

Life cycle of the jellyfish *Rhizostoma pulmo* (Scyphozoa: Rhizostomeae) and its distribution, seasonality and inter-annual variability along the Catalan coast and the Mar Menor (Spain, NW Mediterranean)

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Received: 3 October 2010 / Accepted: 26 May 2011 / Published online: 21 June 2011
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Abstract *Rhizostoma pulmo* is one of the most abundant scyphomedusae along the Mediterranean coasts. To understand changes in the population densities of the medusa stage and its relationship with the benthic stage, we describe all developmental stages from the life cycle of *R. pulmo*, from the scyphistoma stage to young medusae reared in the laboratory. Mature scyphistomae showed a mean total body length of 1.7 mm and the average tentacle number was 16. Asexual reproduction occurred by lateral budding, podocyst and pedalocyst production. Each strobila released up to 8 ephyrae that had a mean total body diameter of 3.5 mm. Moreover, we also present data on the temporal and spatial distribution of the species in the Catalan Sea and the coastal lagoon on Mar Menor (NW Mediterranean) during the years 2007–2009. In the Catalan Sea, the presence of adult *R. pulmo* was recorded as extended along the whole coast, but most of the observation was concentrated in the central area; the highest abundances were recorded during the months of July and August. The highest number of observations was detected

in 2008 in coincidence with the inter-annual variation observed in the Mar Menor lagoon.

Introduction

The numbers of jellyfish are perceived to be increasing in many areas worldwide, and this has triggered a growing scientific interest in the ecological importance of these organisms (Arai 2001; CIESM 2001; Mills 2001; Brodeur et al. 2002; Purcell 2005; Kawahara et al. 2006; Purcell et al. 2007; Richardson et al. 2009) and species seem to be undergoing range expansions into new areas (Mills 2001). Studies on life cycles, ecology and distribution of the most important blooming jellyfish species are necessary because of the ecological and social impacts of their outbreaks. The impacts of jellyfish outbreaks in the ecosystem and on many human activities have been summarized in several papers (Goy et al. 1989; Dawson et al. 2001; Kideys and Romanova, 2001; Mills 2001; Purcell and Arai 2001; Purcell 2005; Richardson et al. 2009), and today there are no doubts about the importance of these phenomena.

Several jellyfish species are frequently observed in high abundances along the NW Mediterranean coast (Gili and Pagès 2005). The most abundant species are, in descending order, the scyphozoans *Pelagia noctiluca* (Forsskål, 1775), *Rhizostoma pulmo* (Macri 1778), *Cotylorhiza tuberculata* (Macri, 1778), *Chrysaora hysoscella* (Linnaeus, 1767) and the hydromedusa *Aequorea forskalea* (Forsskål, 1775) (Gili and Pagès 2005; Gili et al. 2009). Moreover, *R. pulmo* has shown to be the most abundant coastal species in recent years, showing important inter-annual fluctuations in the population densities as typical for most scyphozoans blooms presently observed (Mills 2001; Graham et al. 2003; Lilley et al. 2009).

Communicated by J. Purcell.

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During blooming years in the Mediterranean Sea, *Rhizostoma pulmo* occurred in large numbers in several places as for example the Northern and Southern Adriatic Sea, the Ionian Sea, in the Eastern and Western Mediterranean, as well as in the Black Sea (reviewed in Mariottini and Pane 2010). Proliferations of *R. pulmo* also have been recorded in the Mar Menor lagoon, south-eastern Spain, NW Mediterranean (Fig. 1) (Mas 1999; Perez-Ruzafa et al. 2002). The Mar Menor is a hypersaline coastal lagoon of 135 km² surface area, average depth of 4 m. It is separated from the Mediterranean Sea by a sandy barrier with three shallow inlets connecting both basins (Pagès 2001). The Mar Menor ecosystem had traditionally supported an important artisanal fishery. Jellyfish have always been present, and an important population of *Aurelia aurita* (Linnaeus, 1758) is known from early last century (Mas 1999). The scyphomedusae, *Cotylorhiza tuberculata* and *Rhizostoma pulmo*, were recorded for the first time about 20 years ago, and both species developed a massive bloom in summer first in 1996, which has recurred in different densities (Pagès 2001; Perez-Ruzafa et al. 2002). Both species have completed their life cycle in the lagoon where the conditions seem to be adequate for their development. The maximum numbers of medusae counted between 2002 and 2004 were about 100 million adult *Cotylorhiza tuberculata* and more than 3.5 million *Rhizostoma pulmo* (EUROGEL 2004). The proliferations of *R. pulmo* in these areas have caused serious problems for tourism and to local commercial fisheries (Lakkis 1991; Mariottini and Pane 2010).

The study of scyphozoan life cycles can provide important clues to understand their inter-annual fluctuations. The life cycle of *R. pulmo* begins with a fertilized egg that develops into a planula and hence into a sessile and asexually reproducing scyphistoma, which strobilates

and releases swimming ephyrae that develop into medusae (Fig. 2). Of three species of *Rhizostoma* currently recognized as valid (Holst et al. 2007), *R. pulmo* is the only one found in the Mediterranean Sea and adjacent areas. *Rhizostoma octopus* (Linnaeus, 1788) lives in the North Sea and adjacent Atlantic Ocean coast regions, while *Rhizostoma luteum* (Quoy and Gaimard, 1827) is found off the coasts of Portugal, the Straits of Gibraltar and the west coast of Africa (Russell 1970).

Different stages of the life cycle of *Rhizostoma pulmo* were observed by few authors previously, but the complete life cycle of the species has never been fully described. Claus (1883, 1884) described the early development of sampled ephyrae, and Paspaleff (1938) was the first to rear scyphistomae successfully under laboratory conditions, but the induction of strobilation led to degenerated ephyrae.

Recently, several studies have shown the importance of both planktonic and benthic phases of the jellyfish life cycle to understand the changes in jellyfish population densities (Boero et al. 2008) and population sizes probably reflect the success of the benthic stage in producing jellyfish (Purcell 2007). Moreover, jellyfish that aggregate, bloom or swarm seem to be clustered taxonomically and phylogenetically (Hamner and Dawson 2008) and a suite of life history and phenotypically distinguishing features (podocyst formation, polydisc strobilation, ephyrae, circular and radial canals, large size) appears phylogenetically correlated with clades that bloom or swarm (Arai 2009; Dawson and Hamner 2009). Our study describes all stages of the life cycle of the blooming species, *Rhizostoma pulmo*, one of the largest and most abundant jellyfish in the NW Mediterranean, fills the gaps of information between the scyphistoma and medusa stages and provides information about its distribution, seasonality and inter-annual

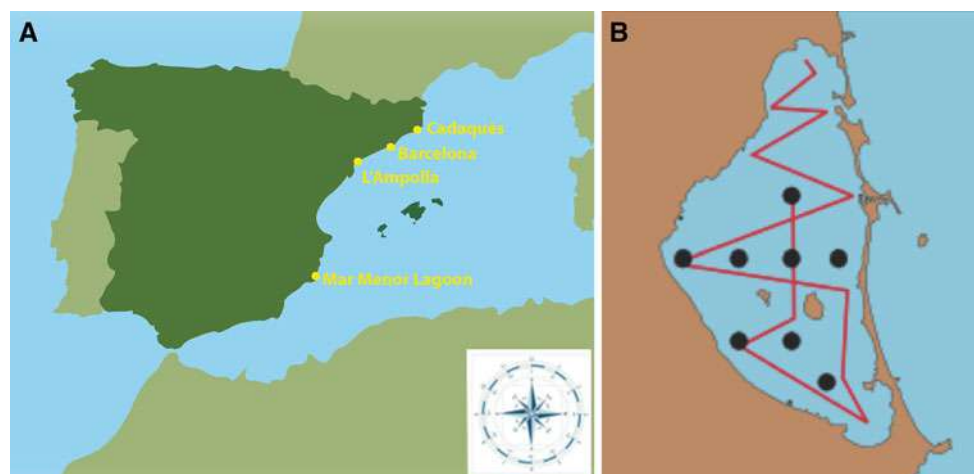


Fig. 1 Locations of jellyfish observations along the Catalan coast and in the Mar Menor Lagoon in 2007–2009. **a** Sampling stations on the Catalan coast and location of the Mar Menor on the Mediterranean

coast of Spain, **b** sampling stations (circles) and video tracks (lines) in the Mar Menor Lagoon

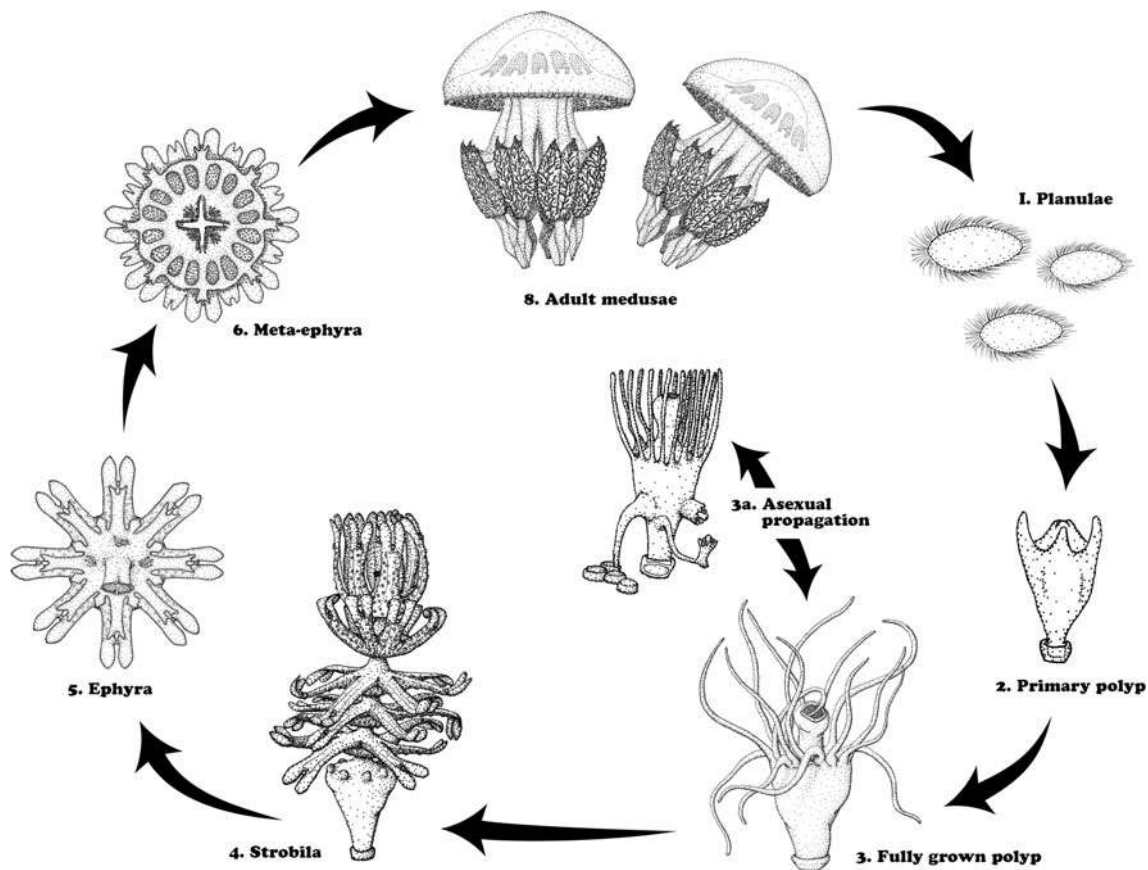


Fig. 2 Schematic representation of the *Rhizostoma pulmo* life cycle

variability along the NW Mediterranean (Catalan) coast and in the Mar Menor, in Spain.

Materials and methods

The presence of large (>5 cm) jellyfish, including *R. pulmo*, has been monitored since 2007. The presence of jellyfish is recorded daily at more than 300 beaches along the entire Catalan coast from May to September. Data are recorded by inspectors who observe organisms on the sand and in the near-shore water at fixed locations and at 200 m offshore beyond the swimming areas. The ACA surveys were supplemented since 2008 by monthly sampling in three areas along the coast (Fig. 1a). Data on water temperature and salinity (SAIV A/S CTD SD204) were collected.

The populations of scyphomedusae in the Mar Menor have been monitored yearly beginning in May with weekly sampling at 8 stations, utilizing a 1-m-diameter plankton net with 1,000- μm mesh (filtered water volume 800–1,000 m^3) to detect the first ephyrae (Fig. 1b). When the strobilation period had finished and the umbrella diameter of young medusae was about 5 cm, they were

quantified by means of a towed video camcorder that records the jellyfish that cross a 1- m^2 surface. The sampling stations and video tracks in the Mar Menor are shown in Fig. 1b.

The occurrences of adult *Rhizostoma pulmo* medusae along the Catalan coast (Fig. 1a) were detected by cooperation between the Marine Science Institute (ICM, Barcelona, Spain) and the Catalan Water Agency (ACA, Barcelona, Spain). *Rhizostoma pulmo* scyphistomae were obtained in the laboratory from the continuous culture established in 2007 at the ICM. Eight adults (about 30-cm umbrella diameter) collected close to the Barcelona Olympic port (Fig. 1a) were placed in a tank (2,000-L capacity) designed for rearing adult *R. pulmo* medusae. The tank was filled with filtered and UV-treated seawater that was pumped directly from the sea. The animals were kept from June to September 2007 at the natural seasonal cycle of sea water temperatures and salinities (Fig. 5) and fed with newly hatched nauplii of *Artemia* sp. and natural plankton from the Catalan coast. While the medusae were in the tanks, PVC settling discs were placed at the corners of the tank.

In late September, when the adult *R. pulmo* medusae were removed from the tanks, the artificial substrates that

were colonized by scyphistomae also were removed. Scyphistomae were carefully collected with a plastic pipette and cultivated further in glass bowls (250-ml capacity) covered by glass lids (Jarms et al. 2002). They were kept in sea water (37–38 salinity, 21°C temperature, light cycle 12-h light–12-h darkness) inside incubators and fed twice weekly with newly hatched *Artemia* sp. nauplii. Scyphistomae for this project were never forced to strobilate by manipulating the temperature or salinity; they strobilated spontaneously in spring 2008 and 2009 and in March 2010. Newly released ephyrae were removed from the cultures, transferred to several 6-L capacity aerated aquaria and reared at approximately 20°C water temperature. The ephyrae were fed daily with newly hatched *Artemia* sp. nauplii.

To compare the scyphistomae, strobilae and ephyrae, all specimens were photographed with a digital camera (ColorView, Soft Imaging System GmbH) under the same conditions. Mature scyphistomae of equal sizes and in different stages of strobilation were transferred to a glass petri dish (5-cm diameter) with culture water in a lateral position. Each ephyra was transferred into a depression slide so that the manubrium faced the objective lens of the camera and then a cover slip was applied. Adaptation times were 2–5 min. A menthol solution was used to relax the animals. When the scyphistomae, strobilae or ephyrae were fully expanded, the pictures were taken immediately to avoid extreme temperature changes. Afterwards the animals were transferred back into their culturing dishes. Development of the gastric system in ephyrae was photographed every second day 4 h after feeding when the opacity of the gastric system was increased by food particles. The scyphistomae and ephyrae were measured from the pictures by use of the program analySIS® (Soft Imaging System GmbH).

The following measurements were used (Table 1): The measurements of scyphistomae were defined as in Straehler-Pohl et al. (2011): total body length (TBL), calyx length (CL), hypostome length (HL), mouth disc diameter (MDD) and stalk length (StL). The measurements of ephyrae were defined as in Straehler-Pohl and Jarms (2010): total body diameter (TBD), central disc diameter (CDD), total marginal lappet length (TMLL), lappet stem length (LStL) and rhopalial lappet length (RLL). To compare relative body dimensions, proportions (%) were calculated as in Straehler-Pohl et al. (2011) for scyphistomae (measurements compared with body length, e.g. $CL/TBL \times 100$, and calyx diameter, $MDD/CL \times 100$) and in Straehler-Pohl and Jarms (2010) for ephyrae (measurements compared with body diameter, e.g. $CDD/TBD \times 100$ and lappet length, e.g. $RLL/TMLL \times 100$). A total of ten scyphistomae and 29 ephyrae of 10 strobilae were measured. Data are presented as mean \pm 1 standard deviation.

Results

Rhizostoma pulmo medusae temporal and spatial distributions

During the summers of 2007, 2008 and 2009 along the Catalan coast, *Rhizostoma pulmo* represented 17% ($n = 70$), 25% ($n = 298$) and 15% ($n = 107$), respectively, of the total number of jellyfish observations. After *Pelagia noctiluca*, *R. pulmo* was the second-most observed species. The most *R. pulmo* were observed during summer 2008 (220 observations) and the fewest in 2007 (70 observations). The distribution of *R. pulmo* medusae extended along the entire Catalan coast, but most observations were concentrated in the central area (Fig. 3).


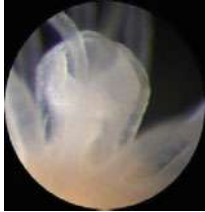
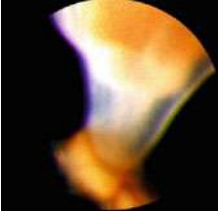


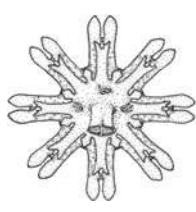
The seasonal distribution of *Rhizostoma pulmo* observations along the Catalan coast was quite similar during the 3 years studied, with most observations during July and August (Fig. 4). During years 2008 and 2009, juvenile *R. pulmo* about 5–10 cm umbrella diameter were observed at the beginning of May. The adults continued to be observed from July to September and disappeared at the end of September in 2008 and 2009 and in August 2007.

Rhizostoma pulmo medusae were very abundant in the Mar Menor. The total abundance of juveniles and adults estimated from the towed video camcorder ranged between 165,000 medusae in 2009 and 325,000 in 2007. In 2008, the number of medusae (167,000) was similar to 2007. Ephyrae first appeared in the plankton samples in the Mar Menor at the end of May and beginning of June. The first ephyrae always appeared near the opening of Albuñón avenue in the western part of the lagoon, but the scyphistomae were not found. The recurrence of ephyrae in the same area each year strongly suggests that the biological cycle of the species is completed in the lagoon. Mature individuals were found in August. The numbers of medusae decreased throughout the summer, probably due to removal by fishermen, which were paid for collecting adult medusae, and also to natural mortality. The adult medusae normally disappeared during January and March; however, in some years, all adults did not disappear until end of June of the following year, with some adults occurring with the new ephyrae.

Environmental parameters

Average surface water temperatures along the Catalan coast (years 2007, 2008 and 2009) fluctuated from 12.2°C in February 2009 to 25.5 in July 2009, and salinity varied from 37 to 39.1 (Fig. 5). During 2007–2009 in the Mar Menor, the average surface temperature ranged between 11°C (February 2009) and 28.6°C (August 2009) and the salinity between 40.8 and 44.8 (Fig. 6).

Table 1 Morphology and body proportions of the polyps and Ephyra of *Rhizostoma pulmo*

Polyp: morphology/body proportions		Ephyra morphology/body proportions	
  		 	
<p>Anatomy:</p> <ul style="list-style-type: none"> • 16 filiform tentacles • Flat to slightly sunken mouth disc • Hypostome: broad club shaped, four-lipped • 4 septal funnels • Calyx shape: bowl-shaped, widest body diameter is the mouth disc <p>Basal region:</p> <ul style="list-style-type: none"> • Basal disc enclosed by periderm beaker which is left behind when changing location <p>Distribution:</p> <p>Mediterranean Sea, Black Sea</p>	<p>Body proportions:</p> <ul style="list-style-type: none"> • HL = 35% of TBL (SD = 0.146) • CL = 40% of TBL (SD = 0.087) • MDD > CL (MDD/CL = 1.4, SD = 0.422) • short stalk (StL/TBL = 24%, SD = 0.087) 	<p>Anatomy:</p> <ul style="list-style-type: none"> • 8 lappet stems • 16 spade to lancet-like rhopalial lappets • 1-3 gastric filaments per quadrant • No marginal tentacles or tentacle bulbs • Long ML, approx. 46% of the CDD (SD = 0.0744) <p>Gastric system:</p> <ul style="list-style-type: none"> • Rhopalial canals are slightly forked: Fork arms level with the rhopalium base • Velar canals are unforked, diamond shaped, tips level with umbrella rim, cause umbrella rim sometimes to protrude outwards <p>Body proportions:</p> <ul style="list-style-type: none"> • RLL = 13% of the TBD (SD = 0.013) • LStL = 16% of the TBD (SD = 0.022) • CDD = 42% of the TBD (SD = 0.10) • RLL = 44% of the TMLL (SD = 0.0383) • LStL = 56% of the TMLL (SD = 0.0465) 	

CL Calyx length, HL hypostome length, MDD mouth disc diameter, SD standard deviation, StL stalk length, TBL total body length, CDD central disc diameter, LStL lappet stem length, RLL rhopalial lappet length, TBD total body diameter, TMLL total marginal lappet length

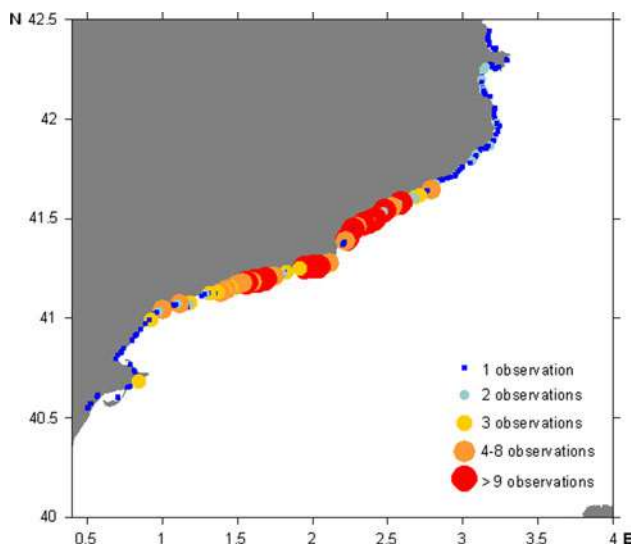


Fig. 3 Distribution of *Rhizostoma pulmo* medusae observed along the Catalan coast from May to September in 2007, 2008 and 2009

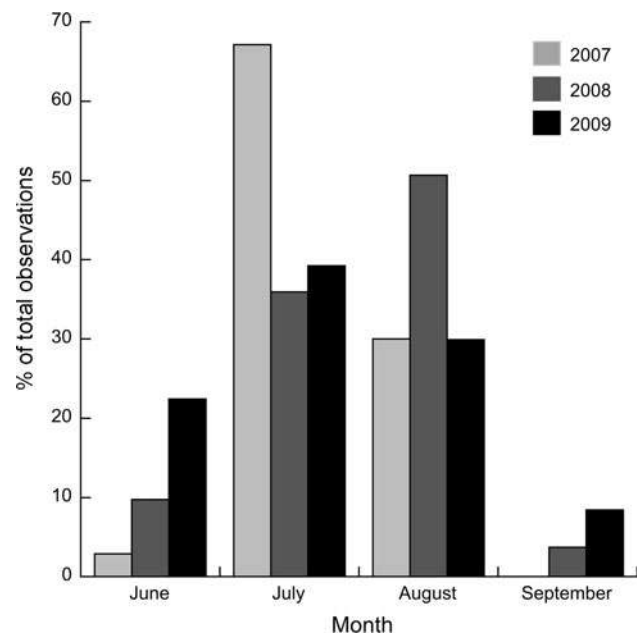


Fig. 4 Seasonal occurrence of *Rhizostoma pulmo* medusae observed from 2007 to 2009 along the Catalan coast

Life cycle

Mature scyphistomae of *Rhizostoma pulmo* (Table 1) averaged 1.7 mm in total body length (TBL) and 0.9 mm in mouth disc diameter (MDD; Table 2). The mature scyphistomae had an average of 16 tentacles in a single whorl

around a slightly sunken mouth disc (peristome) and a very long, club-shaped, four-lipped hypostome that was 35% of the TBL (Table 1). Scyphistomae were white to pale pink in colour depending on the feeding condition. They had a

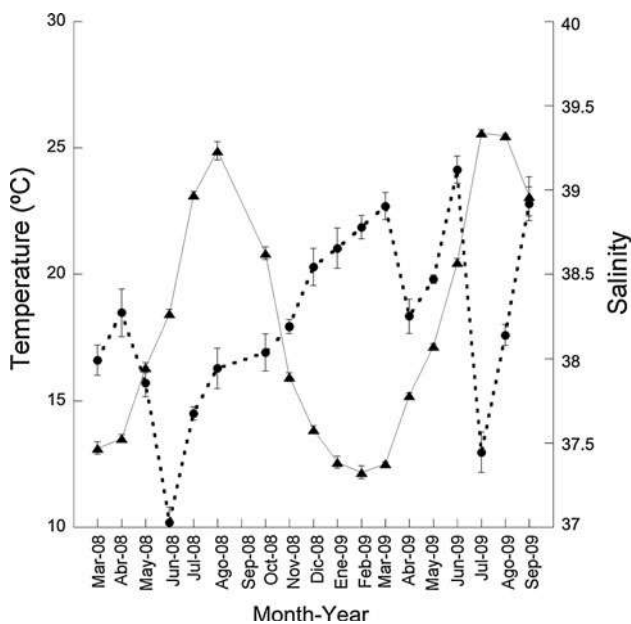


Fig. 5 Monthly measurements of sea temperature (°C) and salinity in the surface waters of the Catalan sea from March 2008 to September 2009. *Solid triangles* salinity. *Crosses* temperature

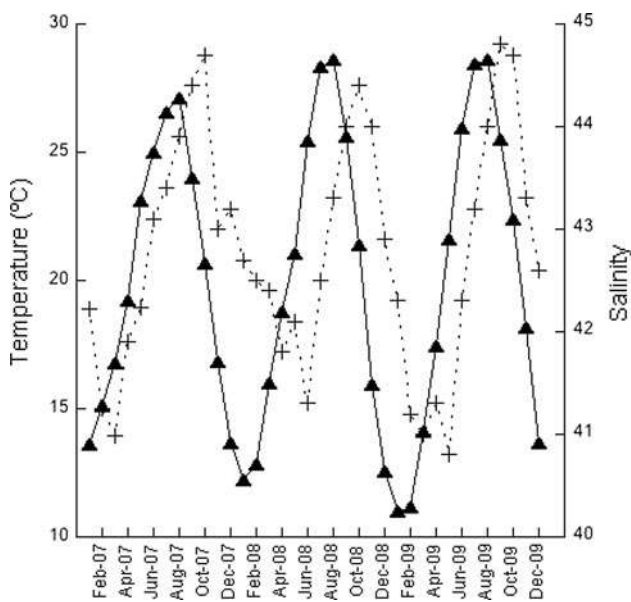


Fig. 6 Monthly measurements of sea temperature (°C) and salinity in the surface waters of the Mar Menor from February 2007 to December 2009. *Solid triangles* salinity. *Crosses* temperature

bowl-shaped calyx that was distinctly wider than high. The widest part was the mouth disc that was perched on a short stalk (~24% of TBL). The basal disc at the foot of the stalk was enclosed by a periderm beaker that was left behind when the scyphistoma changed locations.

Asexual proliferation of scyphistomae occurred by typical lateral scyphistoma budding (origin: junction point of

calyx and stalk), podocysts, pedalocysts and lateral budding by the stolon (Fig. 2). Podocyst production was more frequent than scyphistoma budding and was done by stolons that appeared at the junction of the calyx and stalk. The stolons attached to the substrate, and a periderm-enclosed podocyst was formed around the attached part of the stolon. The podocyst was sealed off and the tissue above the podocyst detached, retracted, and was resorbed by the scyphistoma. The pedalocysts were formed underneath the basal disc and had the same external appearance as the podocysts. The stolonal scyphistoma budding resembled the beginning of podocyst production, but a tiny scyphistoma formed at the tip of the stolon instead of a podocyst. The daughter scyphistoma attached to the substrate, and the stolon detached and was absorbed by the scyphistoma.

At the first phase of strobilation, the calyx elongated and the mouth disc rim thickened (Table 3). Constrictions formed right below the tentacle crown in the 2nd phase. Up to 8 primordia of ephyrae (Table 3) formed chronologically. The scyphistoma tentacles were gradually resorbed while the first primordium differentiated into an ephyra. The mouth disc and hypostome of the residuum were reconstructed after the last primordium was formed. The other primordia differentiated almost synchronously. The stack of developing ephyrae were colourless during the whole strobilation process. The fully developed ephyrae pulsed in rhythmic waves by contracting their lappets until their release. The residuum developed 4–8 tentacle buds when the first ephyra detached. The ephyrae matured and were released almost synchronously. The residuum, with newly regenerated tentacles and hypostome, was much smaller than the mature, pre-strobilation scyphistomae. After strobilation, the residuum required up to 2 weeks to regenerate into a polyp of mature size and tentacle number.

Newly liberated ephyrae had a total body diameter (TBD) of ~3.5 mm and a central disc diameter (CDD) of ~1.5 mm, about 42% of the TBD (Tables 1, 3). Typical ephyrae had 8 marginal arms, although the number ranged from 5 to 9. No irregular ephyrae were produced. Ephyrae had a single rhopalium per lappet stem between the two-pointed spatula and lancet-shaped rhopalial lappets (Table 4). The rhopalial lappets were 30% of the total marginal lappet length. The manubrium was 0.7 mm long, which was ~46% of CDD. There were 1–3 gastric filaments per quadrant in the central stomach. Ephyrae were opaque white with small white nematocyst warts scattered over the exumbrella.

Because the ephyrae would achieve their developmental stages at different times depending on the temperature and feeding conditions, the chronological order of the different stages is given below without time periods. Definitions of gastric canals and their sequence are in Table 4.

Table 2 Polyp morphology and references of rhizostome species

Species	Culture conditions (temperature)	Polyp size range (mm)	MDD (mm)	Number of tentacles	Stalk (shape/length (mm)/proportion)	Hypostome (shape/length (mm)/proportion)	Periderm shape	Asexual reproduction forms	Zooxanthellae	Strobilation rate (ephyrae per strobila, strobilation type)	Reference
<i>Rhizostoma pulmo</i>	–	12	–	32	Short	Long and flexible	–	Lateral polyp buds, polyp buds by means of stolon, swimming buds, podocysts	–	12–18 primordia without detachment of ephyrae	Paspaleff (1938)
	5–20°C	1.45	0.80	16	Short/0.36/25% of TBL	Long, club-shaped/0.64/44% of TBL	Solid beaker	Podocysts, lateral polyp buds	Absent	8, oligodisc	Straehler-Pohl (2009)
	21°C	0.96–2.15, mean: 1.69	0.53–1.16, mean: 0.88	14–18, mean: 16	Short/0.40/24% of TBL	Long/0.60/35% of TBL	Beaker	Lateral polyp buds, stolonal polyp buds, podocysts, pedalcysts	Absent	8, polydisc	Present study
<i>Rhizostoma octopus</i>	5–20°C	2.30	–	Up to 24	Short	Long and flexible/50% of TBL	–	Podocysts, polyp buds (rare)	–	1, monodisc 2–5, polydisc	Holst and Jarms (2006) and Holst et al. (2007)
<i>Catostylus mosaicus</i>	5–20°C	1.90	1.25	Up to 20	Short/0.44/23% of TBL	Long, club-shaped/0.86/45% of TBL	Solid beaker	Podocysts, lateral polyp buds	Absent	5–12, polydisc	Straehler-Pohl (2009)
	21°C	–	–	12–20	short ^p	Long and capable of considerable expansion,	Beaker ^p	Lateral polyp buds, podocysts, pedalcysts, longitudinal fission	Absent	1, monodisc 2–5, polydisc	Pitt (2000)
<i>Rhopilema esculentum</i>	23°C	1.57–1.90	0.69–0.81	16–17	Short/0.28/16% of TBL	Long, club-shaped/0.69/36% of TBL	Solid beaker	Podocysts, lateral polyp buds	Absent	4, polydisc	Straehler-Pohl (2009)
	12–22°C	3.00	1.6 ^{p,z}	16	Short ^p	Moderately long ^p	Beaker ^p	Podocysts	Absent	6–10, polydisc 7–8, up to 17, polydisc	Ding and Chen (1981) and Chen and Ding (1983)
<i>Rhopilema nomadica</i>	5–20°C 20°C	1.00–3.50 1.8–2.0	– –	16 16	– Short	– Extraordinarily large clavate shaped/1/3 of polyp length	– Solid beaker	Podocysts Podocysts	Absent	7–8, polydisc 5–6, polydisc	You et al. (2007) Lotan et al. (1992)
<i>Rhopilema verrilli</i>	9–20°C	0.75–1.0	0.35	8–10	Short ^r to long ^r	0.25	–	Pedalcysts, podocysts	–	Up to 3, polydisc	Cargo (1971)
	10–12°C, 20°C	2.5	–	Up To 20	Short ^r	Large, flexible, and quadrate, irregular in outline	–	Podocysts	–	1, monodisc	Calder (1973)
<i>Lychnorhiza lucerna</i>	16–22°C	1.5	0.55–0.80	18–22	Short to moderate [#]	Prominent dome-shaped (club-shaped [#])	Transparent beaker	Podocysts	–	3, polydisc	Schiariti et al. (2008)
<i>Nemopilema nomurai</i>	13–23°C, 18°C	2.6	0.80–1.10	16	Short to moderate [#]	Dome-shaped, one-third of scyphistoma height	–	Podocysts	–	3–7, polydisc	Kawahara et al. (2006)
<i>Stomolophus meleagris</i>	25–27°C	2.0	–	16	Short to moderate [#]	Large, flexible, and dome- or knob-shaped	–	Podocysts	–	1, monodisc 2–3, polydisc	Calder (1982)
<i>Cephea cephea</i>	20–30°C	1.4–2.9	0.04–0.7	16	Long/1.0–2.0	Short ^r	–	Swimming polyp buds	–	1, monodisc	Sugiura (1966)
	23–25°C, daylight	2.04–2.47	0.44–0.60	14–17	Long, sturdy/1.13–1.33/54–58% of TBL	Short, club-shaped/0.22–0.32/12% of TBL	Cuticle enclosing 1/3 of the stalk	Lateral budding, swimming buds	Present	1, monodisc	Straehler-Pohl (2009)

Table 2 continued

Species	Culture conditions (temperature)	Polyp size range (mm)	MDD (mm)	Number of tentacles	Stalk (shape/length (mm)/proportion)	Hypostome (shape/length (mm)/proportion)	Periderm shape	Asexual reproduction forms	Zooxanthellae	Strobilation rate (ephyrae per strobila, strobilation type)	Reference
<i>Corylorhiza tuberculata</i>	23–24°C	5.0	–	16	Long and slender/ 3.0–4.0/ 60–80% of TBL	Cylindrical ^p	–	Lateral budding, swimming buds	Present	1, monodisc	Kikinger (1992)
<i>Mastigias papua</i>	23–25°C, daylight	3.23–3.59	0.82–0.86	16–17	Long, sturdy/ 2.29–2.50/ 70% of TBL	Short, cylindrical/ 0.34–0.40/11% of TBL	Cuticle enclosing up to 1/3 of the stalk	Lateral budding, swimming buds	Present	1, monodisc	Strachler-Pohl (2009)
	–	–	–	16	Long	–	–	–	–	–	Uchida (1926)
	>15–24°C	1.0–2.3	0.4–0.8	15–18, mean: 16	Long/0.7–1.8/ 70–78% of TBL	–	Tube enclosing parts of stalk, ^{z,p}	Planula-like larvae	Present	1, monodisc	Sugiura (1963, 1964, 1965)
<i>Phylorhiza punctata</i>	23–25°C, daylight	8.14–10.22	0.76–0.92	15–17	Very long, delicate/ 7.45–9.64/ 93% of TBL	Very short, cylindrical/ 0.08–0.20/1–2% of TBL	Tube enclosing 90% of stalk	Planuloids	Present	1, monodisc	Strachler-Pohl (2009)
<i>Cassiopea andromeda</i>	25°C	–	–	16	Long ^z	–	Tube around parts of stalk ^z	Ciliated buds	–	1, monodisc	Rippingale and Kelly (1995)
	–	–	–	32	Very long/4x calyx length/–	–	Chitin-beaker	Swimming buds	Present	1, monodisc if calyx is long and stalk is short then 2 to many but rate	Gohar and Eisawy (1960a, b)
	19–22°C	5.0–10.0	1.95	32	Long, slender/ 3.0–8.0/ 60–80% of TBL	Conspicuously long, tetragonal/0.88/9–18% of TBL, 0.8-fold of calyx length	Chitinous periderm barrel	Swimming buds	Present	1, monodisc	Ludwig (1969)
	23–25°C, daylight	4.72–6.85	–	–	Long, slender/ 3.35–5.86/ 71–82% of TBL	Ephyra-manubrium-shaped/0.53–0.80/8–14% of TBL	Tube enclosing up to 70% of stalk	Planuloids	Present	1, monodisc	Strachler-Pohl (2009)
<i>Cassiopea xamachana</i>	–	–	1.5–2.0	Up to 42, mean: 32	–	–	–	Planula-like larvae	Present	1, monodisc	Bigelow (1900)

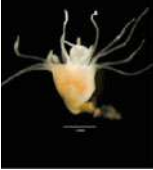






MDD Mouth disc diameter, TBL total body length, – no statement

^p Data taken from photos

^z Data taken from sketches

Moderate length in comparison with stalks of other Rhizostomida polyps but short in comparison with stalks of Cepheida polyps (e.g. *Cepheia cephea*, *Mastigias papua*)

Table 3 Strobilation phases of *Rhizostoma pulmo*

Species	Polyp	Strobilation				Ephyra	
		Phase 1	Phase 2	Phase 3	Phase 4	Residium	
<i>Rhizostoma pulmo</i>							
		<ul style="list-style-type: none"> Elongation of the calyx 	<ul style="list-style-type: none"> Formation of the 1st primordia of ephyrae by forming a constriction directly below the tentacle crown Chronological formation of up to 8 additional primordia of ephyrae 	<ul style="list-style-type: none"> Absorption of tentacles Residium forms hypostome after developing last primordium Synchronical differentiation of primordia 	<ul style="list-style-type: none"> Ephyrae detach nearly in synchronical order from strobila Residium forms 4-8 tentacle buds before detachment of the last ephyra 	<ul style="list-style-type: none"> Size growth and development of last missing tentacles after strobilation 	

Stage 0: The gastric system of newly released ephyrae (Table 1) consisted of a central stomach, 8 slightly forked rhopalial canals and 8 non-forked, diamond-shaped velar canals (radial canals = primary canals). The tips of the rhopalial canal-spikes ended at the base of the rhopalium. The tips of the velar canals ended at the umbrella rim, sometimes causing the rim to protrude slightly outwards.

Stage 1: The tip of the velar canals broadened and a velar lappet bud appeared at the umbrella rim between the marginal lappets right above the velar canal. The first mouth tentacles developed around the mouth opening (Table 4).

Stage 2: A pair of short side branches (secondary canals) was developed by the rhopalial canals. The velar lappet buds split each into a pair of short lappets that were still fused at the base (Table 4).

Stage 3: The velar canals lengthened centrifugally. The velar canal tips developed one branch on each side, which fused with side branches developed by the rhopalial canals to form a primary ring canal. The tips of the velar lappet pairs reached the rhopalial lappet base level in length. The rim of the manubrium began to split into 4 mouth arms (Table 4).

Stage 4: The connections of the primary ring canal between the velar and rhopalial canals were closed and eliminated (Table 4). The velar canals lengthened further centrifugally. The velar lappet pairs broadened, the tips nearly reaching the level of the rhopalial lappet tips, completing the umbrella.

Stage 5: The side branches of the rhopalial canals were eliminated. The disconnected side branches of the velar canals grew two new canals each, two developing centripetally parallel to the radial canals (tertiary canals) and the other two developing perpendicular to the rhopalial canals (Table 4). The rhopalial and velar canals grew two new side branches midway. The tips of the 4 mouth arms split forming 4 pairs of mouth arms.

Stage 6: The midway-side branches of the radial canals fused with the centripetally growing tertiary canal of the velar tips to form a second ring canal. The perpendicularly growing canals fused with the rhopalial canals directly below the rhopalia to form a third ring canal (Table 4). Below the second ring canal, the velar and rhopalial canals developed the last set of side branches to form a final ring canal by fusing with the last part of the centripetally growing tertiary canals. The tips of the centripetally growing canals remained free and protruded into the space between the radial canals.

Stage 7: As soon as the final ring canal formed, the spaces between the canals extended by “Inselbildung”.¹ The “Inseln” (=islands) were woven through by “Austuepungen”² (quaternary canals), forming a fine-meshed network of slender anastomosing canals (Table 4).

Stage 8: The final ring canal separated the upper extra-circular network of anastomosing canals from the lower intra-circular arcades, consisting of the radial canals, the tips of the centripetal canals, the final ring canal and the central stomach (Table 4). A fully developed juvenile *R. pulmo* is pictured in Fig. 7.



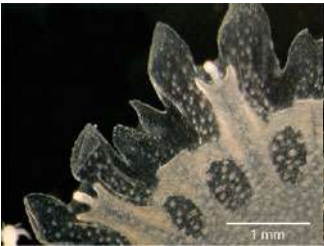

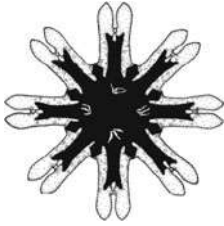



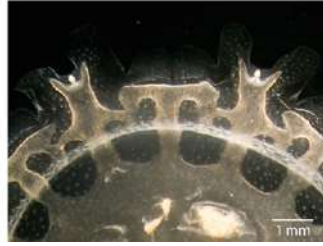







Discussion

This work represents the first complete description on the life cycle of *Rhizostoma pulmo* and emphasizes that such baseline studies on important blooming species are a key aspect of understanding jellyfish fluctuations. We focused

¹ Fusion of roof and bottom of the gastric cavity, defined by Stiasny (1923) and Uchida (1926).

² Diverticula of gastric system growing into extra-gastric tissues, defined by Stiasny (1923) and Uchida (1926).

Table 4 Developmental stages of gastric system of the ephyra of *Rhizostoma pulmo*

Species (Ephyra, Stage 1 ^{#1})	Development of Gastric system ^{#2}		
	Stage 2	Stage 3	Stage 4
			
			
<p><i>Rhizostoma pulmo</i></p> <ul style="list-style-type: none"> • rhopial canals (primary canals) with forked tips, fork tips level with the base of the statolith • diamond-shaped, unforked velar canals (primary canals) end at umbrella rim, sometimes causing the rim to protrude outside 	<ul style="list-style-type: none"> • the rhopial canals form midway 1 short pair of side branches (secondary canals)^{#3} • the velar canals tips grow centrifugally and form one pair of side branches each just below their tips • twin velar lappets grow between the marginal lappets 	<ul style="list-style-type: none"> • the side branches of the velar canals fuse with the pair of side branches of the rhopial canals to form a primary ring canal 	<ul style="list-style-type: none"> • the connection of the primary ring canal between the velar and rhopial canals close up and phase out. • the velar canals grow further in centrifugal direction • the velar lappet pairs broaden, the tips nearly reaching the level of the rhopial lappet tips, completing the umbrella
Development of Gastric systems^{#2}			
Stage 5	Stage 6	Stage 7	Stage 8
			
			
<ul style="list-style-type: none"> • the side branches of the rhopial canals phase out • the disconnecting side branches of the velar canals grow two new canals each (tertiary canals^{#4}) - two developing centripetally in parallel to the radial canals, the other two developing horizontally towards the rhopial canals • The rhopial and velar canals grow midway two new side branches 	<ul style="list-style-type: none"> • the midway-side branches of the radial canals fuse with the centripetally growing tertiary canals of the velar canal tips to form a secondary ring canal • the horizontally growing canals fuse with the rhopial canals directly below the rhopalia, forming a third ring canal • below the second ring canal, the velar and rhopial canals develop the last set of side branches to form a final ring canal by fusing with the last part of the centrifugally growing tertiary canals. 	<ul style="list-style-type: none"> • the tips of the centripetally growing canals stay clear of the fusion and protrude into the space between the radial canals and the stomach • as soon as the final ring canal is finalised, the spaces between the canals extend by "Inselbildung"^{#5} • The "Inseln" are woven through by "Ausstülpungen"^{#5} (quarternary canals) forming a fine-meshed network of slender anastomosing canals 	<ul style="list-style-type: none"> • the final ring canal separates the upper extra-circular network of anastomosing canals from the lower intra-circular arcades consisting of the radial canals, the tips of the centripetal canals, the final ring canal and the central stomach

#1: newly detached; #2: white = umbrella, black = gastric system; #3: secondary canals: form ring canal or connect the ring canal with rhopial, velar and secondary canals; always direct connection with ring canal; #4: tertiary canals: connect secondary canals with each other or with rhopial or velar canals, no direct connection to ring canal; #5: "Inselbildung" = fusion of roof and bottom of the gastric cavity, defined by Stiasny (1923) and Uchida (1926); "Ausstülpungen" = diverticula of gastric system growing into extra-gastric tissues, defined by Stiasny (1923) and Uchida (1926)



Fig. 7 Photograph of a fully developed juvenile of *Rhizostoma pulmo* reared at the ICM, Barcelona

on the early developmental stages, from scyphistoma to the fully developed juvenile medusa.

Distribution and seasonality of medusae

Rhizostoma pulmo is one of the most important scyphozoan jellyfish species blooming along the Spanish coasts, as well as, *Pelagia noctiluca* and *Cotylorhiza tuberculata*. The scyphozoans have life history traits (scyphistoma and free living stages) that can result in rapid increases in numbers, growth and dispersal rates. In addition to the descriptive studies conducted to date, more detailed characterizations of jellyfish populations are needed to understand their distributions, abundances and blooming events. In this regard, it is important to monitor the population dynamics at temporal and spatial scales.

Our data about the presence, distribution and inter-annual variability of *Rhizostoma pulmo* medusae in the Catalan Sea (NW Mediterranean) show that the distribution of the species seems to be restricted to the central Catalan coast (Fig. 3). This agrees with the review on *Rhizostoma* spp. in European waters by Lilley et al. (2009) who cited newspaper reports that >1,500 *R. pulmo* (35–40 cm) were stranded near Barcelona. Environmental factors could be determined the distributions of the species. The Catalan Sea has a clear zonation with three hydrographic areas (Castellón et al. 1990; Masó and Tintoré 1991; Salat 1996). The central shelf-area (Fig. 1a) is characterized by a high mesoscale activity due to the dynamic coupling of coastal and oceanic waters. The northern and southern regions are characterized by specific hydrodynamics, such as influence of the Ebro River runoff associated with higher temperatures and lower salinities (southern) or dominance by Liguro-Provençal-Catalan current with low water temperatures and north winds (northern).

By contrast, in the coastal lagoon, the Mar Menor, the response of plankton food web dynamics to environmental changes can be observed and studied more easily. In the Mar Menor, there was a native population of *Aurelia aurita* (Franco and Gili 1989; Franco 1990); however, in 1993, *Cotylorhiza tuberculata* and *Rhizostoma pulmo* medusae first appeared as a result of environmental degradation of the lagoon. Since 1996, both species have completed their life cycle inside the lagoon. The appearance and establishment of these two species coincided with increased nutrient inputs from human activities, especially agriculture (Perez-Ruzafa et al. 2002). *R. pulmo* medusae were present in the lagoon throughout the year, and its distribution had no relationship with the wind regime (EUROGEL 2004). Abundances varied between 25,147 medusae (September 2004) and 3,603,379 (June 2003), which agree with the densities in the present study.

In spite of the environmental differences, *Rhizostoma pulmo* strobilated and first ephyrae appeared in similar periods in the Mar Menor (April–May) and along the Catalan coast (May; Gili et al. 2009). These results suggest that the scyphistomae of *R. pulmo* survive and reproduce in different water temperature and salinity regimes, which can explain the wide distribution of *R. pulmo* in the Mediterranean Sea and adjacent waters (Lilley et al. 2009). In the Mar Menor, the ephyrae appeared in one area and the juveniles and adult medusae are distributed in the lagoon due to the hydrographic regime. The ephyrae appeared mainly in the central Catalan coast (near Barcelona), coinciding with the most observations of adult medusae. The characteristics of the coastal areas and substrates where ephyrae appear and scyphistomae can be located need to be evaluated.

In this work, we updated data on *Rhizostoma pulmo* dynamics in the Mar Menor in 2007–2009 and compared it with the coastal Mediterranean waters. During 2007–2009, large aggregations of adult *Rhizostoma pulmo* medusae were observed frequently by fishermen along the Catalan coast. In July 2007, important damage to fisheries in the area was reported, and a similar situation occurred in summer 2010 (data not shown; Fig. 8).

Life cycle

There are three groups of rhizostome jellyfish (Cepheida, Rhizostomida and Cassiopeida), which can be clearly separated by distinctly different anatomical features of the polyps, strobilation rates and developmental stages of the gastric systems as the ephyrae develop into medusae (Thiel 1970, 1976; Straehler-Pohl 2009). *Rhizostoma pulmo* has a typical rhizostome life cycle that alternates between pelagic and benthic phases, as described for *Rhizostoma octopus*, *Catostylus mosaicus*, *Rhopilema esculentum*,



Fig. 8 Photograph of *Rhizostoma pulmo* medusae collected by fishermen in Premià de Mar (Catalunya, Spain) in Summer 2010

Stomolophus meleagris, *Lychnorhiza lucerna* and *Nemopilema nomurai* (Ding and Chen 1981; Calder 1982; Pitt 2000; Kawahara 2006; Holst et al. 2007; You et al. 2007; Holst 2008; Schiariti et al. 2008; Straehler-Pohl 2009). The life cycle, partly described by Paspaleff (1938), starts with pelagic planulae, produced sexually by mature medusae (Krumbach 1930), that settle on hard substrates. The settled planulae metamorphose into benthic primary scyphistomae that grow into mature scyphistomae that asexually reproduce by polydisc strobilation (Paspaleff 1938). The detaching, pelagic, 8-rayed ephyrae (Claus 1883, 1884) grow into mature medusae, which reproduce sexually. We observed the life cycle from planula to young medusa of *Rhizostoma pulmo* under laboratory conditions (Fig. 2).

Paspaleff (1938) described the grown scyphistoma as follows (translated by the authors): "...the scyphistoma develops up to 32 tentacles with a body size of 12 mm. The grown scyphistoma has a yellow, perisarc covered basal disc.... The rump is nearly funnel-shaped. The peristome (hypostome) consists of 4 lobes, rounded, very pliable and expendable and about as long as the rump.... The tentacles are filiform, contractile, solid and equipped with two types, large and small, of nematocysts." We can confirm the general aspects of the observations on *Rhizostoma pulmo* by Paspaleff, especially the very large hypostome that is nearly as long as the calyx. Only the total body size and the number of tentacles given by Paspaleff differ markedly from our data. The differences in body size might be explained by a calculation or typing error by Paspaleff, because all scyphistomae measured in our study and in the study of Straehler-Pohl (2009) were smaller by a factor of approximately 10. Tentacle numbers in scyphistomae can change under artificial culture conditions and may explain those different data. The characters of the *Rhizostoma pulmo* scyphistoma, a short stalk, bowl-shaped calyx and a

very long, club-shaped hypostome seem to be typical of scyphistomae of the Rhizostomida group (proposed by Thiel 1970) (Table 2). By contrast, scyphistomae of the Cepheida feature long stalks, short, platter-shaped calices and very short hypostomes (Holst et al. 2007; Table 2).

Paspaleff (1938) noted podocysts, lateral scyphistoma buds, scyphistoma buds produced by stolons and swimming buds (planuloids) as methods of asexual reproduction in *Rhizostoma pulmo*. The only method of scyphistoma asexual reproduction that we did not observe was by swimming buds (planuloids), which are typical in asexual reproduction of Cepheida scyphistomae like *Cephea cephea*, *Cotylorhiza tuberculata*, *Mastigias papua*, *Phyllorhiza punctata* and in the Cassiopeida (Table 2), but were never described for any other known Rhizostomida life cycles. Paspaleff may have described a different species than *R. pulmo*, or he may have added planuloid production without personally observing it because they were described for other rhizostome species like *Cotylorhiza tuberculata* by Claus (1892) or *Cassiopea xamachana* by Bigelow (1900). The first possibility is unlikely because the anatomy of adult *R. pulmo* medusae is very different from all other jellyfish species in the Black and Mediterranean seas.

Strobilation by *Rhizostoma pulmo* is polydisc as described for all other Rhizostomida species (Table 3), which passes through all phases detailed by Chuin (1930). We noted up to 8 primordia per strobila similar to Straehler-Pohl (2009), half the number described by Paspaleff (1938). Spangenberg (1968) noted a strobilation rate of 1–3 ephyrae per strobila in 1-year-old scyphistomae of *Aurelia aurita*, while up to 8 ephyrae were produced by 2-year-old scyphistomae, and older scyphistomae produced as many as 25–30 ephyrae per strobilation. Thus, the number of ephyrae in polydisc-strobilating species relates to the age, size and nutritional status of the scyphistomae as mentioned by Uchida and Nagao (1963), Spangenberg (1968), Kato et al. (1980) and Holst (2008). This may explain the differences between our data and those of Paspaleff (1938). All primordia in the strobilae observed by Paspaleff (1938) degenerated and never developed into normal ephyrae but into disc-shaped, swimming scyphistomae with 8 tentacles and without rhopalia.

The ephyrae of *Rhizostoma pulmo* we observed developed normally into the 8-rayed type typical of scyphozoan taxa (Straehler-Pohl 2009; Straehler-Pohl and Jarms 2010; Table 5). Distinctive characters of *R. pulmo* are the entire rhopalial lappet rim, as in *Rhizostoma octopus*, *Rhopilema verrilli*, *Stomolophus meleagris*, and in the Cepheida species without the additional finger-like appendices described for *Rhopilema esculentum*, *Rhopilema nomadica*, *Lychnorhiza lucerna* and *Nemopilema nomurai* (Table 5).

Several stages of *Rhizostoma pulmo* ephyra development, including the changes in the gastric system, were first

Table 5 Ephyra morphology and references of rhizostome species

Species	Culture conditions (temperature)	TBD (mm)	CDD (mm) and/or proportions	No. of marginal lappets	Lappet proportions: LStL/RLL compared to TMLL	Shape of rhopalial Lappet/ distinctions	Gastric system/zooxanthellae	Colour	Reference
<i>Rhizostoma pulmo</i>	–	–	–	–	–	–	–	–	Paspaleff (1938)
	15–25°C	3.19–3.34, mean: 3.27	1.66–1.67, mean: 1.67/51% of TBD	8	60%/40% of TMLL	Spade like/1 bis 2 gastric filaments per quadrant	Slightly forked rhopalial canals; unforked, rhombic velar canals/absent	Milky transparent	Straehler-Pohl (2009) and Straehler-Pohl and Jarms (2010)
	21°C	2.28–3.93, mean: 3.17	0.96–1.62, mean: 1.35/43% of TBD	8	56%/44% of TMLL	Spade to lancet-shaped/2–4 gastric filaments per quadrant; small, white nematocyst clusters scattered over whole exumbrella	Forked rhopalar canals, tips overtop rhopalial base; unforked, diamond-shaped velar canals, tips reach umbrella rim/absent	Opaque white	Present study
<i>Rhizostoma octopus</i>	15–20°C	3.6–5.4, mean: 4.5	1.5–2.3, mean: 1.9/42% of TBD	8	57%/43% of TMLL ^p	–/2–4 gastric filaments per quadrant	Slightly forked rhopalial canals, unforked velar canals ^p /–	Milky white, transparent ^p	Holst and Jarms (2006) and Holst et al. (2007) and Holst (2008)
	15–25°C	3.30–5.96, mean: 4.81	1.32–2.24, mean: 1.95/41% of TBD	8	50%/50% of TMLL	Bread knife shaped/1–2 gastric filaments per quadrant	Slightly forked rhopalial canals; unforked, rhombic velar canals/absent	Milky transparent	Straehler-Pohl (2009) and Straehler-Pohl and Jarms (2010)
<i>Catostylus mosaicus</i>	21°C	2.0	–/46% of TBD ^p	8	58%/42% of TMLL ^p	Antler palm shaped with finger-like appendages ^p /1–2 gastric filaments per quadrant ^p	Slightly forked rhopalial canals, unforked velar canals ^p /–	–	Pitt (2000)

Table 5 continued

Species	Culture conditions (temperature)	TBD (mm)	CDD (mm) and/or proportions	No. of marginal lappets	Lappet proportions: LStL/RLL compared to TMLL	Shape of rhopalial Lappet/ distinctions	Gastric system/zooxanthellae	Colour	Reference
	20°C	1.90–2.26, mean: 2.11	0.88–0.94, mean: 0.93/44% of TBD	8	56 ^P /44% of TMLL	Antler palm shaped with 3–5 finger-like appendages ^P /1–2 gastric filaments per quadrant ^P , Eight long nematocyst batteries along the arms of marginal lobes, eight, circular batteries around manubrium	Slightly forked rhopalial canals; unforked, spade shaped velar canals/–	Milky transparent	Straehler-Pohl (2009) and Straehler-Pohl and Jarms (2010)
<i>Rhopilema exculentum</i>	18–20°C	1.5–3.0	–/39%–42 ^P % of TBD	8	50 ^P –53 ^P %/47 ^P –50 ^P % of TMLL	Talon-shaped with 4–6 branches/1 gastric filament per quadrant	Unforked rhopalial canals ^Z , velar canals not visible in drawing/–	–	Ding and Chen (1981), Chen and Ding (1983), You et al. (2007)
	17–20°C	2.0–4.0	–	–	–	–	–	–	–
	20°C	2.11	9.91/43% of TBD	8	60%/40% of TMLL	Hand shaped with 4–6 finger-like appendages/1 gastric filament per quadrant, 8 large, white, halfmoon shaped nematocyst clusters above central stomach on exumbrella, 2 white, elongated nematocyst clusters on lappet stems	Unforked, spatula shaped rhopalial canals, unforked triangular velar canals/absent	Milky to transparent	Straehler-Pohl (2009) and Straehler-Pohl and Jarms (2010)
<i>Rhopilema nomadica</i>	20°C	1.5–2.0	50 ^P % of TBD	8	53 ^P %/47 ^P % of TMLL	Single or twin-typed, lancet-shaped/0 gastric filaments per quadrant, batteries of nematocysts on the exumbrella, arranged in two whorls, the inner one on the bell and the outer one on the lappets on both sides of each radial canal	Distal end of each radial canal is convex with arched corners on both sides/–	–	Lotan et al. (1992)
<i>Rhopilema verrilli</i>	20°C	–	–	–	–	Rounded	–	Peach to orange-red coloured; birefringent, bright yellow gold statocysts	Cargo (1971)

Table 5 continued

Species	Culture conditions (temperature)	TBD (mm)	CDD (mm) and/or proportions	No. of marginal lappets	Lappet proportions: LStL/RLL compared to TMLL	Shape of rhopalial Lappet/ distinctions	Gastric system/zooxanthellae	Colour	Reference
<i>Lychmorhiza lucerna</i>	20°C	3.0	47% of TBD	8	>50%/ <50% of TMLL	Slender, pointed distally/3–4 gastric filaments, exumbrella has scattered nematocyst batteries	Rhopalar pouches have prominent “horns” extending outward into the lappets/–	Endoderm of the gastrovascular cavity is rose-coloured, manubrium endoderm is orange	Calder (1973)
<i>Lychmorhiza lucerna</i>	19–22°C	1.4–1.9	40% of TBD	8	56 ^P %/44 ^P % of TMLL	Hand shaped ^P , variable number of tips ranging between two and nine/1–2 gastric filaments; Nematocysts batteries on exumbrella formed a defined pattern of two concentric whorls (inner whorl surrounded manubrium, larger outer whorl surrounded marginal lobes)	Radial canals square-shaped ends with slight lateral horns which extended into the lappet on both sides/–	Translucent	Schiariti et al. (2008)
<i>Nemopilema nomurai</i>	18–22°C	2.2–3.8	43 ^P % of TBD	8	61 ^P %/39 ^P % of TMLL	Hand shaped ^P , 2–6 pointed tips/1–2 gastric filaments; nematocyst batteries in the centre and along radial canals the exumbrella	Unforked, spatula shaped rhopalial canals ^S , unforked triangular velar canals ^P /–	Translucent	Kawahara et al. (2006)
<i>Stomatolophus meleagris</i>	RT-25°C	1.5–2.0	46 ^S % of TBD	8	<50%/ >50% of TMLL (47 ^P %/53 ^P % of TMLL)	Slender, distally pointed/1–2 gastric filaments; exumbrellar: ring of small nematocyst batteries about the periphery of the stomach and a large, elongate battery on each marginal lobe.	Blunt-ended rhopalar canals, small adradial bulges (velar canals)/–	Ectoderm pale straw coloured, remainder of ephyra translucent	Calder (1982)
<i>Cephea cephea</i>	28°C	1.6–2.1	–	8	–	–/1 Gastric filament per interradius	8 Sacs radiate/–	Pale yellow or yellowish brown	Sugiura (1966)
	25–28°C	2.36–3.24, mean: 3.02	0.95–1.22, mean: 1.12/37% of TBD	8	59%/41% of TMLL	Round spoon shaped/0–1 gastric filament per quadrant	Rhopalar canals slightly forked, velar canals unforked and slightly rhombic/present	Yellowish brown	Straehler-Pohl (2009) and Straehler-Pohl and Jarms (2010)

Table 5 continued

Species	Culture conditions (temperature)	TBD (mm)	CDD (mm) and/or proportions	No. of marginal lappets	Lappet proportions: LStL/RLL compared to TMLL	Shape of rhopalial Lappet/ distinctions	Gastric system/zooxanthellae	Colour	Reference
<i>Netrostoma setouchianum</i>	25–28°C	2.24–2.44, mean: 2.37	0.96–1.02, mean: 0.98/41% of TBD	8	59%/41% of TMLL	Round spoon shaped/0–1 gastric filament per quadrant	Rhopalar canals slightly forked, velar canals unforked and slightly rhombic/present	Reddish to yellowish brown	Straehler-Pohl (2009) and Straehler-Pohl and Jarms (2010)
<i>Coylorhiza tuberculata</i>	– 20–24°C	1.5–2.0 1.5–2.0	–/40% of TBD –	8 8	66%/34% of TMLL ^z –	Rounded/1 gastric filament per quadrant –	Rhopalar canals slightly forked, velar canals unforked ^z /present Rhopalar canals slightly forked, velar canals unforked ^z /zooxanthellae line the gastric system	– –	Claus (1884) Kikinger (1992)
	25–28°C	2.72–3.25, mean: 2.99	1.10–1.49, mean: 1.27/42% of TBD	8	61%/39% of TMLL	Round spoon shaped/1 gastric filament per quadrant	Rhopalar canals slightly forked, velar canals unforked and slightly rhombic/zooxanthellae line the gastric system	Transparent with yellow hemmed gastric system	Straehler-Pohl (2009) and Straehler-Pohl and Jarms (2010)
<i>Mastigias papua</i>	– 25°C	1.5 1.5–2.7	–/47% of TBD ^z –/45% of TBD ^z	8 8 ^z	52%/48% of TMLL ^z 50%/50% of TMLL ^z	Rounded ^z /1 gastric filament per quadrant Rounded ^z /1 gastric filament per quadrant	Rhopalar canals slightly forked, velar canals unforked ^z /present Rhopalar canals slightly forked and reach base of rhopalial lappets, velar canals unforked ^z /present	Brown –	Uchida (1926) Sugiura (1963)
	25–28°C	2.64–3.91, mean: 3.23	1.16–1.59, mean: 1.39/43% of TBD	8	51%/49% of TMLL	Tapered, broad spoon shaped/1 gastric filament per quadrant	Rhopalar canals slightly forked, velar canals unforked and slightly rhombic/present	Orange brown	Straehler-Pohl (2009), Straehler-Pohl and Jarms (2010)

Table 5 continued

Species	Culture conditions (temperature)	TBD (mm)	CDD (mm) and/or proportions	No. of marginal lappets	Lappet proportions: LSiL/RLL compared to TMLL	Shape of rhopalial Lappet/ distinctions	Gastric system/zooxanthellae	Colour	Reference
<i>Phyllophiza punctata</i>	28°C	1.5–2.5	~44% of TBD ^p	8	57%/43% of TMLL ^p	Rounded/4 gastric filaments; small, white warts on exumbrella	–/Present	Yellowish brown ^p	Tronolone et al. (2002)
	25–28°C	0.46	0.22/48% of TBD	8	67%/33% of TMLL	Pointed spoon shaped/0–1 gastric filaments per quadrant, white spots on exumbrella	Rhopalar canals slightly forked, velar canals unforked and slightly rhombic/present	Ochre	Straehler-Pohl (2009) and Straehler-Pohl and Jarms (2010)
<i>Cassiopea andromeda</i>	–	–	–	12–18, mean: 16	–	Spatula like ^z /4 gastric filaments, 11–17 velar lappets	–/Present	–	Gohar and Eisawy (1960a, b)
	25–28°C	3.69–3.95, mean: 3.79	2.43–2.69, mean: 2.56/68% of TBD	17–23, mean: 19	48%/52% of TMLL	Spatula like/0 gastric filaments; 16–21 (mean: 18) velar lappets; velar lappets and rhopalial lappets are connected by a thin lamella	Severely forked rhopalial canals with rounded tips, fill nearly the whole the rhopalial lappet; unforked, spatula like velar canals, fill nearly the whole velar lappet/present	Yellowish green	Straehler-Pohl (2009) and Straehler-Pohl and Jarms (2010)

CDD Central disc diameter, LSiL lappet stem length, RLL rhopalial lappet length, TBD total body diameter, TMLL total marginal lappet length, RT room temperature, – no statement given in the publication

^p Data taken from photos

^z Data taken from drawings

described by Claus (1883) while studying the development of the ephyrae of *Cotylorhiza tuberculata*. Thiel (1970) used those descriptions and the specifications of the development of the gastric systems of other rhizostome species (Stiasny 1921, 1922a, b, 1923, 1932) to show the differences between two rhizostome groups, Kolpophorae and Dactylophorae, which he renamed as Cepheida and Rhizostomida, respectively. The Cepheida develop the gastric system exclusively centrifugally while the Rhizostomida develop their gastric system centripetally as well (Thiel 1970, 1978; Holst et al. 2007; Straehler-Pohl 2009), as shown in the present study.

Rhizostoma pulmo belongs to the group of the Rhizostomida, and its ephyral development resembles the types described for *Rhizostoma octopus* by Holst et al. (2007), for *Stomolophus meleagris* in parts by Mayer (1910) and in detail by Stiasny (1922a) and *Catostylus mosaicus* as detailed by Straehler-Pohl (2009).

Acknowledgments We thank the Catalan Water Agency for funding the Medusa Project. We are indebted to all institutions collaborating with the reporting network. Furthermore, we would like to thank PD Dr. G. Jarms (Hamburg, Germany) for kind advice and laboratory facilities. We also thank the Regional Government of the Region of Murcia (Comunidad Autónoma de la Región de Murcia—CARM) that financed the monitoring programs in the Mar Menor and to the EUROGEL European project that financed sampling there in 2003–2005. We thank also Eduardo Ovis and Georgios Tsounis for the photographs of the jellyfish.

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