911) in several locations in the Eastern Pacific and Angulo *et al.* (2014) has recorded this species for Isla del Coco. The genus *Praya* has also been collected on the Oceanographic Cruises to the Costa Rica Thermal Dome, DOMO I to IV between 1979 and 1982 (Vicencio-Aguilar & Fernández-Álamo, 1996).

Class HYDROZOA Owen, 1843
Order SIPHONOPHORAE Eschscholtz, 1829
Family Apolemiidae E. Huxley, 1859
Genus *Apolemia* Eschscholtz, 1829
(N = 2)
(Figure 4C, D)

RECORDED MATERIAL

Wall 0475: 05°34.753′N 87°03.504′W; and Piedra Drop: 5°34.640′N 87°03.557′W. A single colony was recorded each time. Observed on 13 November 2009 and 1 December 2010, close to the bottom at 300 and 400 m, respectively.

DESCRIPTION AND DISTRIBUTION

Nectophore hollowed axially, forming a pair of large axial wings. The nectosac is extensive and its lateral radial canals follow an S-shaped course of varying complexity. One of the colonies with 10 smooth nectophores and without palpons (Figure 4C), the other colony has 9 nectophores with numerous warts and palpons (Figure 4D). *Apolemia* is widely distributed in all oceans (Alvariño, 1971). There is no previous record of this genus in the ETP.

Phylum CTENOPHORA Eschscholtz, 1829
Class TENTACULATA Eschscholtz, 1825
Order CYDIPPIDA Gegenbaur, 1856
Family PLEUROBRACHIIDAE Chun, 1880
Genus *Hormiphora* L. Agassiz, 1860
(N = 1)
(Figure 4E)

RECORDED MATERIAL

Wall 0475: 05°34.753′N 87°03.504′W. Only one organism observed on 28 May 2007 at Wall 0475, at a depth of 300 m.

DESCRIPTION AND DISTRIBUTION

Body oblong, moderately compressed. Broadly rounded to flattened at the aboral end. Comb rows equal, extending from near the aboral pole to at least 4/5 the distance to the mouth. Canals underlying the comb rows without branches. Tentacle bulbs are about 1/3 of the body, located midway along the body and close to the pharynx. Tentacle sheaths parallel to the pharynx and exiting the body near the aboral end. Transparent body.

This genus has been recorded worldwide in warm and temperate seas. The species *Hormiphora* cf. *palmata* (Chun, 1898) has been reported in the Galápagos Islands (Tirado, 2012), but the author states that the identification and occurrence of this species in the archipelago is doubtful.

Class TENTACULATA Eschscholtz, 1825
Order THALASSOCALYCIDA Madin & Harbinson, 1978
Family THALASSOCALYCIDAE Madin & Harbinson, 1978
Genus *Thalassocalyce* Madin & Harbinson, 1978

Thalassocalyce inconstans Madin & Harbinson, 1978
(N = 3)
(Figure 4F, Supplementary Figure)

RECORDED MATERIAL

Wall 0475: 05°34.753′N 87°03.504′W; Piedra 165: 05°34.670′N 87°03.473′W. Three individuals observed between July and December in 2007, 2009 and 2010, at a depth of ~200 m at Wall 0475 site and near the bottom (326 m) at Piedra 165 and Wall 0475.

DESCRIPTION AND DISTRIBUTION

Body shaped like a broad medusa, up to 15 cm when fully expanded. Slit-like mouth on a central conical peduncle. Eight short comb rows. Tentacle bulbs located on sides of central peduncle. Tentacles with simple lateral filaments that are not enclosed in tentacle sheaths.

Known to occur in the Atlantic Ocean, Bahamas, Mediterranean and several locations off California (Wrobel & Mills, 1998). There is no previous record of this species for the ETP.

DISCUSSION

Observations of gelatinous zooplankton were not made systematically because the 'DeepSee' submersible is used for tourism, and recordings focused mostly on large, conspicuous animals. Therefore, small hydromedusae and siphonophores may have been overlooked. However, this study complements and increases existing information of these organisms in the Eastern Tropical Pacific (Morales-Ramírez, 2008; Angulo *et al.*, 2014). For instance, the scyphozoans *Pelagia noctiluca* and *Phacellophora camtschatica* are distributed from California to Chile (Larson, 1990), and were observed several times during the 'DeepSee' inmersions. *Pelagia noctiluca* has been previously found in Costa Rica (Rodríguez-Sáenz & Segura-Puertas, 2009), whereas *P. camtschatica* has not been recorded in Costa Rican waters. At Isla del Coco, aggregations of *P. noctiluca* (N = 6) were observed close to the bottom at the site 'Wall 0475' (Figure 2C).

Hydromedusae are well studied in the region (e.g. Segura-Puertas, 1984). Costa Rican waters contain at least 76 species of hydromedusae (Rodríguez-Sáenz & Segura-Puertas, 2009), with 53 species in the Gulf of Papagayo alone, a seasonal upwelling region in the ETP (Rodríguez-Sáenz & Vargas-Zamora, 2012). *Mooderia rotunda* has not been previously recorded in the region, which may be due to its deeper vertical distribution in the tropics: although this species is present in shallow waters of temperate regions (Wrobel & Mills, 1998), it is probably limited to deeper waters in the tropics, a phenomenon also common in coronate medusae (Lucas & Critch, 1974; Pielou, 1979).

Rodríguez-Sáenz & Gasca (2009) estimated that ~90 species of siphonophores inhabit the Pacific Ocean adjacent to Costa Rica, based on Alvariño (1972, 1974), Stepanjants (1977) and Gasca (2002). Although *Praya* was frequently observed with the 'DeepSee', only *P. reticulata* has been recorded with enough detail to identify the species based on morphological characteristics of the nectophores (Angulo *et al.*, 2014). Regarding *Apolemia*, we suggest that there may be additional species in the ETP, because the specimens

recorded here had different numbers of palpons (Figure 4C, D) and one specimen had opaque spots on its nectophores (Figure 4D). *Apolemia lanosa* Siebert, Pugh, Haddock & Dunn, 2013, recently described from Monterey Bay (Siebert *et al.*, 2013), has both characteristics previously mentioned, but collection of specimens is needed to verify this identification.

Records of ctenophores in the Eastern Pacific are scarce compared to other taxa of gelatinous zooplankton because their fragile bodies are usually destroyed by net trawls (Swift *et al.*, 2009). Mathews (1954) recorded in Hawaii only *Hormiphora palmata, Beroe forskalii* and the platycteniid ctenophore *Coeloplana duboscqui* Dawydoff, 1930. Wrobel & Mills (1998) recorded 28 species of ctenophores between the Gulf of Alaska and the Baja California Peninsula. In the Eastern Tropical Pacific, specifically in the Galapagos Islands, Tirado (2012) lists *Beroe* sp., *Hormiphora* cf. *palmata* and *Cestum* sp. Eight species of ctenophores have been recorded in the Pacific coast of Mexico, where *Ocyropsis maculate* (Rang, 1828), *Bolinopsis vitrea* (L. Agassiz, 1860) and *B. forskalii* have been recently found in surface waters of the Oaxacan coast (Ruiz-Escobar *et al.*, 2015). *Thalassocalyce inconstans* is a unique ctenophore that presents a medusoid bell (Supplementary Figure B) without any discrete lobes (Madin & Harbison, 1978).

Behavioural and ecological information of the recorded species is limited due to the short time lapses (0.5–3 min) in which the organisms were observed. Some specimens of *P. camtschatica* had symbiotic hyperiid amphipods on the subumbrella (Figure 2F). This association has been reported in other regions of the Pacific Ocean (Towanda & Thuesen, 2006). *Solmissus* sp. shows the typical tentacle-first foraging behaviour (Mills & Goy, 1988; Raskoff, 2002) and an ingested prey (Figure 3C, D). On the other hand, the radial canals of *H. maasi* seem to be empty (Figure 3E) compared with other individuals that might have oil droplets in those structures, which has been interpreted as evidence of recent prey ingestion (Wrobel & Mills, 1998). The images of *T. incostans* show individuals with their feeding disc retracted (Figure 4F, Supplementary Figure A) and extended (Supplementary Figure B), which relates to the type of prey captured by the ctenophore. Big, fast swimming prey such as euphausiids are engulfed by the contracted feeding disc (Swift *et al.*, 2009) while small copepods are entrained in the mucus at the inner side of the feeding disc when it is expanded (Madin & Harbison, 1978). The videos taken by the 'DeepSee' have also led to the description of the association between a fish larva of the genus *Paracaristius* sp. with the siphonophore *P. reticulata* (Angulo *et al.*, 2014).

The use of submersibles has provided new information on the diversity and natural history of gelatinous organisms in meso- and bathypelagic environments (Russell, 1967; Larson *et al.*, 1988; Matsumoto *et al.*, 2003; Raskoff & Matsumoto, 2004). However, most studies of gelatinous zooplankton in the Eastern Tropical Pacific have sampled only the epipelagic stratum. The videos recorded by the 'DeepSee' submersible have been useful so far to broaden our knowledge on gelatinous species occurrence in this region, but the lack of a systematic sampling through time by the submersible impedes the use of the videos for relative abundance and seasonality estimations for the species in the area. New records will increase as more studies targeted on gelatinous zooplankton are conducted in the Eastern Tropical Pacific. Information about their behaviour and ecology can also increase as more systematic sampling and/or observations with submersibles are conducted in this region. Future research should also be focused on obtaining detailed environmental parameters and quantitative information about the behaviour and abundance of these organisms.

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at https://doi.org/10.1017/S0025315417000558.

ACKNOWLEDGEMENTS

We acknowledge the support provided by the Vicerrectoría de Investigación (project 808-B0-654) and CIMAR, Universidad de Costa Rica. We thank the owners, captains and crews of the Undersea Hunter Group, also Shmulik Blum and his pilots of the 'DeepSee' submersible for the video recording. We appreciate the help of Astrid Sánchez-Jiménez, Alex Rodríguez-Arrieta and Cinthya Pérez with the video analysis, and Laurence P. Madin, Jennifer E. Purcell, Agustín Schiariti and an anonymous reviewer for their comments and corrections to this manuscript. This is a contribution of the Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Universidad de Costa Rica.

REFERENCES

Agassiz L. (1860) *Contributions to the natural history of the United States of America*, Vol. 3. Boston: Little, Brown & Co.

Alvariño A. (1971) Siphonophores of the Pacific with a review of the world distribution. *Bulletin of the Scripps Institution of Oceanography* 16, 1–432.

Alvariño A. (1972) *Zooplancton del Caribe, Golfo de México y regiones adyacentes del Pacífico*. México: Memorias del IV Congreso Nacional de Oceanografía, pp. 223–247.

Alvariño A. (1974) Distribution of siphonophores in the regions adjacent to the Suez and Panama canals. *Fisheries Bulletin* 22, 41–76.

Angel M.V. (2003) The pelagic environment of the open ocean. In Tyler P.A. (ed.) *Ecosystems of the World 28. Ecosystems of the Deep Oceans*. Amsterdam: Elsevier Science B.V., pp. 39–79.

Angulo A., Naranjo-Elizondo B., Corrales-Ugalde M. and Cortés J. (2014) 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). *Marine Biodiversity Records* 7(e132), 1–6.

Bigelow H.B. (1909) Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross", from October, 1904, to March, 1905. XVI. The Medusae. *Memoirs of the Museum of Comparative Zoology at Harvard College* 37, 1–243.

Bouillon J. (1999) Hydromedusae. In Boltovskoy D. (ed.) *South Atlantic zooplankton*. Leiden: Backhuys Publishers, pp. 385–465.

Brandt J.F. (1835) Prodromus descriptionis animalium ab Mertensio in orbis terrarum circumnavigatione observatorum. Fascicule I. *Recueil Actes des séances publiques de l'Acadadémie Impériale des Science de St. Petersbourg* 183, 201–275.

Cortés J. (2012) Marine biodiversity of an Eastern Tropical Pacific oceanic island, Isla del Coco, Costa Rica. *Revista de Biología Tropical* 60 (Supplement 3), 131–185.

Cortés J. and Blum S. (2008) Life to 450 m depth at Isla del Coco, Costa Rica. *Revista de Biología Tropical* 56 (Supplement 2), 189–206.

Cortés J., Enochs I.C., Sibaja-Cordero J., Hernández L., Alvarado J.J., Breedy O., Cruz-Barraza J.A., Esquivel-Garrote O., Fernández-García C., Hermosillo A., Kaiser K.L., Medina-Rosas P., Morales-Ramírez Á., Pacheco C., Pérez-Matus A., Reyes-Bonilla H., Riosmena-Rodríguez R., Sánchez-Noguera C., Wieters E. and Zapata F.A. (2017) Marine biodiversity of Eastern Tropical Pacific coral reefs. In Glynn P.W., Manzello D. and Enochs I. (eds) *Coral reefs of the world 8. Coral reefs of the Eastern Pacific: persistence and loss in a dynamic environment*. Dordrecht: Springer Science+Business Media, pp. 203–250.

Costello M.J., Coll M., Danovaro R., Halpin P., Ojaveer H. and Miloslavich P. (2010) A census of marine biodiversity knowledge, resources, and future challenges. *PLoS ONE* 5 (Issue 8), 1–15.

Eschscholtz F. (1829) *System der Acalephen. Eine ausführliche Beschreibung aller Medusenartigen Strahltiere*. Berlin: Ferdinand Dümmler.

Forsskål P. (1775) *Descriptiones Animalium, Avium, Amphibiorum, Piscium, Insectorum, Vermium; quae in Itinere Orientali Observavit Petrus Forskål*. Prof. Haun. Post Mortem Auctoris Ed. Carsten Neibuhr. Adjuncta est Materia Medica Kahirina atque Tabula Maris Rubri Geographica. Hauniae, pp. 1–20 + i–xxxiv + 1–164.

Gasca R. (2002) Lista faunística y bibliografía comentada de los sifonóforos (Cnidaria) de México. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México* 73, 123–143.

Haeckel E. (1879–80) *Das System der Medusen*. 1, 1–360, 2, 361–672. Jena: Gustav Fischer.

Hamner W.M., Madin L.P., Alldredge A.L., Gilmer R.W. and Hamner P.P. (1975) Underwater observations of gelatinous zooplankton: sampling problems, feeding biology, and behavior. *Limnology and Oceanography* 20, 907–917.

Kramp P. (1961) Synopsis of the medusae of the world. *Journal of the Marine Biological Association of the United Kingdom* 40, 7–382.

Larson R.J. (1990) Scyphomedusae and cubomedusae from the Eastern Pacific. *Bulletin of Marine Science* 47, 546–556.

Larson R.J., Madin L.P. and Harbison G.R. (1988) In situ observations of deepwater medusae in the genus *Deepstaria*, with a description of *D. reticulum*. sp. nov. *Journal of the Marine Biology Association of the United Kingdom* 68, 689–699.

Lindsay D., Umetsu M., Grossmann M., Miyake H. and Yamamoto H. (2015) The gelatinous macroplankton community at the Hatoma Knoll Hydrothermal Vent. In Ishibashi J., Okino K. and Sunamura M. (eds) *Subseafloor biosphere linked to hydrothermal systems: TAIGA concept*. Tokyo: Springer, pp. 639–666.

Longhurst A.R. (2001) Pelagic biogeography. In Steele J.H. (ed.) *Encyclopedia of ocean sciences*. Oxford: Elsevier, pp. 2114–2122.

Lucas J. and Critch P. (1974) *Life in the oceans*. New York, NY: Thames & Hudson.

Lucas C.H., Jones D.O.B., Hollyhead C.J., Condon R.H., Duarte C.M., Graham W.M., Robinson K.L., Pitt K.A., Schildhauer M. and Regetz J. (2014) Gelatinous zooplankton biomass in the global oceans: geographic variation and environmental drivers. *Global Ecology and Biogeography* 23 (Supplement 7), 701–714.

Madin L.P. and Harbison G.R. (1978) *Thalassocalyce inconstans*, new genus and species, an enigmatic ctenophore representing a new family and order. *Bulletin of Marine Sciences* 28, 680–687.

Mapstone G.M. (2009) *Siphonophora (Cnidaria) of Canadian Pacific waters*. Ottawa: National Research Council Press.

Mathews D.C. (1954) Records of Hawaiian Ctenophora. *Transactions of the American Microscopical Society* 73, 282–284.

Matsumoto G.I., Raskoff K.A. and Lindsay D.J. (2003) *Tiburonia granrojo* n. sp., a mesopelagic scyphomedusa from the Pacific Ocean representing the type of a new subfamily (Class Scyphozoa: Order Semaeostomae: Family Ulmaridae: Subfamily Tiburoniinae subfam. nov.). *Marine Biology* 143, 73–77.

Mianzan H. (1999) Ctenophora. In Boltovskoy D. (ed.) *South Atlantic zooplankton*. Leiden: Backhuys Publishers, pp. 561–573.

Mianzan H. and Cornelius P. (1999) Cubomedusae and Scyphomedusae. In Boltovskoy D. (ed.) *South Atlantic zooplankton*. Leiden: Backhuys Publishers, pp. 513–559.

Mills C., and Goy J. (1988) In situ observations of the behavior of mesopelagic *Solmissus* Narcomedusae (Cnidaria, Hydrozoa). *Bulletin of Marine Science* 43, 739–751.

Morales-Ramírez A. (2008) Caracterización cualitativa del zooplancton del Área de Conservación Marina Isla del Coco (ACMIC), Océano Pacífico de Costa Rica. *Revista de Biología Tropical* 56 (Supplement 2), 159–169.

Pugh P.R. (1999) Siphonophorae. In Boltovskoy D. (ed.) *South Atlantic zooplankton*. Leiden: Backhuys Publishers, pp. 467–511.

Pielou E.C. (1979) *Biogeography*. New York, NY: John Wiley & Sons.

Quoy J.R.C. and Gaimard J.P. (1827) Observations zoologiques faites à bord de l'Astrolabe, en mai 1826, dans le détroit de Gibraltar. *Annales des sciences naturelles* 10, 1–12, 172–193, 225–239.

Quoy J.R.C. and Gaimard J.P. (1833) Zoologie: Zoophytes. In Tatsu J. (ed.) *Voyage de la corvette de l "Astrolabe", exécuté par l'ordre du roi pendant les années 1826–1829 sous le commadement de M.J. Dumont d'Urville*. Paris: Tatsu Imprimeur, pp. 1–390, pls. 1–26.

Raskoff K.A. (2002) Foraging, prey capture and gut contents of the mesopelagic narcomedusa *Solmissus* spp. (Cnidaria, Hydrozoa). *Marine Biology* 141, 1099–1107.

Raskoff K.A. and Matsumoto G.I. (2004) *Stellamedusa ventana*, a new pelagic scyphomedusa from the eastern Pacific representing a new subfamily, the Stellamedusinae. *Journal of the Marine Biology Association of the United Kingdom* 84, 37–42.

Richardson A.J. (2008) In hot water: zooplankton and climate change. *ICES Journal of Marine Science* 65, 279–295.

Robison B.H. (2004) Deep pelagic biology. *Journal of Experimental Marine Biology and Ecology* 300, 253–272.

Rodríguez-Sáenz K. and Gasca R. (2009) Siphonophores. In Wehrtmann I.S. and Cortés J. (eds) *Marine biodiversity of Costa Rica, Central America*. Berlin: Springer Science-Business Media, pp. 151–156, (text), pp. 101–104 (Species list in CD).

Rodríguez-Sáenz K. and Segura-Puertas L. (2009) Hydrozoa, Scyphozoa and Cubozoa (Medusozoa). In Wehrtmann I.S. and Cortés J. (eds) *Marine biodiversity of Costa Rica, Central America*. Berlin: Springer Science-Business Media, pp. 143–149, (text), pp. 94–100 (Species list in CD).

Rodríguez-Sáenz K. and Vargas-Zamora J.A. (2012) Medusae (Cnidaria: Hydrozoa) from a coastal upwelling zone, Culebra Bay, Pacific, Costa Rica. *Revista de Biología Tropical* 60, 1731–1748.

Ruiz-Escobar F., Valadez-Vargas D.K. and Oliveira O. (2015) Ctenophores from the Oaxaca coast, including a checklist of species from the Pacific coast of Mexico. *Zootaxa* 3936, 435–445.

Russell F.S. (1967) On a remarkable new scyphozoan. *Journal of the Marine Biology Association of the United Kingdom* 47, 469–473.

Segura-Puertas L. (1984) *Morfología, sistemática y zoogeografía de las medusas (Cnidaria: Hydrozoa y Sciphozoa) del Pacífico Tropical Oriental*. Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Publicación Especial, no. 8, 320 pp.

Segura-Puertas L., Franco-Gordo C., Suárez-Morales E., Gasca R. and Godínez-Domínguez E. (2010) Summer composition and distribution of the jellyfish (Cnidaria-Medusozoa) in the shelf area off the central Mexican Pacific. *Revista Mexicana de Biodiversidad* 81, 103–112.

Siebert S., Pugh P.R., Haddock S. and Dunn C. (2013) Re-evaluation of characters in Apolemiidae (Siphonophora), with description of two new species from Monterey Bay, California. *Zootaxa* 3702, 201–232.

Spalding M.D., Agostini V.N., Rice J. and Grant S.M. (2012) Pelagic provinces of the world: a biogeographic classification of the world's surface pelagic waters. *Ocean and Coastal Management* 60, 19–30.

Stepanjants S. (1977) Siphonophora of the central part of the Pacific Ocean. In *Explorations of the fauna of the seas XX (XXVIII). Marine plankton* (*systematics and faunistics*). pp. 54–81.

Suárez E. and Gasca R. (1991) *Sifonóforos de México. Biología y Ecología*. Chetumal, México: Centro de Investigaciones de Quintana Roo (CIQRO).

Swift H.F., Hamner W.M., Robison B.H. and Madin L.P. (2009) Feeding behavior of the ctenophore *Thalassocalyce inconstans*: revision of the anatomy of the order Thalassocalycida. *Marine Biology* 156, 1049–1056.

Tirado N. (2012) CDF Checklist of Galapagos comb jellies. In Bungartz F., Herrera H., Jaramillo P., Tirado N., Jiménez-Uzcátegui G., Ruiz D., Guézou A. and Ziemmeck F. (eds) *Charles Darwin Foundation Galapagos species checklist*. Puerto Ayora, Galápagos: Fundación Charles Darwin. http://checklists.datazone.darwinfoundation.org/marine-invertebrates/ctenophora/. Last updated: 27 Nov 2012.

Towanda T. and Thuesen E.V. (2006) Ectosymbiotic behavior of *Cancer gracilis* and its trophic relationships with its host *Phacellophora camtschatica* and the parasitoid *Hyperia medusarum*. *Marine Ecology Progress Series* 315, 221–236.

Vicencio-Aguilar M.E. and Fernández-Álamo P.R. (1996) Zooplancton del Domo de Costa Rica: taxonomía y biogeografía. *Revista de Biología Tropical* 44, 631–642.

and

Wrobel D. and Mills C. (1998) *Pacific Coast pelagic invertebrates: a guide to the common gelatinous animals*. Monterey: Global Interprint, Monterey Bay Aquarium Research Institute.

Correspondence should be addressed to:
M. Corrales-Ugalde
Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Ciudad de la Investigación, Universidad de Costa Rica, San Pedro, 11501-2060 San José, Costa Rica
email: mcugalde88@gmail.com