Marine Environmental Research 205 (2025) 106991

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Habitat and identification of scyphozoan polyps in Bages-Sigean lagoon (France)

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ARTICLE INFO

Keywords:
Cnidaria
Jellyfish
Scyphistoma
Mediterranean lagoon
Substrate
Aurelia coerulea
Rhizostoma pulmo

ABSTRACT

Polyps are important stage in the medusozoan jellyfish life cycle, but the ecology of wild populations is still poorly understood. For some species, like *Rhizostoma pulmo*, polyps have never been reported in the wild. The Bages-Sigean lagoon is a Mediterranean, semi-enclosed lagoon with seasonally abundant *Aurelia coerulea* and *R. pulmo* medusae. Given its semi-closed nature and because ephyrae are commonly observed, it is likely that the polyps of both species reside in the lagoon. Our study aimed to characterize the polyp species distribution for this lagoon by performing snorkeling surveys of the potential polyp substrates, such as wood, concrete, buoys and bivalves. We observed polyp colonies at five sites, all on the underside of floating polypropylene docks despite the diversity of available substrates. Identification of the jellyfish species was performed in two ways: by strobilation then development of the ephyrae in aquaria, and by DNA sequencing of the collected polyps. All five sites produced *A. coerulea* medusae, but we were unable to locate polyps of *R. pulmo* despite surveying substrates that the planulae settle on under laboratory conditions. This study underscores the need to improve our ability to locate polyps in the wild by expanding laboratory studies to include more species, increasing sampling efforts and substrates in the field, and applying new methods (e.g., eDNA, hydrodynamic modeling).

1. Introduction

Blooms of scyphozoan jellyfish are notorious (Brotz et al., 2012; Condon et al., 2013; Graham et al., 2014), but bloom magnitude and timing can be driven by the polyp for species with benthopelagic life cycles. For example, if a polyp receives sufficient food and properly timed environmental cues (e.g., temperature, light), the recruitment of the pelagic stage would be larger in a given season than if polyps have poor nutrition and mismatched cues (Liu et al., 2009; Wang et al., 2015; Henschke et al., 2018). Despite the importance of the polyp, we know little about its biology, partially because polyps are difficult to locate and sample in the field. Most of our knowledge comes from experimental laboratory-based studies, but there are many aspects of *in situ* ecology and dynamics that cannot be replicated in the laboratory. However, these laboratory studies have elucidated patterns that have helped to locate polyps in the wild, such as orientation, substrate preferences, and others (e.g., Janβen et al., 2013; Ceh and Riascos, 2017).

Planula larvae, which are released from medusae and settle to become polyps, have an affinity for hard substrates (Yoon et al., 2014; Marques et al., 2015b) and artificial materials (Janβen et al., 2013), especially hard plastics (Holst and Jarms, 2007; Hoover and Purcell, 2009). They also tend to attach on the underside of these materials (Brewer, 1978; Ceh and Riascos, 2017), which is a behavior that likely mitigates negative effects of solar irradiation, silting and biofouling (Brewer, 1976; Svane and Dolmer, 1995). Larvae often settle in an agglomerative pattern (Gröndahl, 1988, 1989), which leads to monospecific colonies of polyps. Individuals also have a few modes of asexual reproduction that allow colonies to grow and persist independently of planula settlement (Han and Uye, 2010). These settling behaviours may be true for many species of polyps, but previous experiments are only based on a handful of species, and the polyp stage of most scyphozoan species has never been observed in the wild. Contrary to the relatively

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https://doi.org/10.1016/j.marenvres.2025.106991
Received 10 October 2024; Received in revised form 30 January 2025; Accepted 31 January 2025
Available online 31 January 2025

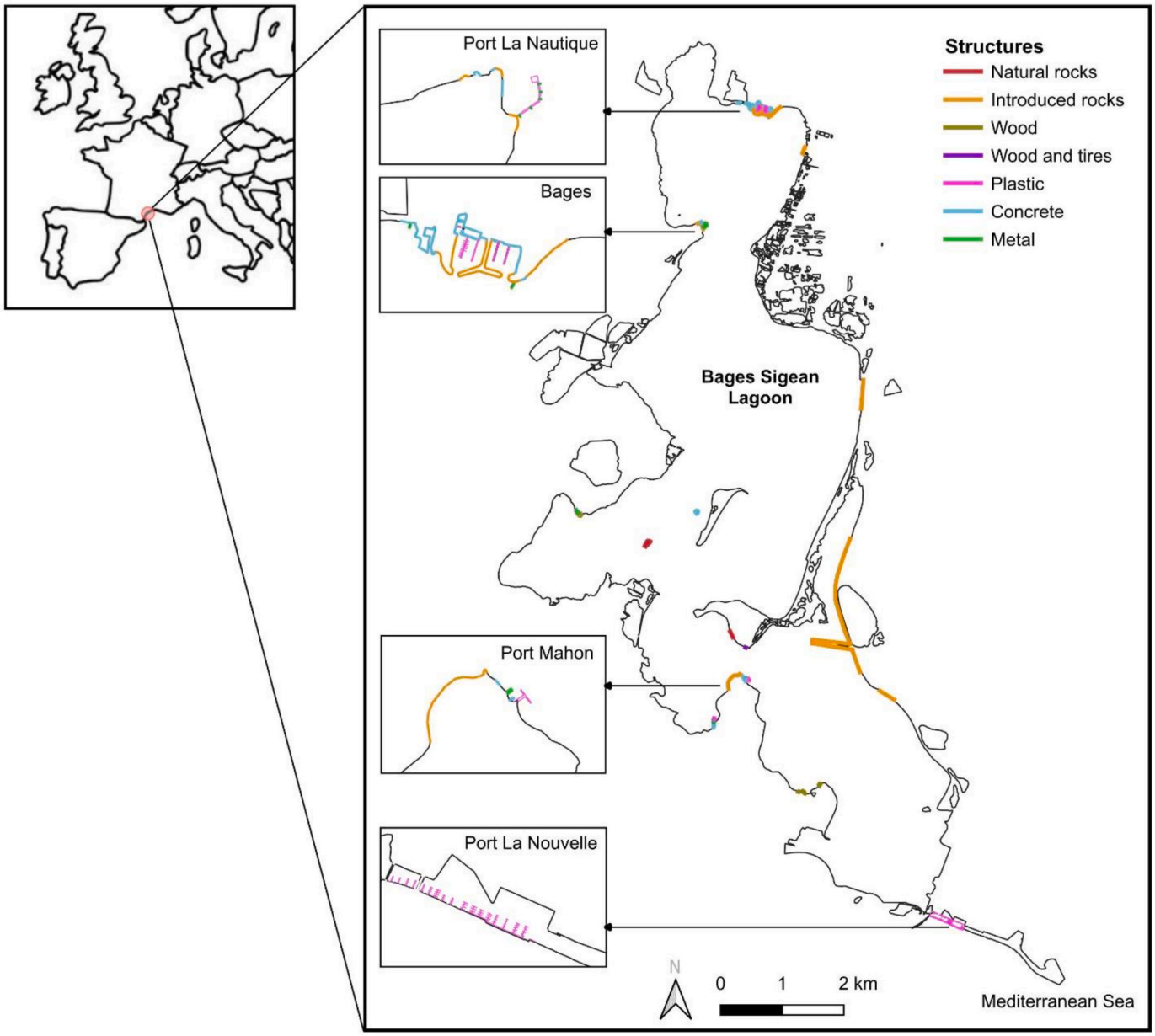

Fig. 1. Map of the hard substrates in Bages-Sigean lagoon (France). In this context, *wood and tires* refers to wooden pontoons with fixed tires to protect hulls while docking, and *wood* refers to wooden pontoons without tires. Similarly, *natural rocks* refers to rocks that are endemic to the lagoon, while *introduced rocks* are those that were introduced to the lagoon for construction purposes.

well-documented *in situ* distribution of *Aurelia* spp. polyps, the benthic stage of Rhizostomeae species, such as the native Mediterranean jellyfish *Rhizostoma pulmo*, are mostly unknown in nature.

The Bages-Sigean lagoon is a semi-enclosed French coastal shallow lagoon that is connected to the Mediterranean Sea at the southern end via a single channel, and is fed by several small freshwater rivers and the Robine Canal in the northern end. It covers an area of 38 km^2 with a mean depth of 2 m and a maximum depth of 4 m. Seasonal temperature and salinity range from approximately 5-27 °C and 28–45, respectively (Marques et al., 2015a; Leoni et al., 2021). The lagoon has seasonal occurrence of both *A. coerulea* (Marques et al., 2015a) and *R. pulmo* (Leoni et al., 2021) ephyrae and medusae each year, although the presence of *R. pulmo* in the lagoon has only been reported since 2014 (Leoni et al., 2021). While there are interannual variations in their period of occurrence, ephyrae of *A. coerulea* appear during the winter and develop into medusae from February and can persist until July, while *R. pulmo* appear later from April and can occur until October (Marques et al., 2015a; Leoni et al., 2021). Bages-Sigean has some commercial and recreational fishing activity, and contains a variety of hard structures that are potentially suitable for polyp settlement (e.g. plastic, stones, wood, metal, tires, etc.- cf Fig. 1). Given its semi-closed nature, it is likely that the polyps of the two species live in the lagoon. As such, it is an ideal location to identify and compare polyp habitat and distribution for these two benthopelagic species. This study aims to characterize the species distribution of polyps in the Bages-Sigean lagoon, and the findings will contribute to our understanding of wild population dynamics for both species.

2. Materials & methods

Hard substrates in the Bages-Sigean lagoon (43.0869°N, 3.0098°E) were mapped from Google Earth images with a field validation done

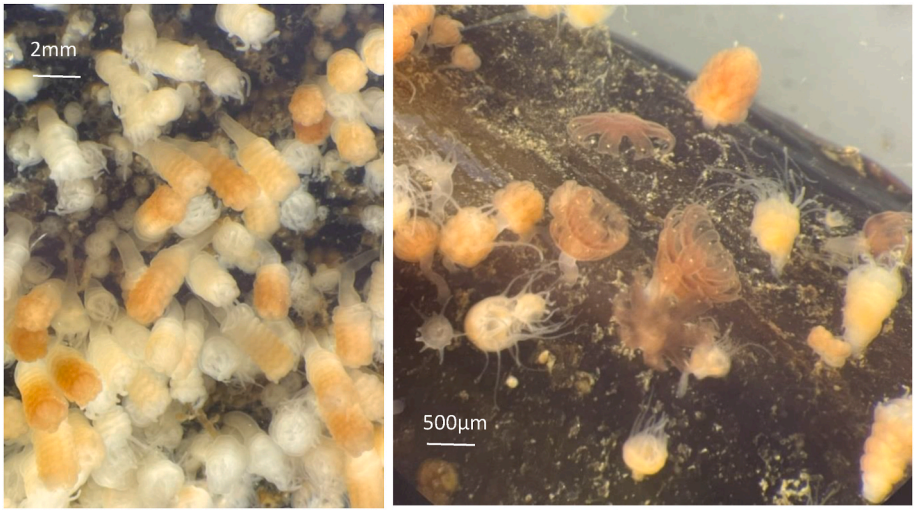

Fig. 2. Strobilation of polyps collected in Bages-Sigean lagoon in November 2022.

during a survey via snorkeling over three days in mid-November 2022, and Port La Nouvelle harbour was explored at the beginning of April 2023 (Fig. 1; see Leoni et al., 2021 for a larger map of the area). Temperature and salinity in the Bages-Sigean lagoon were 14.5 °C and 40, in November 2022 and 13.3 °C and 37.4 in April 2023, respectively. All mapped substrates were surveyed with a comprehensive inspection of every surface using a flashlight. Multiple snorkelers sometimes re-surveyed the same area if the structure was complex. Visibility was at least 2 m at all locations. When a polyp colony was located, it was visually classified according to its size using the system described by Marques et al. (2015b), which resulted in three categories: 1 (0.01–0.1 m^2), 2 (0.1–0.5 m^2) and 3 (0.5–1.0 m^2). A subset of ~200 polyps per station were then collected in 250 mL PET jars with a large aperture, filled with ambient seawater. Polyps for these two species are difficult to identify taxonomically in the field, so individuals were sampled for both morphological and genetic identification. Jars were transported to the laboratory in a cooler to maintain ambient temperature. Using a microscope, polyps were collected in 2 mL Eppendorf tubes and frozen at −20 °C for later DNA extraction with two replicates from each collection location. Each replicate contained approximately 25 polyps.

The remaining polyps were sent to the Paris Aquarium for induction of strobilation, where they were kept at 15 °C and a salinity of 35. Strobilation began spontaneously without any additional influence in November 2022 (Fig. 2), probably due to environmental changes and stress of collection and transport. The resulting ephyrae and medusae were morphologically identified to confirm whether the polyps were *A. coerulea* or *R. pulmo*. Images of the ephyrae and medusae developed from the cultures were taken for morphological identification. Polyps were fed a mixture of *Artemia* nauplii and rotifers.

For polyp identification *via* genomics, total DNA extractions were performed using an automated Maxwell® instrument (Promega) and following 16 LEV Blood DNA kit (Promega) protocols, with a modification of the lysis procedure, which was run 2 h at 56 °C, using 30 µL of Proteinase K (Promega, France). Final DNA concentrations were between 84.7 and 222.3 ng μL^{-1}, which were confirmed *via* NanoDrop one (Thermo scientific). To identify species, the amplification of a 710-bp fragment of the *mtCOI* gene was done using the universal invertebrate primers LCO1490- F (5′- GGTCAACAAATCATAAAGATATTGG- 3′) and HCO2198-R (5′-TAAACTTCAGGGTGACCAAAAAATCA - 3′) designed by Folmer et al. (1994).

Amplifications occurred in a 50 µL reaction volume containing 10 µL of buffer (Promega, France), 4 µL of $MgCl_2$, 1 µL of dNTP (10 mM each), 3 µL of each primer (10 µM concentration), 0.25 µL of GoTaq G2 Flexi DNA polymerase (Promega, France), 3 µL of template DNA and DNase-free water. All polymerase chain reactions (PCRs) were carried out on Eppendorf thermocycler with the following protocol: denaturation at 94 °C for 3 min, then 40 cycles of 94 °C for 30 s, 50 °C for 30 s, and 72 °C for 50 s and final extension at 72 °C for 10 min (Prieto et al., 2013). Amplified DNA was purified with a QIAquick PCR Purification Kit (Qiagen, Venlo, The Netherlands) and sequenced by Macrogen (Amsterdam, The Netherlands).

PCR products were sequenced using the amplification primers identified above in the forward and reverse direction. The resulting sequences were processed and aligned in Geneious Prime (2022).2.2. First, sequences were trimmed on both ends according to an error probability limit of 0.01 (greater than 1% chance of error per base) then reading direction was set and sequences were aligned using the multiple sequence alignment tool in Geneious Prime (cost matrix of 65% similarity, gap open penalty of 12, gap extension penalty of 3, and 2 refinement iterations). Forward/reverse sequence pairs were extracted and combined into consensus sequences with a base calling threshold of 100%, where bases must be identical to be called unambiguously. The consensus sequences were aligned again using the Geneious Prime algorithm according to the above parameters, and a Tamura-Nei neighbour-joining tree was made with bootstrap resampling (100 replicates) and a 50% support threshold. Closely related sequence groups were visually identified and sequences from these groups were blasted against the NCBI nucleotide collection database (updated October 3, 2023), with optimisation for highly similar sequences (megablast) to identify species. If the closest blast hits were not for the species thought to be present, representative sequences from groups were aligned to published COI sequences for the closest blast hits, as well as to the hypothesised species (above parameters), then another Tamura-Nei neighbour-joining tree was made to compare genetic proximities.

3. Results

3.1. Mapping of the polyps' colonies

A variety of hard substrates were recorded and surveyed in the lagoon (e.g., rocks, concrete, wood, metal, plastic; Fig. 1) with depths ranging 1–3 m. However, the sites where polyp colonies were observed were always floating polypropylene docks (Figs. 1 and 3) at depths <1 m. Polyps were located on the underside of the floating docks either directly attached to the polypropylene or on secondary biotic substrates, like mussel shells or ascidians. Five sites were identified and the polyp colonies were mapped and classified according to the surface area of the colonies (Fig. 3; Toyokawa et al., 2011; Marques et al., 2015b). Four of

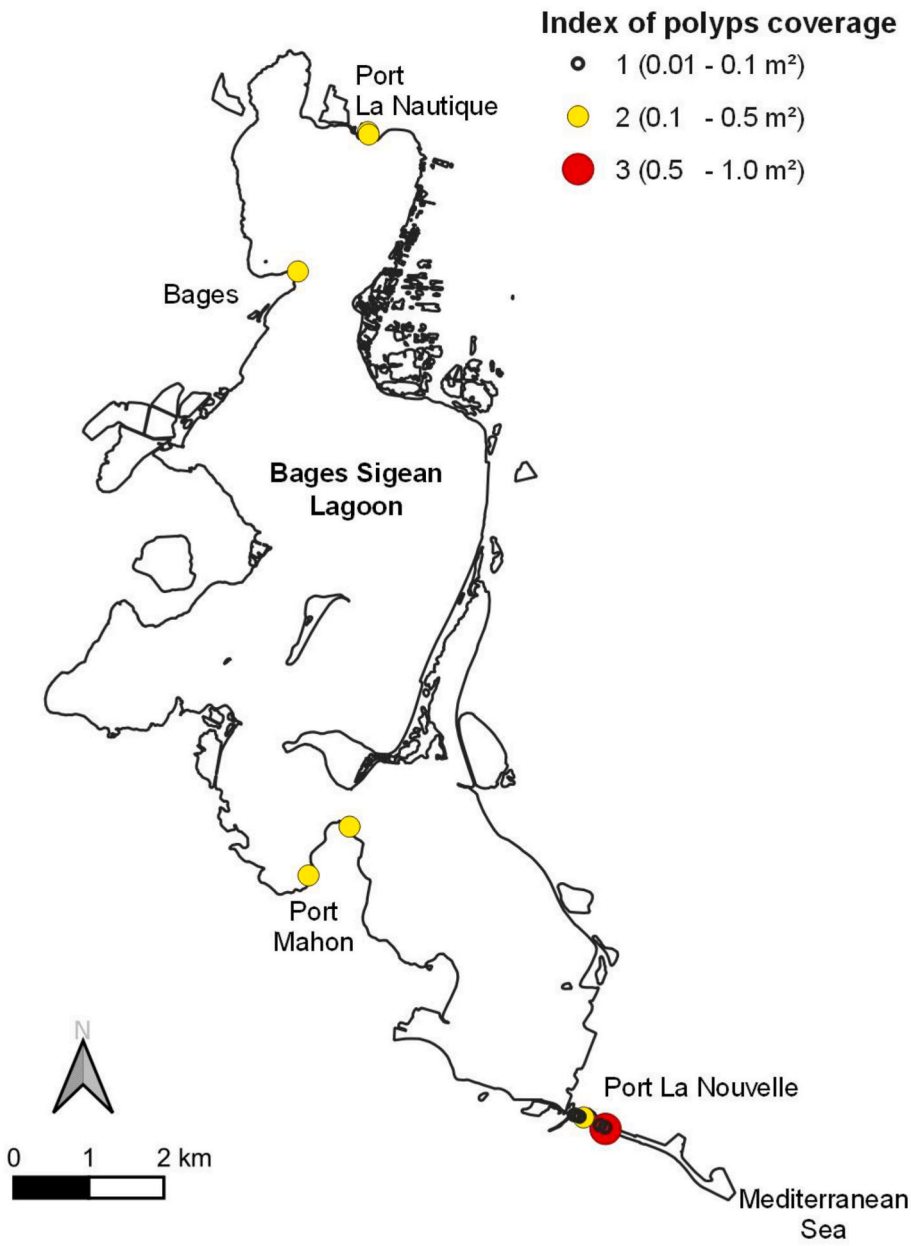

Fig. 3. Map of polyp colonies in Bages-Sigean lagoon. The locations where polyps' colonies were found, and the index of polyp coverage are indicated.

them were of category 2 (0.1–0.5 m^2) in the small harbours of the lagoon, while a category 3 (0.5–1.0 m^2) colony was observed in Port La Nouvelle harbour, the largest port connecting the lagoon to the Mediterranean Sea (Fig. 4).

3.2. Characterising the polyp species

While polyps had various colours and shapes, strobilation and ephyra development of all five colonies produced pelagic stages of *A. coerulea* (Fig. 5). Indeed, ephyrae and medusae stages presented *Aurelia* spp. characteristics described by Gambill and Jarms (2014). Similarly, the sequencing results indicated *A. coerulea* for all sampling sites where polyps were collected (Fig. 6).

4. Discussion

After surveying hard substrates in the Bages-Sigean lagoon, *A. coerulea* colonies were located at five sites exclusively on the underside of floating polypropylene docks at < 1 m depth. In some cases, polyps were located on secondary biotic substrates, like shells of the mussel *Mytilus* sp. and ascidians that were also attached to the floating docks. Consequently, the polyps were observed only in harbours and locations where other boating activities occur (e.g., small-scale and recreational fishing, sailing clubs), which is where this type of floating dock is typically located. Interestingly, the largest colony was observed in the largest harbour of the lagoon. Artificial materials are commonly reported as preferred substrates for planula settlement for *Aurelia labiata* (Hoover and Purcell, 2009), so this result is unsurprising. Similarly,

Fig. 4. Sampling in Port la Nouvelle.

populations of *Aurelia aurita* in the Inland Sea of Japan increased following the installation of a floating pier (Makabe et al., 2014), further emphasising the importance of these materials as polyp substrates. In fact, a summary of the available literature on *in situ* polyp substrates reveals a similar trend (Table 1). Of the naturally-occurring scyphozoan polyp habitats reported around the world, floating docks and piers are among the most common, with bivalve shells often serving as secondary substrates as well. Other common artificial substrates occasionally include concrete, different types of plastic, and the iron and fiberglass hulls of sunken vessels (Table 1). Natural primary substrates are apparently less frequently reported, but include eelgrass, empty bivalve shells, and calcareous stony coral skeletons (Table 1). As with the current study, shallow habitats <10 m depth are common (Table 1), but this may be an artefact of the locations and types of substrates that are surveyed, the survey methods used, and increased visibility at shallow depths.

Reports of *in situ* polyp habitats are dominated by *Aurelia* spp. (Table 1). This is unsurprising given that *Aurelia* is the most studied genus of scyphozoan owing largely to its cosmopolitan distribution, and is often the target of *in situ* studies. Here we expected to find polyps of both *A. coerulea* and *R. pulmo* as pelagic stages for both are present in the Bages-Sigean lagoon seasonally each year (Marques et al., 2015a; Leoni et al., 2021). Despite surveying many hard substrate types across the lagoon (Fig. 1), we did not locate any *R. pulmo* polyps. While this was surprising, there are similar cases in the literature. For example, van Walraven et al. (2016) surveyed 29 sites in the southern North Sea where five species of scyphomedusae are present. Despite locating polyp colonies at most of these sites at varying depths and on various substrates, all were identified *via* DNA sequencing as *A. aurita*. Toyokawa et al. (2011) also surveyed fishing ports in Mikawa Bay in Japan broadly for scyphozoan polyps, and also only found *A. aurita* s.l. polyps despite the occurrence of *Chrysaora pacifica* pelagic stages seasonally. The absence of polyp species is reported in these studies only because other species were found, thus a report was written. Consequently, we should also consider how many studies have found no polyps despite surveying diverse potential polyp substrates, and therefore have not been written. In this case, negative results are important as they may help elucidate potential polyp habitats and ensure costly efforts are not being duplicated.

Hard substrates are typically surveyed during *in situ* polyp studies because the planula larvae prefer to settle on the underside of hard substrates during substrate choice experiments in laboratory conditions (Holst and Jarms, 2007; Janβen et al., 2013; Yoon et al., 2014; Marques et al., 2015b; Ceh and Riascos, 2017). While substrate choice experiments have predominantly been conducted on *Aurelia* spp., *Chrysaora* spp. and *Cyanea* spp., one choice experiment included *Rhizostoma octopus* and the results were similar to those for other scyphozoans (Holst and Jarms, 2007). In fact, *R. octopus* planulae settled on PET, shells, concrete, wood and glass when presented with these options (Holst and Jarms, 2007), which includes many of the substrates that were examined in our survey (Fig. 1). In the absence of a choice, *Rhizostoma* spp. planulae have also successfully settled on glass (*Rhizostoma luteum* and *R. octopus*; Holst et al., 2007; Kienberger et al., 2018) and PVC (*R. pulmo*; Fuentes et al., 2011) in aquaria. These findings suggest that the substrates chosen for our survey align with what is expected,

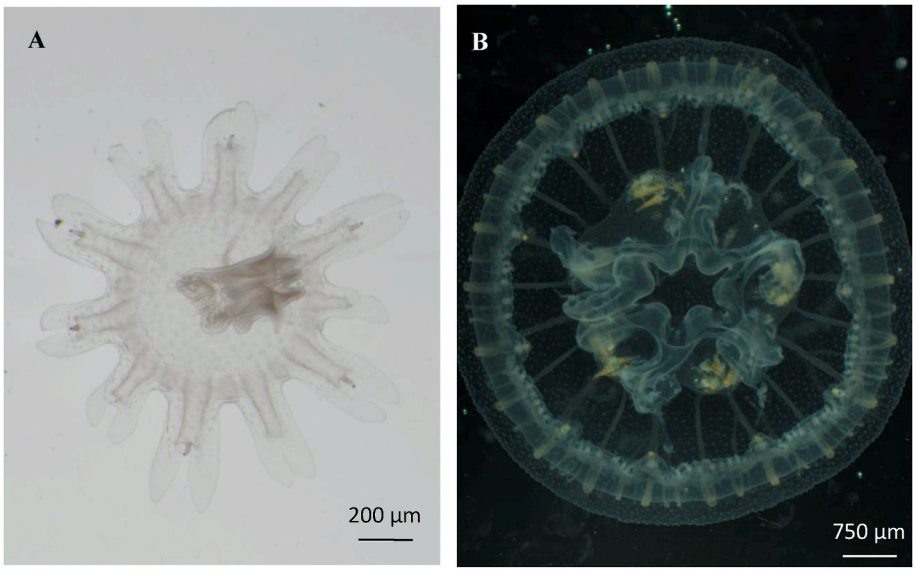

Fig. 5. *Aurelia coerulea* ephyrae (A) and young medusae (B) developed from the polyps collected in Bages-Sigean lagoon.

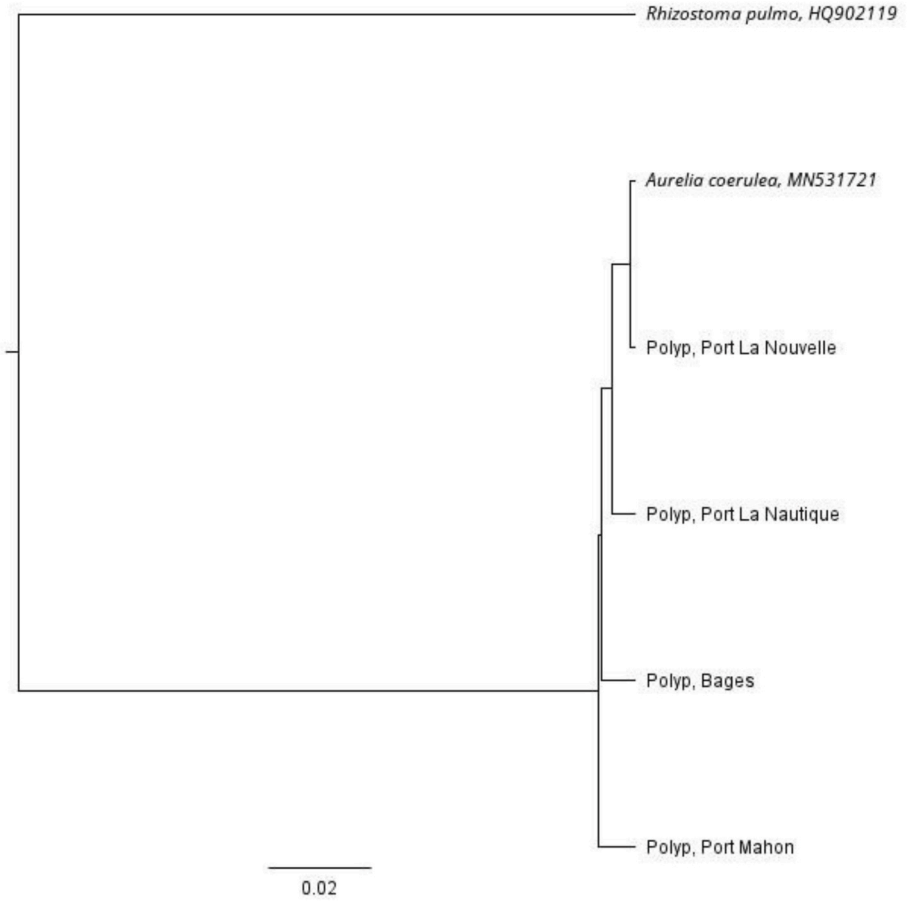

Fig. 6. Tamura-Nei neighbour joining tree of COI sequences from polyps of the various sampling sites in Bages-Sigean lagoon (see sample sites in Fig. 3). The tips labelled with species are GenBank entries with the corresponding accession number.

and the absence of *R. pulmo* polyps is unresolved. It is important to note that substrate choice experiments rarely offer substrates besides hard artificial materials, rocks, and shells. Wild scyphistomae have been located on seagrasses and macroalgae (Kikinger, 1992; Östman, 1997; Rekstad et al., 2021), so perhaps including seagrass and macroalgae beds during *in situ* surveys would improve our ability to locate elusive species.

There are currently approximately 240 described species of scyphozoans, but life cycles have only been described for 49 species (Rodrigues et al., 2024), which include both holopelagic and benthopelagic life cycles. Table 1 highlights that the polyp stage of only a handful of the benthopelagic species have been located in the wild, so this conundrum is not restricted to *R. pulmo*. Other papers have suggested alternative hypotheses for why some species are difficult to locate. For example, Toyokawa (2011) suggest that *C. pacifica* polyps may not be present throughout the year and might instead only appear seasonally, which may also be true for *R. pulmo* and other non-*Aurelia* genera. There are some additional methods that have been applied to locate polyps with some success. For example, Kawahara et al. (2006) combined field observations of medusae and knowledge of the local current patterns to estimate the location of *Nemopilema nomurai* polyps. On a more complex scale, there are promising models under development that could combine pelagic observations with hydrodynamic models to locate polyp beds (Cant et al., 2024). Environmental DNA (eDNA) has also been applied to help locate cubozoan jellyfish polyps in the field (Bolte et al., 2021, Morrissey et al., 2024a; Morrissey et al., 2024b), which is another emerging method that may be useful for locating elusive species. Regardless of the approach, the polyp stage of these scyphozoans is often regarded as the driver of medusa bloom size (Liu et al., 2009; Lucas et al., 2012; Wang et al., 2015; Henschke et al., 2018), where medusa blooms have significant ecological and economic roles in some regions (Graham et al., 2014). Therefore, it is important to fully understand the role of this small and elusive benthic life stage at larger scales, by improving our understanding of their ecology, and by using new methods to locate them.

CRediT authorship contribution statement

Jessica Schaub: Writing – review & editing, Writing – original draft, Visualization, Investigation, Funding acquisition, Formal analysis, Data curation. **Valentina Leoni:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Sandrine Crochemore:** Writing – review & editing, Formal analysis. **Hadrien Blayac:** Writing – review & editing, Methodology, Investigation, Data curation. **Benjamin Kleinerman:** Writing – review & editing, Writing – original draft, Validation, Methodology, Formal analysis, Data curation. **Anaïs Courtet:** Writing – review & editing, Visualization, Investigation, Data curation. **Etienne Bourgouin:** Writing – review & editing, Visualization, Investigation. **Delphine Bonnet:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Table 1
Summary of *in situ* scyphozoan polyp substrates reported in the literature. This summary excludes settling plates that were pre-settled in the laboratory before being deployed in the field.

Order	Species	Primary Substrate	Secondary Substrate	Depth (m)	Location	Reference
Coronatae	*Atolla* sp. (most likely)	Stones, shell fragments		486 to 2610	Chukchi Borderland, Arctic Ocean	Zhulay et al. (2019)
	Atorella sibogae	Plastic bottle (PVC) and soft plastic (PE) debris		898 to 3233	South China Sea, China	Song et al. (2021)
	Atorella sp.	Calcareous stony coral skeletons		417	Atlantic Coast, Brazil	Jarms et al. (2002)
	Nausithoe cf. *rubra*	Plastic bottle (PVC) debris		898	South China Sea, China	Song et al. (2021)
	Nausithoe sp.	Polymetallic nodule		4150	Clarion-Clipperton Zone, central Pacific	Dahlgren et al. (2016)
		Calcareous stony corals		147 to 417	Atlantic Coast, Brazil	Jarms et al. (2002)
Rhizostomeae	*Cotylorhiza tuberculata*	Seagrass		Not given	Lefkada, Greece	Kikinger (1992)
Semaestomeae	*Aurelia aurita*	Shipwreck (iron)	Bivalves (mussels, oysters)	14	Adriatic Sea, Italy	Di Camillo et al. (2010)
		Pylon		2 to 5	Tokyo Bay, Japan	Ishii and Katsukoshi (2010)
		Concrete settlement plates mimicking wind farm piles and foundations		0 to 10	SW Baltic Sea	Janβen et al. (2013)
		Floating docks		1	NE Pacific, USA	Kozloff (1983), cited in Holst and Jarms (2007)
		Floating pier (steel and concrete)		1	Hiroshima Bay, Japan	Makabe et al. (2014)
		Floating dock		0.2 to 2	Wakasa Bay, Japan	Matsumura et al. (2005)
		Floating docks, buoys, rock, concrete, polystyrene, cellophane wrapper and leaf	Polychaete tubes, amphipod tubes, barnacles, bivalves, solitary ascidians, algae	1.5	Kagoshima Bay, Japan	Miyake et al. (2002)
		Floating docks	Bivalves, ascidians, and amphipod tubes	1.5	Yamaguchi, Japan	Miyake et al. (2002)
		Rock, kelp, brick, glass bottle, iron plate, cinder block, concrete		0.1 to 2	Trondheimsfjorden, Norway	Rekstad et al. (2021)
		Floating piers, moored boats, wharfs (concrete, fibreglass, steel, vinyl)		0.2 to 2	Korenaga Port, Japan	Takao et al. (2014)
		Wreck, marina, harbor, oyster reef (PVC, rubber, iron, wood, granite, glass)	Bivalves (mussels, oysters, clams), barnacles, encrusting bryozoan, colonial and solitary ascidians, sponges	1 to 38.5	Southern North Sea	van Walraven et al. (2016)
	Aurelia aurita s.l.	Pillars	Oysters	2.2 to 6	Port of Koper, Northern Adriatic Sea, Slovenia	Hočevar et al. (2018); Melica et al. (2014); Malej et al. (2012)
		Floating piers, moored boats, wharfs (concrete, fibreglass, steel, vinyl)	Bivalves (mussels and oysters)	Likely <1	Mikawa Bay, Japan	Toyokawa et al. (2011)
	Aurelia coerulea	Concrete dam	Polychaete tubes	3	Fenghuang Lake, China	Dong et al. (2018); Sun et al. (2023)
		Piers, pontoons, oysters culture rafts (metal, plastics, concrete, tires, rocks, boats, wood)	Red and brown algae, ascidians, sponges, bryozoans, bivalves, barnacles, calcareous polychaete tubes and muddy amphipod tubes	0.2 to 6.1	Thau Lagoon, Mediterranean Sea, France	Marques et al. (2015b)
		Fiberglass boat	Encrusting red algae, oysters, mussels	2 to 6	Thau Lagoon, Mediterranean Sea, France	Marques et al. (2019)
		Not given		Not given	Jaran Bay, South Korea	Seo et al. (2021)
		Electric power transmission towers, dike, port, pier, breakwater, wharf, bridge pier	Oysters	Not given	Lake Shihwa, Lake Saemangeum, and Masan Bay, Korea	Yoon et al. (2018)
		Floating polypropylene dock	Mussels, ascidians	<1	Bages-Sigean Lagoon, Mediterranean Sea, France	Current study

(*continued on next page*)

Table 1 (*continued*)

Order	Species	Primary Substrate	Secondary Substrate	Depth (m)	Location	Reference
	Aurelia labiata	Settling plates of common docking building material (polystyrene, wood, rubber, polyethylene), floating docks		0.5	Cornet Bay, Washington, USA	Hoover and Purcell (2009); Purcell et al. (2009)
	Aurelia limbata	Aluminum can, plastic bottle		296 and 392	Coastal Japan	Shibata et al. (2015)
	Aurelia sp.	Cinder block, rock	Barnacles, solitary ascidians, oyster, mussel shells, seagrass, algae and plastic	0.5 to 2	Trondheimsfjorden, Norway	Rekstad et al. (2021)
		Cement breakwaters and floating docks		1.5 to 3.5	Tasmania, Australia	Willcox et al. (2008)
		Rocks, algae, mussels		0.3 to 10	Gullmar Fjord, Sweden	Östman (1997)
	Chrysaora hysoscella	Empty clam shells		Unknown; 25 to 38.5	Dogger Bank and Oostende Beach, North Sea, Belgium	van Walraven et al. (2020)
	Chrysaora pacifica	Rocks, empty clam shells		<5	Sagami Bay, Japan	Toyokawa (2011)
	Chrysaora quinquecirrha	Not given	Oysters	Not given	Great Wicomico and Rappahannock Rivers, USA	Webb, 1972
		Not given	Oysters	3 to 11	Chesapeake Bay, USA	Cargo and Schultz (1966, 1967)
	Cyanea lamarckii (podocyst only)	Empty clam shells		Unknown	Oostende Beach, Belgium	van Walraven et al. (2020)
	Cyanea sp.	Rocks, algae, mussels		0.3 to 10	Gullmar Fjord, Sweden	Östman (1997)

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jessica Schaub reports financial support was provided by Kimberly Foundation. Jessica Schaub reports financial support was provided by Natural Sciences and Engineering Research Council of Canada. Valentina Leoni reports financial support was provided by National Agency for Research and Innovation. Benjamin Kleinerman reports financial support was provided by Campus France. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The authors are grateful to Nicolas Nouguier for his assistance during the field work, and to Fabien Gaboyard for the use of his boat. They also thank Corine Bouvier for her support during the DNA extraction and amplification.

This study was funded by the Kimberley Foundation's Hugh Morris Fellowship (HMF) and JS was supported by the HMF and the Vanier Canada Graduate Scholarship. VL was supported by the National Agency for Research and Innovation, ANII, Uruguay (code POS_CFRA_2017_1_147109). BK was supported by the MOPGA grant: ANR-19-MPGA-0004.

Data availability

Data will be made available on request.

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