

First occurrence of the rare siphonophore *Lilyopsis* Chun, 1885 (Hydrozoa, Siphonophora, Prayinae) in South Africa

Gillian M. Mapstone¹, Craig N. Foster², Mark J. Gibbons³

1 Department of Life Sciences, The Natural History Museum, London, UK **2** Seachange Science Lab, 41 Freesia Rd., Murdock Valley South, Simonstown, South Africa **3** Department of Biodiversity and Conservation Biology, University of the Western Cape, Private Bag X17, Belleville 7535, South Africa

Corresponding author: Mark J. Gibbons (mgibbons@uwc.ac.za)

Academic editor: S. Stainbank | Received 26 August 2022 | Accepted 21 September 2022 | Published 25 October 2022

<https://zoobank.org/86C22FAA-9951-48F4-8B4A-5E919BA82197>

Citation: Mapstone GM, Foster CN, Gibbons MJ (2022) First occurrence of the rare siphonophore *Lilyopsis* Chun, 1885 (Hydrozoa, Siphonophora, Prayinae) in South Africa. African Invertebrates 63(2): 121–130. <https://doi.org/10.3897/AfrInvertebr.63.94095>

Abstract

A colony of the rare hydrozoan siphonophore *Lilyopsis* Chun, 1885, was observed for the first time in shallow water in False Bay, South Africa, swimming amongst kelp. A study of a high-quality image of this individual found it to share some characters with the prayine prayid *L. fluoracantha* Haddock, Dunn & Pugh, 2005, so far known only from Monterey Bay, California, in the eastern Pacific. No *Lilyopsis* species has previously been reliably identified from either the South Atlantic or the Indian Ocean, so this record represents an expansion of the known worldwide distribution for this genus.

Keywords

Agulhas Current, Benguela ecosystem, Calycophorae, community science, diversity, photo identification, Prayid

Introduction

Siphonophores can be abundant members of coastal and oceanic zooplankton (e.g. Gili et al. 1991), where they play a role as predators (Purcell 1981; Choy et al. 2017; Hetherington et al. 2022) and prey (Bieri 1966; Bjorndal 1997; Nakamura et al. 2015; Eduardo et al. 2020; Hetherington et al. 2022). Although their populations

may fluctuate in size (Blackett et al. 2014, 2015, 2016), they are widely regarded as indicators of water mass movement (Russell 1935). However, their value in the latter context relies on up-to-date information regarding distribution, as this allows us to track potential range expansions in response to, for example, changing ocean circulation. Traditionally, the reporting of new species in areas outside known distributional ranges has been the purview of professional scientists, but this is rapidly changing as we harness the interest, enthusiasm and effort of community scientists (e.g. Gibbons et al. 2021). Here, we report on a genus of siphonophore not previously recorded from the South Atlantic from an image taken by one such community scientist.

Materials and methods

A specimen of a siphonophore was photographed by CF taken on 10 May 2018, at a depth of 1.5 m from within a kelp bed along the western shore of False Bay (34°12.484'S, 018°27.662'E, Fig. 1), and a high-resolution copy of the photograph (Fig. 2) used to identify the specimen. The photo was taken using natural light. The length of the colony was estimated at 7 cm based on the distance of the specimen from the camera.

Glossary of terminology used in this paper:

Basigaster – proximal thickened region of gastrozoid where nematocysts are produced.

Bract – protective asexual zooid of cormidium, typically rounded in prayids with lobed distal margin but in *Lilyopsis* extending into a spur on one side.

Calyconula larva – later larval stage of a calycothoran siphonophore.

Cormidium – serially repeated (iterative) group of zooids on the main stem, or siphosome, each including a gastrozoid, one or more gonophores and typically a bract.

Cormidial bell – a special nectophore in the cormidia of *Lilyopsis*, some other prayines and some other siphonophores.

Gastrozoid – asexual feeding zooid in a cormidium, with tentacle arising from proximal end.

Nectophore – asexual swimming bell present in most siphonophores, having a muscular nectosac for locomotion opening distally via an aperture termed the ostium.

Siphosome – posterior part of the stem, bearing cormidia in all siphonophores.

Tentilla – specialized side branches on a siphonophore tentacle comprising a complex nematocyst battery.

Results and discussion

The specimen illustrated in Fig. 2, can be identified as the fragile prayine siphonophore genus *Lilyopsis* Chun, 1855, for its distinctive closely spaced cormidia on the siphosome, each with a cormidial bell, and a pair of extremely transparent nectophores, swimming away from the camera on the right. *Lilyopsis* nectophores have very large nectosacs relative to those of other prayines. Each nectosac opens via an enlarged ostium oriented

at a 45° angle relative to the long axis of the nectophore and one such ostium is just visible in Fig. 2B. The bracts in the siphosomal cormidia of *Lilyopsis* are spurred, also clearly visible in Fig. 2B (see Fig. 3).

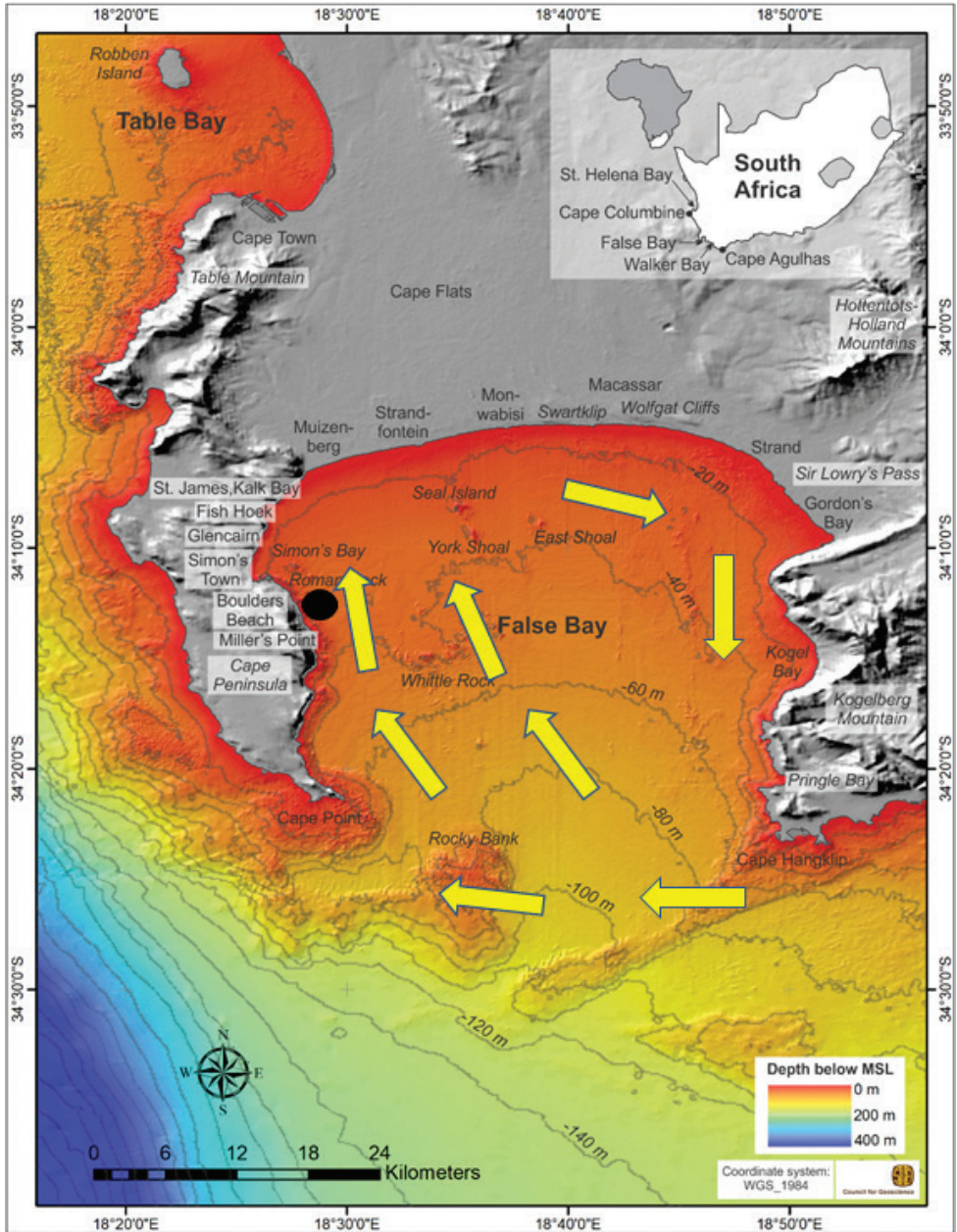


Figure 1. Bathymetric chart of False Bay (From Pfaff et al. 2019, <https://doi.org/10.1525/elementa.367.f1>). Location where the image was taken indicated by black circle; approximate direction of prevailing surface circulation during SE winds shown by yellow arrows.

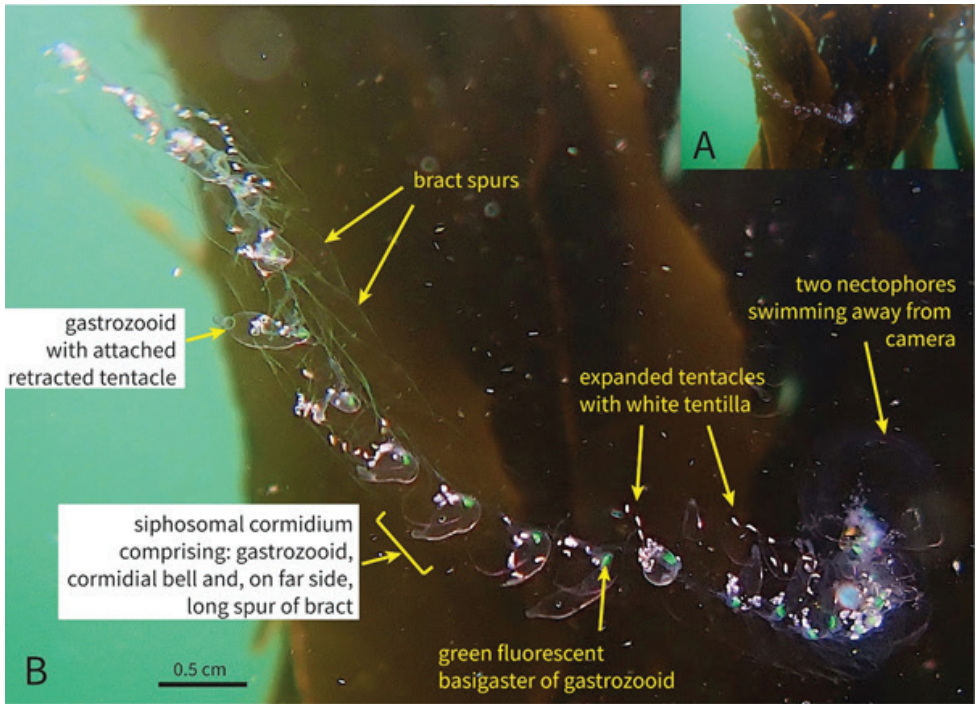


Figure 2. A photograph of a specimen of *Liliopsis* taken against a background of the kelp *Ecklonia maxima* at a depth of 1.5 m in False Bay on 10 May 2018 **A** original image **B** enlarged *Liliopsis* colony with explanatory labels. The length of the colony was estimated to be 7 cm.

There are two species currently identified as belonging to the genus *Liliopsis*: *L. medusa* (Metschnikoff & Metschnikoff, 1871) and *L. fluoracantha*, Haddock, Dunn and Pugh 2005. *Liliopsis medusa* was first introduced as *Praya diphyes* by Graeffe (1860), but because this name was already preoccupied by another prayine prayid, precedence for the species name *medusa* went to the specimen described by Metschnikoff and Metschnikoff (1871) from Villefranche as *Praya medusa*. Later, Chun (1885) introduced a new genus *Liliopsis* for three prayine species with the generic characters noted above. These included Chun's own species *L. rosea* from Naples which he considered different from the *L. medusa* of Metschnikoff and Metschnikoff (1871) and from the *Praya diphyes* of both Kölliker (1853) and Vogt (1854). *Liliopsis rosea* has been considered a junior synonym of *L. medusa* for some time, although usage of the specific name did not change until the error was pointed out by Pugh (2009). *Praya diphyes* of Kölliker and Vogt is now referred to as *Desmophyes annectens* (Totton 1965).

Liliopsis medusa was last studied in detail by Carré as *L. rosea*, based on specimens collected at Villefranche in the Mediterranean, including drawings and photographic images of the siphosome and of male and female cormidia (Carré 1969, figs 1, 2, pl. I fig. 5, pl. II fig. 5). More recently, the same species was imaged in the Southern California Bight by Luo et al. (2014, fig. 3ad), with a second image from the same site

included in Mapstone (2015, fig. 14E). In all these figures, and earlier ones reproduced by Totton (1965, figs 72A–C) and Bedot (1896, fig. 1), the bracts of the cormidia can be seen to have a spur extending from one side in a posterior direction, but this spur is not particularly elongate. In contrast, the bracteal spurs of *L. fluoracantha* are conspicuously longer as clearly shown by Haddock et al. (2005, fig. 5A–C) and noted in their species diagnosis.

The siphosome of the present colony from False Bay (Fig. 2) became twisted during swimming, and the most mature cormidia on the stem are on the left in Fig. 2B. In these cormidia each bract has a long posteriorly directed spur and further long spurs are also visible from bracts in cormidia on the right, closer to the nectosome. These bracteal spurs are longer than those shown for *Lilyopsis medusa* and are most similar to those illustrated and described for *L. fluoracantha* (Haddock et al. 2005), as shown in Fig. 3. Other similarities include the whitish tentilla on the tentacles of the gastrozooids in both the False Bay specimen and *L. fluoracantha*, which, although said to be yellowish in life in *L. fluoracantha*, appear whitish in the published figures (Haddock et al. 2005, fig. 6A, C, E). The gastrozooids of *L. fluoracantha* also appear similar to those of the present colony, except that they are relatively smaller in the published figure of *L. fluoracantha* and also have white basigasters (Haddock et al. 2005, fig. 6E).

Some characters of the present colony from South Africa fit well with those of both *Lilyopsis medusa* and *L. fluoracantha* (large transparent nectophores and closely spaced siphosomal cormidia, each with a cormidial bell), although nectophore details could not be directly compared since in the False Bay image only one of the two nectophores was visible, and in posterior view (Fig. 2B). Our colony measured c. 7 cm in length, which falls within the range of 5–10 cm for *L. medusa* (Carré 1969) and 3.6–12 cm for *L. fluoracantha* (Haddock et al. 2005, fig. 6A and p. 702). At least 18 cormidia can be identified in our colony (Fig. 2B). In *L. medusa*, 10 to 20 cormidia have been identified by Carré (1969) and up to 25 by Luo et al. (2014), and in *L. fluoracantha* up to 35 cormidia have been observed (Haddock et al. 2005). The main difference between our colony and those of *L. medusa* and *L. fluoracantha* is the bright green basigasters on the gastrozooids (Fig. 2B). In *L. fluoracantha* the gastrozooids were clear or whitish and cylindrical (Haddock et al. 2005) with a whitish basigaster, as noted above, and it is assumed here that those of *L. medusa* are similar, since no previous authors have commented on any pigment in this zooid (for example Carré 1969; Chun 1885). Cormidial bells are clearly present in each cormidium of our specimen, but further detail is not discernible (Fig. 2B). In *L. medusa* a small red disc is present on the two most anterior of the four cormidial radial canals and fine red spots are distributed all around the ostium, but in *L. fluoracantha* no red pigment was identified in the cormidial bells (Haddock et al. 2005).

Lilyopsis fluoracantha was described from just five specimens collected, or captured on video, between 1998 and 2004 near Monterey Bay, California, at depths between 327 and 476 m (Haddock et al. 2005), although 13 more have been identified in the same region (pers. comm. Kyra Schlining). There are more records for *L. medusa* which is considered a warmer water species worldwide, but rare. Most

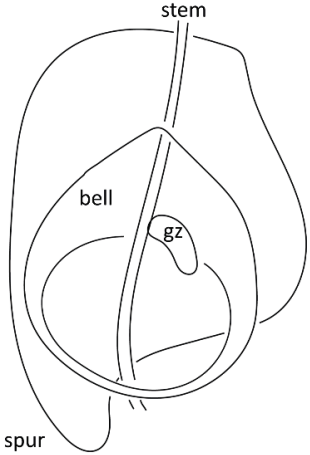
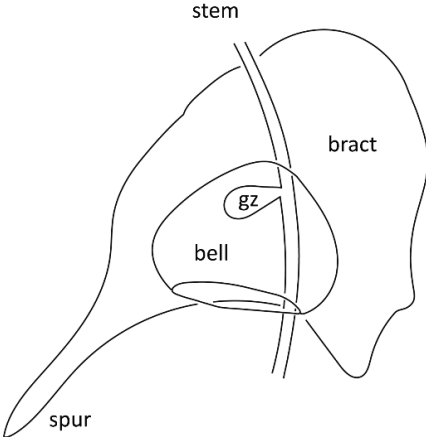
<i>Lilyopsis medusa</i> bract, from below	<i>Lilyopsis fluoracantha</i> bract, from below
<p data-bbox="170 305 577 407">Quite flattened cushion, concave below with rounded right border and left border with short spur</p> 	<p data-bbox="648 305 1097 480">Fluorescent green in life. Lower surface concave & draped over the stem, partly enclosing cormidial elements. Conspicuous elongate spur on left side, directed posteriorly.</p> 

Figure 3. Bracts of the two known *Lilyopsis* species from below. *L. medusa* modified from Carré 1969 Fig. 1; *L. fluoracantha* modified from Haddock et al. (2005 Fig. 5A; bell – of cormidium; gz – gastrozoid).

specimens have been collected at Villefranche-sur-Mer in the Ligurian Sea of the Mediterranean where upwelling has been known since antiquity (Madin 1991). From this location, or nearby off Nice, *L. medusa* has been described by Graeffe (1860), Metschnikoff and Metschnikoff (1871), Fewkes (1883), Moser (1917), Carré (1969) and Carré and Carré (1969). However, it has also been reliably reported twice in the Tyrrhenian Sea off Naples (Chun 1885; Schneider 1898), in the North Atlantic once from the Canaries by Chun (1888), in the Caribbean (Minemizu et al. 2015) and elsewhere by Haddock et al. (2005). In the Pacific, *L. medusa* has been recorded from the Southern Californian Bight (Luo et al. 2014, at 84 m), from the central tropical Pacific in the Bay of Ambon (Moluccas Indonesia, Bedot 1896), in Sagami Bay (Lindsay and Miyake 2009) and in Suguru Bay (Minemizu et al. 2015) in the western Pacific, and also off Australia (Haddock et al. 2005). This species has been additionally collected as a calyconula larva by SCUBA divers in Monterey Bay, California (Pugh 2009). Other records for the genus exist but the specific identity is unknown (e.g. Hoving et al. 2020).

So far *Lilyopsis fluoracantha* has only been observed or collected in deep water from Monterey Bay where the water temperature varied between ~6.5 and 8.5 °C (pers. comm. from Kyra Schlining at MBARI, July 2020). In contrast, reliable records for *L. medusa* show that it typically inhabits shallower and warmer water worldwide, between, for example, 14 and 24 °C in Villefranche Bay (Villefranche Sea Temperature 2021), 13 and 28 °C in the Bay of Naples (Bay of Naples Sea Temperature 2021) and 27 and 29 °C in the Bay of Ambon, in the Moluccas (Bay of Ambon Sea Temperature 2021), although one record is from 84 m in the Southern California Bight, where the water temperature was only 8 to 11 °C (Luo et al. 2014). Our *Lilyopsis* specimen was imaged in False Bay during the austral autumn where the water temperature was c. 15 °C. False Bay is one of the largest true embayments in South Africa (Fig. 1), and although circulation is approximately clockwise, it is influenced by prevailing winds. Because the bay sits at the NW edge of the Agulhas Bank, it is also subject to the vagaries of the Agulhas Current (Gründlingh and Largier 1991, de Vos et al. 2021). SE winds predominate in summer, which lead to upwelling at Cape Hangklip in the SE corner of the bay, offshore water transport and the development of a strong northward temperature gradient (Pfaff et al. 2019). During winter, NW winds serve to mix waters in the bay, and they promote onshore water movement (Pfaff et al. 2019). While we can speculate as to its origin, it is clear that *Lilyopsis* is not resident in False Bay because it has only been observed once during the many years that one of us (CF) has been snorkeling daily at the site in False Bay. Neither has it been observed by another frequent community scientist, Peter Southward (see Gibbons et al. 2021).

Conclusions

In general, our specimen shares more characters with *L. fluoracantha* than it does with *L. medusa*, but the bright green basigasters of the gastrozooids do seem to be unique, although may not be a robust character for species separation. Perhaps, therefore, it represents a third *Lilyopsis* species, or maybe a variant of *L. fluoracantha*, since in both species the bracts have elongate spurs. It will be necessary to collect a specimen in the future for genetic analysis if this is ever possible, which could confirm its identity as *L. fluoracantha*. Meanwhile, we assign our specimen to the genus *Lilyopsis* Chun, 1885, in the subfamily Prayinae Chun, 1897, of the calycophoran family Prayidae Kolliker, 1853.

Acknowledgements

We thank Kyra Schlining of Monterey Bay Aquarium Research Institute for information about observations and samples of *Lilyopsis fluoracantha* from the Monterey Bay area. GMM thanks The Natural History Museum, London for access to literature and other facilities as an NHM Scientific Associate. We are grateful to Bert Hoeksema and Dhugal Lindsay for their comments on the manuscript, which have helped to clarify the text.

References

- Bay of Ambon Sea Temperature (2021) Ambon Water Temperature. <https://www.seatemperature.org/asia/indonesia/ambon.htm> [Accessed 27/05/2021]
- Bay of Naples Sea Temperature (2021) Naples Sea Temperature. <https://www.seatemperature.org/europe/italy/naples.htm> [Accessed 27/05/2021]
- Bedot M (1896) Les siphonophores de la Baie d'Amboine. Etude suivie d'une revision de la famille des Agalmidae. *Revue Suisse de Zoologie* 13(3): 367–414. <https://doi.org/10.5962/p.318236>
- Bieri R (1966) Feeding preferences and rates of the snail, *Ianthina prolongata*, the barnacle, *Lepas anserifera*, the nudibranchs, *Glaucus atlanticus* and *Fiona pinnata*, and the food web in the marine neuston. *Publications of the Seto Marine Biological Laboratory* 14(2): 161–170. <https://doi.org/10.5134/175429>
- Bjorndal KA (1997) Foraging ecology and nutrition of sea turtles. In: Lutz PL, Musick JA (Eds) *The biology of sea turtles*. CRC Press, Boca Raton, USA, 199–231.
- Blackett M, Licandro P, Coombs SH, Lucas CH (2014) Long-term variability of the siphonophores *Muggiaea atlantica* and *M. kochi* in the Western English Channel. *Progress in Oceanography* 128: 1–14. <https://doi.org/10.1016/j.pocean.2014.07.004>
- Blackett M, Lucas CH, Harmer RA, Licandro P (2015) Population ecology of *Muggiaea atlantica* (Cnidaria, Siphonophora) in the Western English Channel. *Marine Ecology Progress Series* 535: 129–144. <https://doi.org/10.3354/meps11423>
- Blackett M, Lucas CH, Cook K, Licandro P (2016) Occurrence of the siphonophore *Muggiaea atlantica* in Scottish coastal waters: Source or sink? *Journal of Plankton Research* 39(1): 122–137. <https://doi.org/10.1093/plankt/fbw082>
- Carré C (1969) Sur le genre *Lilyopsis* Chun 1885, avec une redescription de l'espèce *Lilyopsis rosea* Chun 1885 (Siphonophore, Prayinae) et une description de sa phase calyconula. *Cahiers de Biologie Marine* 10: 71–81.
- Carré C, Carré D (1969) Le développement larvaire de *Lilyopsis rosea* (Chun, 1885) siphonophore, calycoflore, Prayidae. *Cahiers de Biologie Marine* 10: 359–364.
- Choy CA, Haddock SHD, Robison BH (2017) Deep pelagic food web structure as revealed by *in situ* feeding observations. *Proceedings of the Royal Society B* 284(1868): 20172116. <https://doi.org/10.1098/rspb.2017.2116>
- Chun C (1885) Über die cyklische Entwicklung der Siphonophoren. *Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin for 1885*, 511–529.
- Chun C (1888) Berichte über eine nach den Canarischen Inseln im Winter 1887/88 ausgeführte Reise. *Sitzungsberichte der Preussischen Akademie der Wissenschaften zu Berlin for 1888*: 1141–1173. [English translation in *The Annals and Magazine of Natural History, Series 6*, 3: 214–246.]
- Eduardo LN, Bertrand A, Mincarone MM, Santos LV, Frédou T, Assunção RV, Silva A, Ménard F, Schwamborn R, Le Loc'h F, Lucena-Frédou F (2020) Hatchetfishes (Stomiiformes: Sternoptychidae) biodiversity, trophic ecology, vertical niche partitioning and functional roles in the western Tropical Atlantic. *Progress in Oceanography* 187: 1–14. <https://doi.org/10.1016/j.pocean.2020.102389>

- Fewkes JW (1883) The Siphonophores. V. The Diphyae. *American Naturalist* 17(8): 833–845. <https://doi.org/10.1086/273435>
- Gibbons MJ, Haddock SHD, Matsumoto GI, Foster C (2021) Records of ctenophores from South Africa. *PeerJ* 9: e10697. <https://doi.org/10.7717/peerj.10697>
- Gili JM, Pagès F, Fusté X (1991) Mesoscale coupling between spatial distribution of planktonic cnidarians and hydrographic features along the Galician coast (Northwestern Iberian Peninsula). *Scientia Marina* 55: 419–426.
- Graeffe E (1860) Beobachtungen über Radiaten und Würmer in Nizza. *Neue Denkschriften der allgemeinen Schweizerischen Gesellschaft für die gesammten Naturwissenschaften* 17: 1–59.
- Gründlingh ML, Largier JL (1991) Physical Oceanography in False Bay – a review. In: Jackson WPU (Ed.) *False Bay 21 years on – an environmental assessment*. Proceedings of the Symposium. *Transactions of the Royal Society of South Africa* 47: 387–400.
- Haddock SHD, Dunn CD, Pugh PR (2005) A re-examination of siphonophore terminology and morphology, applied to the description of two new prayine species with remarkable bio-optical properties. *Journal of the Marine Biological Association of the United Kingdom* 85(3): 695–707. <https://doi.org/10.1017/S0025315405011616>
- Hetherington ED, Damian-Serrano A, Haddock SHD, Dunn CW, Choy CA (2022) Integrating siphonophores into marine food-web ecology. *Limnology and Oceanography Letters* 7(2): 81–95. <https://doi.org/10.1002/lol2.10235>
- Hoving HJT, Neitzel P, Hauss H, Christiansen S, Kiko R, Robison BH, Silva P, Körtzinger A (2020) In situ observations show vertical community structure of pelagic fauna in the eastern tropical North Atlantic off Cape Verde. *Scientific Reports* 10(1): e21798. <https://doi.org/10.1038/s41598-020-78255-9>
- Kölliker A (1853) *Die schwimmpolypen oder Siphonophoren von Messina*. Leipzig: Wilhelm Engelmann, Leipzig, 96 pp. <https://doi.org/10.5962/bhl.title.12447>
- Lindsay DJ, Miyake H (2009) A checklist of midwater cnidarians and ctenophores from Japanese waters: Species sampled during submersible surveys from 1993–2008 with notes on their taxonomy. *Kaiyo Monthly* 41: 417–438. [In Japanese with English abstract]
- Luo JY, Grassian B, Tang D, Irisson J-O, Greer AT, Guigand CM, McClatchie S, Cowen RK (2014) Environmental drivers of the fine-scale distribution of a gelatinous zooplankton community across a mesoscale front. *Marine Ecology Progress Series* 510: 129–149. <https://doi.org/10.3354/meps10908>
- Madin LP (1991) *Distribution and Taxonomy of Zooplankton in the Alboran Sea and adjacent western Mediterranean. A literature survey and field guide*. Technical Report Woods Hole Oceanographic Institution, 91–26. <https://doi.org/10.1575/1912/954>
- Mapstone GM (2015) Systematics of Siphonophores. In: Gopalakrishnakone P, Malhotra A (Eds) *Evolution of Venomous Animals and Their Toxins*, 1–37. https://doi.org/10.1007/978-94-007-6727-0_14-1
- Metschnikoff E, Metschnikoff L (1871) Contributions to the knowledge of siphonophores and medusae. *Mémoires de la Société des Amis des Sciences Naturelles, de l'Anthropologie et de l'Ethnographie* 8(1): 295–370. [In Russian]
- Minemizu R, Kubota S, Hirano Y, Lindsay DJ (2015) *A photographic guide to the jellyfishes of Japan*. Heibonsha, Tokyo, 360 pp.

- Moser F (1917) Die siphonophoren der Adria und ihre Beziehungen zu denen des Weltmeeres. Kaiserliche Akademie der Wissenschaften in Wien. Mathematisch-naturwissenschaftliche Klasse. 126(9): 703–763.
- Nakamura I, Goto Y, Sato K (2015) Ocean sunfish rewarm at the surface after deep excursions to forage for siphonophores. *Journal of Animal Ecology* 84(3): 590–603. <https://doi.org/10.1111/1365-2656.12346>
- Pfaff MC, Logston RC, Raemaekers SJPN, Hermes JC, Blamey LK, Cawthra HC, Colenbrander DR, Crawford RJM, Day E, du Plessis N, Elwen SH, Fawcett SE, Jury MR, Karenyi N, Kerwath SE, Kock AA, Krug M, Lamberth SJ, Omardien A, Pitcher GC, Rautenbach C, Robinson TB, Rouault M, Ryan PG, Shillington FA, Sowman M, Sparks CC, Turpie JK, van Niekerk L, Waldron HN, Yeld EM, Kirkman SP (2019) A synthesis of three decades of socio-ecological change in False Bay, South Africa: Setting the scene for multidisciplinary research and management. *Elementa* 7: 32. <https://doi.org/10.1525/elementa.367>
- Pugh PR (2009) A review of the family Sphaeronectidae (Class Hydrozoa, Order Siphonophora), with the description of three new species. *Zootaxa* 2147(1): 1–48. <https://doi.org/10.11646/zootaxa.2147.1.1>
- Purcell JE (1981) Dietary composition and diel feeding patterns of epipelagic siphonophores. *Marine Biology* 65(1): 83–90. <https://doi.org/10.1007/BF00397071>
- Russell FS (1935) On the value of certain plankton animals as indicators of water movements in the English Channel and North Sea. *Journal of the Marine Biological Association of the United Kingdom* 20(2): 309–332. <https://doi.org/10.1017/S0025315400045239>
- Schneider KC (1898) Mittheilungen über Siphonophoren. III. Systematische und andere Bemerkungen. *Zoologischer Anzeiger* 21: 51–57, 73–97, 114, 133, 153–173, 185–200.
- Totton AK (1965) A Synopsis of the Siphonophora. Trustees of the British Museum (Natural History), London, UK, 230 pp.
- Villefranche Sea Temperature (2021) Villefranche-sur-Mer Sea Temperature. <https://www.seatemperature.org/europe/france/villefranche-sur-mer.htm> [Accessed 27/04/2021]
- Vogt C (1854) Recherches sur les animaux inférieurs de la Méditerranée. 1. Sur les Siphonophores de la mer de Nice. *Mémoires de l'Institut National Genévois* 1: 1–164.
- Vos de M, Vichi M, Rautenbach C (2021) Simulating the Coastal Ocean Circulation Near the Cape Peninsula Using a Coupled Numerical Model. *Journal of Marine Science and Engineering* 9(4): e359. <https://doi.org/10.3390/jmse9040359>