Estuarine, Coastal and Shelf Science 318 (2025) 109250

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

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

Jellyfish journey live tracking using floating electronic tag

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ARTICLE INFO

Keywords:
Rhizostoma pulmo
Biologging
LoRa
Trajectory
Swimming speed
Lagoon

ABSTRACT

Gelatinous organisms are key players of marine ecosystems, however underlying processes of their dynamics and behaviour are still to be cleared up. Understanding the areas of production, where the blooms go and what they become are therefore of major interest in marine ecosystem management. We used floating electronic tags developed in our laboratory for jellyfish live tracking. A special attention was put on the welfare of the organisms as the tag was floating and simply attached with a fishing line around the manubrium. *In situ* experiments were carried out in Bages Sigean lagoon (France) where a perennial population of the Mediterranean jellyfish *Rhizostoma pulmo* is established. Up to 47 deployments, from 20 min to 28h, took place in 2022 and 2023 summers. Live tracking indicated that the floating device did not influence the jellyfish trajectory nor its speed. A 28-h trajectory showed that jellyfish movement can be influenced by the wind but also by other environmental factors. The relatively small area covered by the jellyfish compared to the control float one, suggests that movements significantly influence its trajectory as a response to the environment. Jellyfish were successfully recovered suggesting in a near future repeated individual measurements processes over longer deployments.

1. Introduction

While jellyfish are some of the most ancient organisms on earth (Dunn et al., 2022), among the 3000 known jellyfish species to date, the entire life cycle for 5–10 % of them is still to be described (Jarms and Morandini, 2019). However, the increasing anthropogenic pressure on coastal waters has recently induced a regain of interest on jellyfish, and it is now presumed to strongly affect their population dynamics and specially the frequency and intensity of their blooms (i.e. Leoni et al., 2020). Those episodes of proliferation can have negative effects on ecosystem services (e.g. Aubert et al., 2018; Lee et al., 2023). To date, predictive models of jellyfish dynamics or migration routes are still really scarce as information regarding the biology, behaviour and ecology of many species are not known (i.e. Berline et al., 2013; Ramírez-Romero et al., 2018; Ramírez-Romero et al., 2023).

Several non-invasive methods (e.g. satellite images, aerial surveys, underwater video, acoustics: see Fossette et al., 2016) have been developed to study jellyfish blooms and movements at large and medium spatial scales. However, when it comes to depicting *in situ* individual behaviour, only a few studies have been conducted (e.g. Diamant et al., 2023; Fannjiang et al., 2019; Fossette et al., 2015; Hays et al., 2008, 2012; Mooney et al., 2015; Moriarty et al., 2012). While biologgers have been developed for decades and can be extremely sophisticated (Holton et al., 2021), applying traditional methods of tagging and tracking to marine gelatinous organisms composed of 96 % of water is still a real challenge. Nevertheless, three different approaches have been more or less successfully developed so far with tags either glued, sucked on the jellyfish umbrella, or attached to the manubrium with a cable tie, whereas direct implantations in the mesoglea *via* incision then suture or glue were always discarded (e.g. Fossette et al., 2016).

Real-time data transmission from the tag potentially offers a number of advantages, including data acquisition even if the tag is lost, and most importantly, the ability to retrieve the tag, and therefore the tagged organism, whenever it is needed. Such an operation is a tricky challenge mainly because of the need to transmit over a long distance in a harsh environment. In addition, it is generally a costly technology in terms of energy consumption and design (Holton et al., 2021; Naito et al., 2004). Many of the existing technologies use either ultrasound-based techniques for underwater communication (Kataoka et al., 2006), or radiofrequency (RF) communication techniques (VHF, UHF, GSM, LoRa, …). As electromagnetic waves hardly propagate in salted water (Ste-Marie et al., 2022), RF communication is possible when the animal surfaces or requires self-detaching tag popping-up at the surface at the end of the

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https://doi.org/10.1016/j.ecss.2025.109250
Received 4 July 2024; Received in revised form 6 March 2025; Accepted 12 March 2025
Available online 13 March 2025

deployment. In order to overcome the transmission issue, we have designed a floating tag. Our main objective was to realise a tracking device as small as possible to minimise disturbance on jellyfish behaviour. The choice was made to use LoRa communication technology. LoRa technology has been developed for Internet-Of-Things (IOT) applications. It is energy efficient (Cattani et al., 2017), small to embed, and effective for long distance ranges. In addition, the flexibility of the LoRa protocol allows configuring a lot of parameters influencing energy consumption, providing the ability to choose between high frequency transmission, to acquire precise data on short deployments, and slower transmission for long term deployments (Mutescu et al., 2021).

Along the continental French Mediterranean coastline, more than thirty lagoons are classified as transitional water masses under the Water Framework Directive. Those semi-enclosed ecosystems are generally shallow with high variations of temperature and salinity over the year. Coastal lagoons can be considered as large mesocosms to survey ecological processes that are difficult to assess in open sea conditions (i.e. population growth), and to identify the environmental conditions these organisms face during the ontogeny (Marques et al., 2015; Fernandez-Alias et al., 2020).

The Bages-Sigean lagoon presents the rare particularity to harbour a complete resident population of the jellyfish *Rhizostoma pulmo,* the biggest jellyfish of the Mediterranean Sea (Leoni et al., 2021). This offers an exceptional framework to understand the possible trophic processes regulating jellyfish populations over time. While the polyps of this species are still not located within the lagoon, the dynamics of the pelagic stages are now well known (Leoni et al., 2021). First juveniles appear in April; then three cohorts overlapping each other follow, with the latest individuals recorded in October or November. The maximum biomass is observed during summer (Leoni et al., 2021).

We took the opportunity of the recurrent presence of this jellyfish in Bages Sigean lagoon to develop an electronic floating tag to live track tagged medusae so that their trajectory and behaviour could be investigated. The tag was developed in the perspective of being able to recapture the individuals for e.g. morphological measurements involving long term deployment (several weeks to months) and to allow the jellyfish growth monitoring.

2. Material and method

2.1. Fieldwork location

The study was performed in the Bages Sigean lagoon, on the French Mediterranean coast (43°05′12.72″N; 3°00′35.3″E, see Fig. 1), in 2022, between May and August and in 2023, in June and July. It is a small (38 km^2) and shallow lagoon (mean depth 2 m, maximum 4 m) connected to the Mediterranean Sea by a unique and narrow channel (Port-La-Nouvelle, 60 m width). The main freshwater and nutrients inputs come from the northern coast of the basin. Therein, many economic activities coexist, including artisanal fisheries (e.g. eels and sea bass), sport (e.g. kitesurfing, sailing) and tourism. The lagoon is included in a protected area (Parc Naturel Régional de la Narbonnaise en Méditerranée).

2.2. Floating electronic tag

The system consists of a floating device, a fishing line, a quick-release clip and an attachment system. The tag is a floating sphere of 45 mm diameter, weighing 41 g (Fig. 2). It embeds a battery, antennas and an electronic board, composed of a microcontroller, a GPS and a LoRa communication chip which remotely communicates its position on the lagoon in real time at intervals ranging from 1 to 10 min for data storage on a server. The package is 3D printed. The whole floating tag cost is approximately 200 €. Its autonomy varies from 7 h to 12 days of operation, depending on the frequency of GPS data transmission. The fishing line links the device to the jellyfish, with a length of around 3–4 m, which is the maximum depth of the lagoon. The attachment system allows tying up the fishing line around the manubrium. Two types of elastic attachment systems were studied: a rubber band (0.5 g) and a spiral hair ties (3 g).

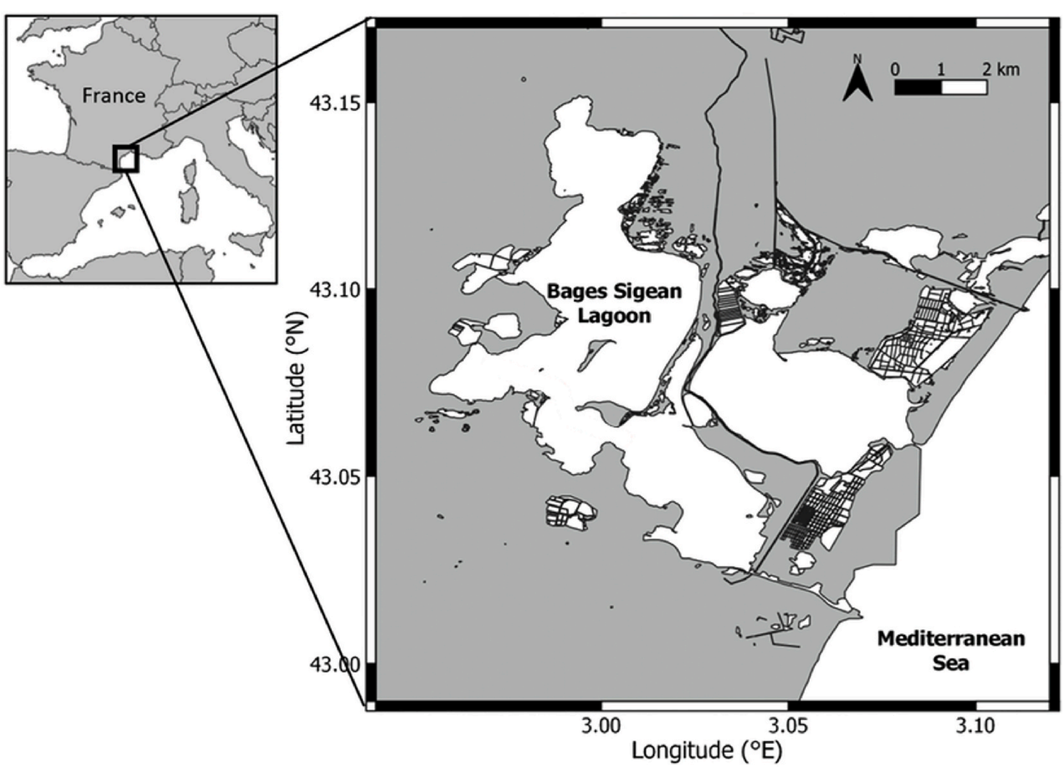

Fig. 1. Map of Bages Sigean lagoon (Aude, France).

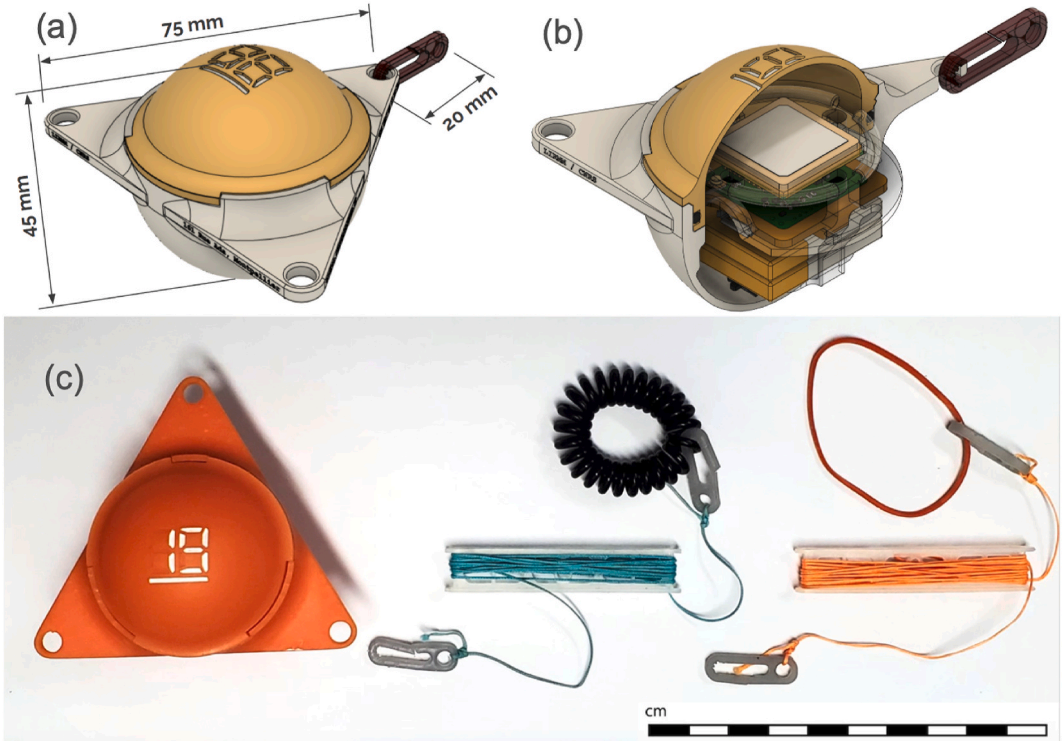

Fig. 2. Floating electronic tag, a) 3D model of the floating device and quick-release clip, b) opened 3D model of the floating device, it reveals the electronic parts of the tag, such as GPS, LoRa communication circuit, antennas, battery and microcontroller, c) Top view of the floating device and two different attachment systems made of two quick-release clips, a fishing line (coiled for storage purpose) and a spiral hair ties (3 g) or a rubber band (0.5 g) for attachment purpose on the jellyfish manubrium.

2.3. Tagging technique

Jellyfish collection was conducted with a fisherman boat (5.56 m long). *R. pulmo* medusae were first visually located and then captured with a handnet (Fig. 3). Once picked, the total lengths of the jellyfish (top of the umbrella to the end of the oral arms) were measured, while the jellyfish were still in the water, using an ichtyometer with a reading precision of 0.5 cm. Afterwards, the tagging device was attached to the manubrium by carefully passing the oral arms through the stretched elastic band. The fishing line connects the floating tag to the elastic attachment system. Quick-release clips are added to facilitate deployment of the attachment device. To avoid any disturbance related to air bubbles which could affect the buoyancy of the jellyfish and prevent it from swimming, tagged individuals were kept submerged throughout the process.

2.4. Tagging operations

A total of 47 deployments took place during the summers of 2022 and 2023. In 2022, there were only 2 days of deployments, but 13 deployments were still carried out thanks to the abundance of jellyfish. Of these 13, 11 were of very short duration (<20 mn). In 2023, 34 deployments were carried out, between 06/20 and 09/27. This time, most deployments (24 out of 34) were between 20 min and 1h30, but there were also 8 long deployments (>1h30), including one lasting for 28h. For each deployment, a control float was deployed for a similar period than the tagged jellyfish. The trajectory of this free-floating tag was mainly influenced by the wind and also by currents driven by wind which are significant in this shallow water lagoon (Fiandrino et al., 2017). As a consequence, the free-floating device was deployed to compare the movement of the tagged jellyfish with the movement of a control floating tag which is only induced by environmental conditions.

Whether the jellyfish is towing or being towed by the float was a central question at the heart of our investigation. Consequently, we decided to compare the speed of the tagged and untagged jellyfishes. Therefore, we determine the average speed of untagged jellyfish of different sizes in Bages-Sigean lagoon using an aerial video approach with a DJI Mavic 2 Pro drone which had filmed the tagging operation on 07/28/2022. Only 1min30 of static-flight video including the fisherman boat were extracted out of the original video filmed for tagging methodology purposes. Tracker software (https://physlets.org/tracker/) was used to automatically track the position of 16 free moving jellyfish. Matlab R2020b was used to clean side effects of movement tracking by smoothing the trajectory and to compute the speed of the jellyfish.

2.5. Data processing

Data transmission played a crucial role in our project, especially since our primary objective was to retrieve the jellyfish's position in real time. To achieve this, the LoRa Orange network was used. LoRa is a radio communication mode specifically designed for networked objects. The LoRa coverage of the Orange network extends over most of the lagoon of Bages. The distance between the transmitting and receiving antennas can be several kilometres in marine environments, while ensuring reliable reception (Gogendeau et al., 2018; Jovalekic et al., 2018). The data sent by the floating device using this communication mode was encoded using the Cayenne Low Power format. This encoding method aims to minimise the power consumption of the transmitting antenna - an essential consideration as we aim for the longest possible deployment time.

Once the data is transmitted, the retrieval process is initiated. We used a Raspberry Pi connected to the Orange LoRa network. The Raspberry Pi detects the reception of messages *via* an Orange LoRa receiving antenna. It then decodes the data using Node-RED and stores it in an InfluxDB database in CSV format. To enhance the user experience, a Discord interface was connected to the communication chain. Its

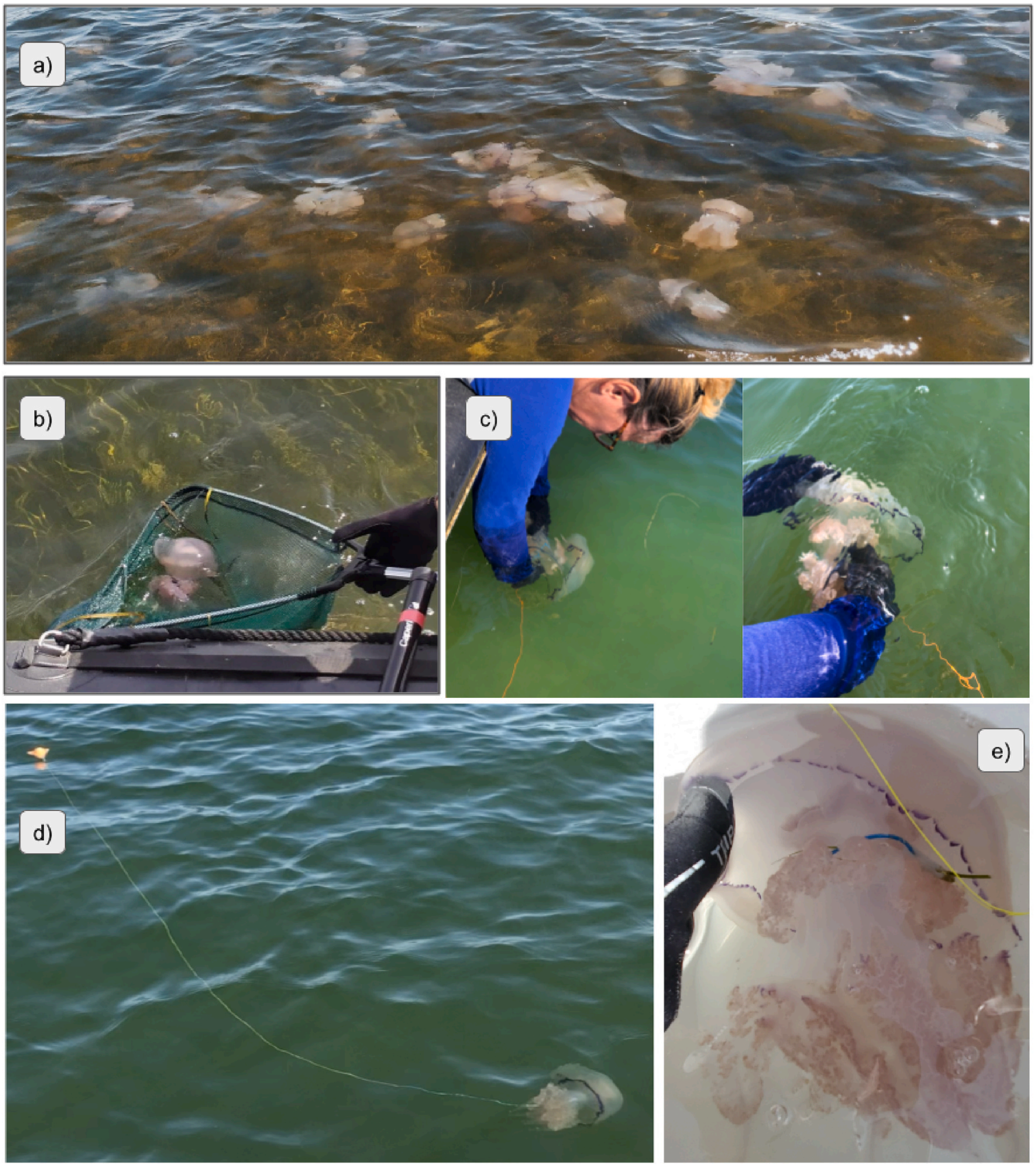

Fig. 3. *In situ* tagging technique: a) Jellyfish spotting, b) Jellyfish carefully collected using a handnet, c) Jellyfish handled in the water for biometry and tag attachment, d) release of the tagged jellyfish, e) recovered tagged jellyfish.

purpose was to transfer the data directly to the user's phone in a more direct and visual way. Users are then able to view various float-related information such as location, speed and direction directly from their phones (Fig. 4).

GPS position is used for jellyfish retrieval but also for trajectory analysis. Potential inaccuracies in GPS data caused by satellite signal interference, such as cloud cover, have first to be corrected. Two filters have been implemented: firstly, GPS points with speeds exceeding 0.5 m/s, based on an upper threshold for jellyfish speed (see swimming speed values in Fossette et al., 2015; Hays et al., 2008; Malul et al., 2019), were removed. Then, a moving average was used to smooth directional changes and reconstruct natural trajectories. To do so, the nearest neighbours were adjusted on a case-by-case basis depending on the number of outliers detected by the first filter and the amount of GPS points generated during the tagging period with a developed Matlab code. The application of both filters in sequence during data processing have allowed producing the jellyfish trajectory.

In order to interpret the trajectories, environmental data, e.g. wind, waves and currents, were collected from databases such as Windy (www.windy.com), InfoClimat (www.infoclimat.fr) and Meteomatics (www.meteomatics.com). For the 28 h deployment, the directions of the environmental parameters were compared with the control float and the tagged jellyfish trajectories. Matlab "*findchangepts*" function was applied on the heading difference between the wind and the jellyfish to identify breaking points (i.e. abrupt breaks) in the dataset. Then, for each identified period, a Pearson correlation analysis was run to determine the influence of environmental parameters to the control float and jellyfish trajectories.

3. Results

3.1. Influence of the attachment device on jellyfish swimming

Understanding the impact of the tag attachment on the jellyfish was a central point of our investigation. Choosing where and how to attach the tag on the jellyfish was paramount for the success of the deployment. The jellyfish's manubrium emerged as a logical anchoring site. The type of attachment was also a crucial aspect of our study. In the perspective of

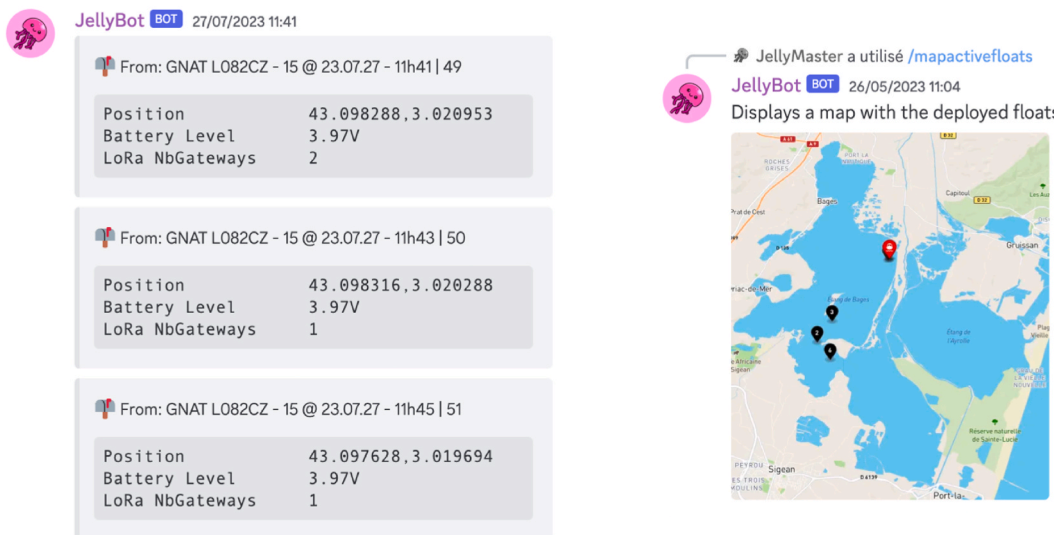

Fig. 4. Discord server used as an end node to display useful data for real-time float monitoring. The '*JellyBot*' bot automatically displays LoRa messages sent by the floats and responds to various user commands. The left side shows the reception of three key parameters for monitoring. The right-hand side shows a map generated using the '*/mapactivefloat*' command to display with pins, the last position of the deployed floats in black and the current user position in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

monitoring the jellyfish over several days and knowing their ability to grow several millimetres daily, the attachment should adapt to their development. Two types of attachment system, able to expand together with the jellyfish, were therefore studied: a 3g spiral hair tie and a 0.5g rubber band, both purchased from a commercial store (Fig. 2c). Fig. 5 shows the average speed of the tagged jellyfish using both types of attachment. The average speed was derived from GPS data collected by the float throughout the tagging period. A Mann-Whitney test (p-value $= 0.448 > 0.05$) indicated that the jellies tagged with the spiral hair tie and the rubber band did not display significantly different average swimming speeds. It is worth noticing that this speed is not just the intrinsic speed of the jellyfish, but a resultant vector influenced by environmental factors such as current, wind and swell. The distinction between 'jellyfish swimming' and 'jellyfish not swimming' was made by visual observation after marking. The results on Fig. 5 show that jellyfish tagging failed exclusively when using a spiral hair tie.

3.2. Comparison of natural and tagged jellyfish speed

Investigating if the float influenced the jellyfish swimming activity

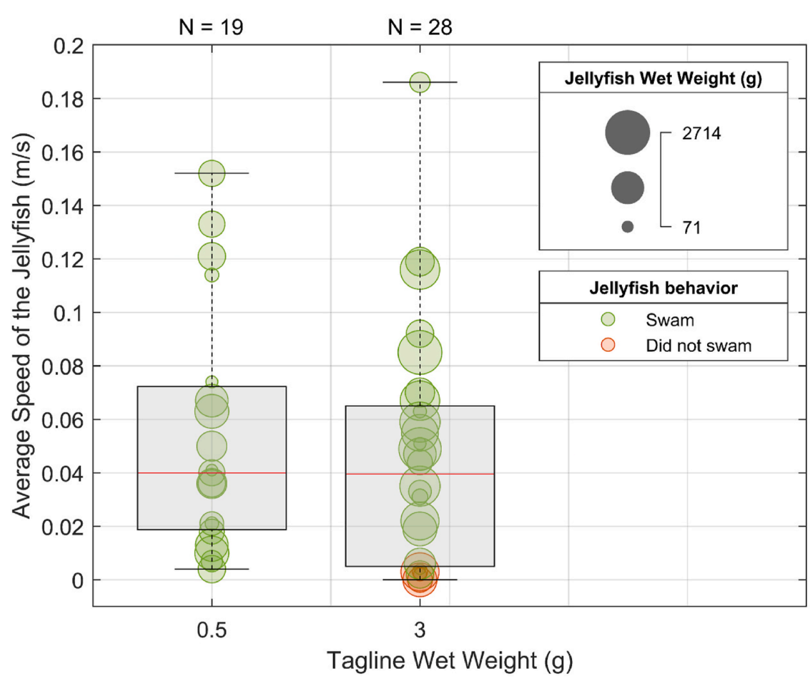

Fig. 5. Box plot showing the average speed of *R. pulmo* tagged according to two types of attachment systems: a 0.5g rubber band and a 3g spiral hair tie. The average speed was calculated using GPS data collected by the float, as explained in the Methods section. The box plot for each size category displays the median (red horizontal line) and the 25th and 75th percentiles (lower and upper box borders). The letter 'N' indicates the number of medusae for which speed has been measured in each respective size class. Green points indicate significant travel distance and red ones indicate no movement after deployment. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

was a central question. Therefore a comparison of speed measurements of untagged jellyfish (Fig. 6A) and tagged jellyfish that swam (Fig. 6B) was made. Average speeds of unmarked jellyfish were consistently different from zero, in contrast to marked jellyfish for which speeds could sometimes approach zero. Nevertheless, the speeds of tagged jellyfish were not statistically different from those of untagged jellyfish (ANOVA type II, p-value = 0.111) and the size of the individuals did not significantly influence their swimming speed (ANOVA type II, p-value = 0.673).

3.3. The 28-h journey of a jellyfish

In line with previous results and with the aim of confirming our observations, an extended deployment of 28-h was carried out with a tagged jellyfish of 26 cm total length. A control float was also deployed. Fig. 7 shows a detailed geo-mapping of both devices during this deployment. Trajectories of the free-drifting control float and the jellyfish-attached float (continuous lines) were derived from the GPS positions data and present some similarities in trajectories, orientations and chronology.

3.4. Environmental influences

Environmental data (i.e. wind, waves and currents) were analysed to shed light on the origin of the trajectories. However, only the wind-related parameters were found to be relevant at the lagoon scale. Fig. 8 shows the directions of the tagged jellyfish, the control float and the wind. Three breaking points have been determined identifying four different phases. Phases of divergence and similarity between the direction of the floats and the wind can be observed (Fig. 8, Table 1). Throughout the deployment, the wind did intermittently influence the direction of both the control float and the jellyfish. For example, the control float trajectory was always strongly positively correlated to the wind apart in the initial very short phase of the survey. In contrast, the jellyfish presented similar directions with the wind only during phases 2 and 4 while in phases 1 and 3, its trajectory was not influenced by the wind (Fig. 8, Table 1). In phase 1 (Fig. 8), the control and the jellyfish floats are strongly correlated together but show an inverse correlation with the wind direction (Table 1).

4. Discussion

Electronic tagging of marine vertebrates is a research topic that benefits from important research efforts for more than 50 years. In the case of fish tagging, optimising tag retention time involves either surgically implanting tags (Rouyer et al., 2023) or attaching them externally using invasive methods such as anchoring systems (Jepsen et al., 2015). The latter approach allows for deployment durations ranging from months to years (Rouyer et al., 2022). However, tagging jellyfish remains a challenging task primarily due to the morphological characteristics of the animal. Indeed, jellyfish are soft-bodied animals whose fragileness of tissues prevents invasive attachment technique or internal tagging. Furthermore, despite limited studies, it is commonly accepted that jellyfish have slightly negative buoyancy (0.5 % denser than water) (Yang et al., 2018). Jellyfish constantly swim to offset their sinking. As a consequence an efficient tagging of jellyfish should limit the impact on the wet weight of it and consequently on its buoyancy to avoid strong impact on its ability to swim up and down in the water column. When designing tagging devices for jellyfish, the size and weight of the floats are crucial. Inadequate design can affect animal movements and lead to erroneous data. While bird tagging studies generally follow the 5 % rule, where the mass of the tags must be less than 5 % of the bird's body mass (see in Fossette et al., 2016), this approach is less suitable for marine organisms where the buoyancy and drag of the float must be taken into account.

4.1. Influence of the attachment device on jellyfish swimming

Our approach is inspired by the results of Fossette et al. (2016), which indicated that a tag attached close to the centre of mass of the jellyfish should not exceed 10 % of its wet weight to avoid disturbing its swimming. In preliminary experiments, we investigated and used different types of attachments: a Serflex, a cat collar, a rubber band and a spring hair tie (data not shown). The first two solutions are interesting because of their ease of use. They minimise the impact on the handling of the jellyfish because they close by clipping the tie around the manubrium. However, they are semi-rigid ties that cannot adapt to the growth of the jellyfish. As jellyfish can grow by several millimetres a day, the fastener must be able to adapt daily to their development. In addition, after several days of wearing the Serflex, we observed lesions and necrosis around the manubrium. The integrity and well-being of the

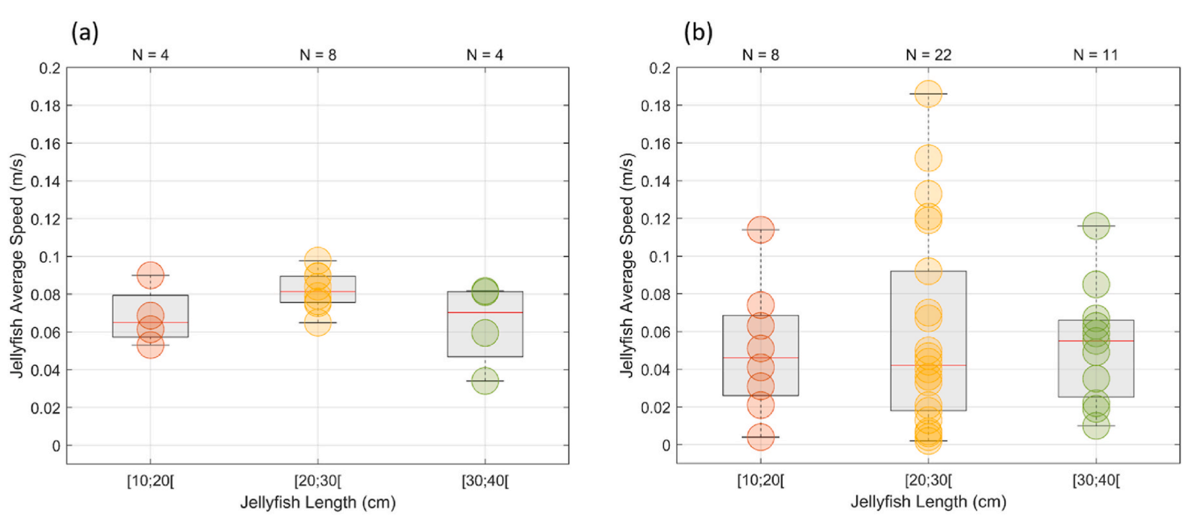

Fig. 6. Box plots showing the average speed of *R. pulmo* according to three size classes. The median (red horizontal line) and the 25th and 75th percentiles (lower and upper box borders) are shown. The letter 'N' indicates the number of medusae for which speed was measured in each respective size class.
(a): Average speed was calculated using 1mn 30s video recording of non tagged jellyfish swimming from a drone.
(b): Average speed was calculated using GPS data collected from the float as explained in the Methods section. Only jellyfish that swam are considered. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

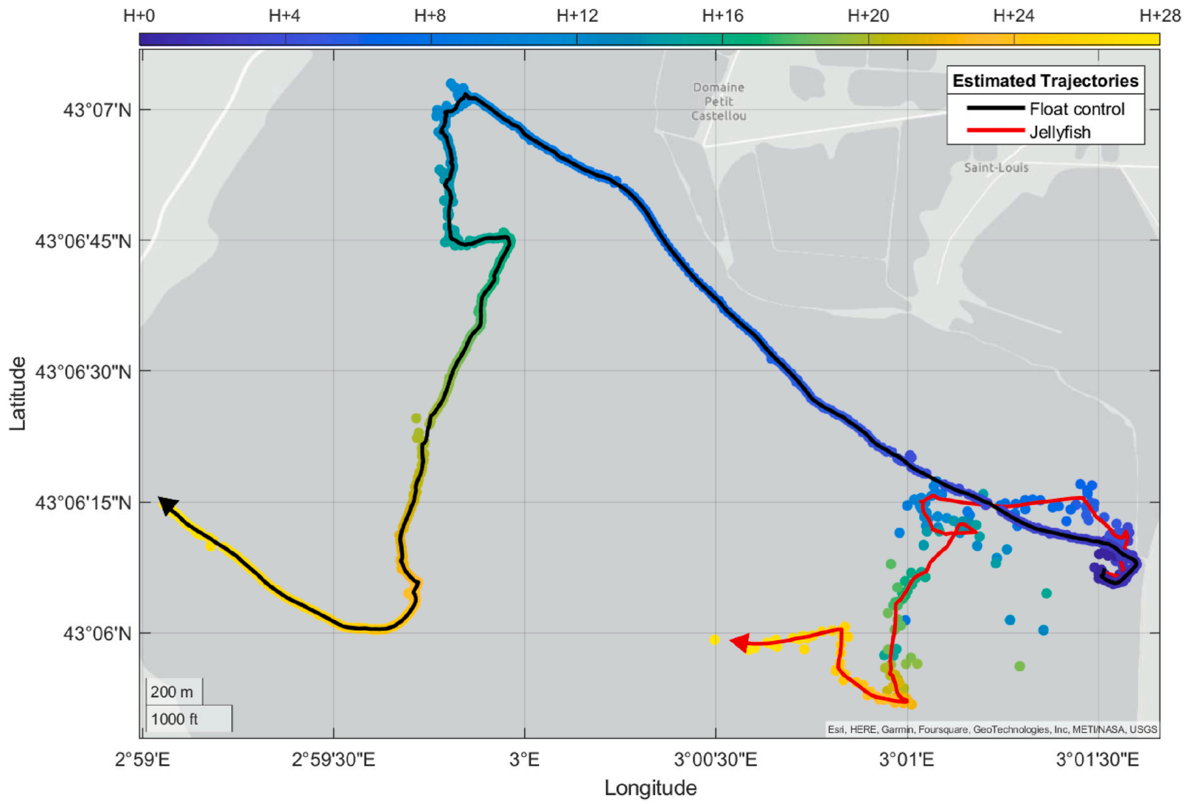

Fig. 7. Map of a 28-h deployment from 09/27/23 to 09/28/23, with a control device (black line) and a tagged jellyfish (red line). Geolocation points are colour coded, transitioning from dark blue (start of deployment) to light yellow (end of deployment). The trajectories, derived from the position data, have been smoothed for enhanced clarity and to estimate the trajectories of the devices. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

animal is our priority. We have therefore abandoned these solutions in favour of the rubber band and the spring hair tie. These two options can expand as the jellyfish grows and, due to their round shape and softness, have less impact on the tissues of the asset. No tissue degradation was observed after wearing these two attachments. In our results the two devices, a 0.5 g rubber band and a 3g spiral hair tie, both of which were less than 10 % of the weight of the smallest tagged jellyfish, were used. Both systems induced different jellyfish responses. Indeed, jellyfish tagged with the rubber band showed a 100 % recovery of swimming activity just after being marked, while those tagged with the spiral hair tie showed only a 75 % recovery. This difference can be explained by the greater weight and volume of the scrunchie, which could have hindered the movement of the jellyfish. However, according to Hays et al. (2008), it has been observed that after tagging, jellyfish can sometimes migrate to the bottom before getting back to a normal swimming activity, suggesting a need for adaptation or recovery after tagging.

Combining the attachment and float, our device achieves a total wet weight of 42–45 g, which is more than half the wet weight of the lighter jellyfish (71 g). As the electronic tag floats, the only element of the system that can sink the jellyfish is the attaching system whose weight is between 0.5 g and 3 g. It enables tagging very small jellyfishes and following them during their growth (e.g. a few weeks). A floating tag could restrain the diving. This was not an issue in our study as the depth of the lagoon is shallow (mean 2 m, maximum 4 m) and the fishing line between the jellyfish and the floating tag was 4 m long.

4.2. Deployment duration and type of data collected

According to Fossette et al. (2016), Diamant et al. (2023) and Fannjiang et al. (2019), tag deployment using suction cup or glue leads to small deployment durations to a maximum of 24 h, whereas attachment using cable tie enables to increase deployment duration to 28 days. Data retrieval in the case of long duration deployment relies on the tag retrieval once stranded. Previously published studies on tagging have focused on underwater movements, using acoustic geographical location (Diamant et al., 2023; Fossette et al., 2016), inertial sensors such as accelerometer, gyroscope and magnetometer (Fannjiang et al., 2019; Fossette et al., 2016), or time-depth recorders (TDR) (Fossette et al., 2016). Our approach is innovative as it aims at live 2D surface tracking over a long time (days to weeks) which potentially enables to follow individual growth and maturation by repeated biometrics, using GPS position to retrieve the animal as often as necessary. This approach could be combined with previously existing solutions to enhance the number of different types of data such as the ones used to study underwater movement.

4.3. Jellyfish swimming speed

Most of jellyfish speed estimates have been measured on Rhizostomeae as they are some of the biggest jellyfish (e.g. Fossette et al., 2015; Gemmell et al., 2013; Hays et al., 2011; Larson, 1987; Malul et al., 2019). In our study, the speeds derived from either the GPS position of the tag or from the drone image analysis indicated no significant difference between tagged and non tagged individuals with an average speed of 0.061 ± 0.039 m. s^{-1}. This value is in the range of speed values previously observed for *Rhizostoma* sp., 0.087 m. s^{-1} in an experimental water flume (Malul et al., 2019) or 0.032–0.078 m. s^{-1} in the Bay of Biscay (Fossette et al., 2015).

In their water flume experiment, Malul et al. (2019) observed that swimming speed varied with the umbrella size in *R. pulmo* individuals but not for *Rhopilema nomadica*, with larger individuals swimming faster. However, this variability was measured among individuals of 3

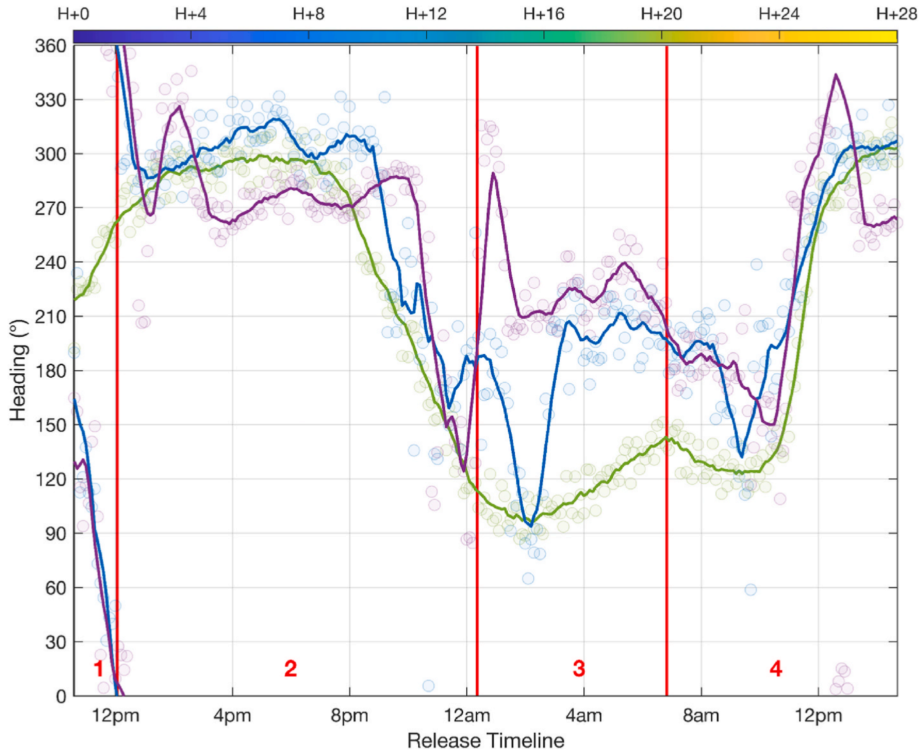

Fig. 8. Directions (in degrees) taken by the jellyfish (purple), the control float (blue) and the wind (green) during the 28-h tagging survey. 0°/360° represents north, 90° east, 180° south and 270° west. Smoothed mean curves facilitate interpretation of directional changes. Breaking points between the wind and the tagged jellyfish trajectories are represented by continuous vertical red lines, distinguishing four phases (1–4 in red). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Analysis of correlation between the wind, the control float and the jellyfish directions during the 4 phases of the 28-h deployment for each binome respectively. Significant correlations are in bold.

	Phase 1	Phase 2	Phase 3	Phase 4
Wind/Control float	**r = -0.983** ***	**r = 0.933** ***	**r = 0.690** ***	**r = 0.979** ***
Wind/Jellyfish	**r = -0.988** ***	**r = 0.772** ***	r = −0.052 ns	**r = 0.892** ***
Control float/ Jellyfish	**r = 0.986** ***	**r = 0.824** ***	r = 0.203 ns	**r = 0.887** ***

*: $p < 0.05$ **:$p < 0.01$ ***: $p < 0.001$ ns: non significant.

size classes included between 10 and 20 cm bell diameter only. In our study, the size range was much larger and we did not observe any significant difference of average swimming speed with size. Indeed, Gemmell et al. (2013) have shown that beyond a certain size, and unlike other animals, jellyfish do not continue to increase swimming velocity with size. This is due to the limit of the thickness of cnidarian muscles for which muscle fibres are housed solely within epitheliomuscular cells. It has to be noticed that the estimated speed using GPS data is an average speed over a filtered trajectory. Indeed due to GPS accuracy (5–20 m according to the using conditions), we assume that small scale movements are in the measurement error and cannot be exploited. Trajectory filtering and smoothing reduces the estimated distance covered by the jellyfish and consequently the averaged speed, which is in agreement with previous conclusions.

4.4. Jellyfish swimming behaviour

Jellyfish aggregation are often considered, with a simplest view, as a result of a current drifting. Wind and hydrodynamics have indeed an important role to play in jellyfish swimming behaviour. For example, sea surface turbulence has been suggested to induce jellyfish sound in the Rhizostomeae *Stomolophus meleagris* (Graham et al., 2001) and disappearance of *Rhizostoma octopus* from surface waters in rough days has also been noticed during aerial surveys (Houghton et al., 2006). Similarly Hays et al. (2008) implied that physical disturbance, like breaking waves that might cause jellyfish physical damage, could be responsible for the observed descent of *R. octopus*. Nevertheless, several publications have also shown that jellyfish can cope with environmental physical forcing in a certain way as they can swim faster counter-current than with it (Fossette et al., 2015; Malul et al., 2019) or can actively reposition themselves in the water column over small timescales (Hays et al., 2008, 2011), suggesting that jellyfish might be able to reduce the risk of stranding.

Swimming behaviour can also vary among medusae according to their feeding strategy (Dabiri et al., 2010). Indeed, the species that forage by continuously cruising (swimming more than 80 % of their time; Colin et al., 2003) swim slowly but efficiently as they need to swim for long durations and to create a feeding current, while ambush foraging jellyfish comparatively swim faster but only for short durations (<30 % of the time; Colin et al., 2003), as they mostly let themselves drift with their tentacles extended waiting for prey capture. Consequently, for those latest jellyfish, swimming is only used to escape predation and reposition themselves in the water column (Colin et al., 2003; Dabiri et al., 2010). Hays et al. (2011) recorded high levels of vertical activity in the water column (in average 620 m d^{-1}) for tagged *Rhizostoma octopus* off Wales. They concluded that this displacement could not be a consequence of diel vertical movement, movements associated with tidal cycles, weather or a consequence of constant wave action over a tag. They rather suggested it was associated with prey searching. In addition, Leoni et al. (2022) have determined *R. pulmo*'s diet during one year in Bages Sigean lagoon which is a really shallow lagoon. They showed that diet composition differs from the availability of prey in the environment with contrasting preferences along ontogeny. The fact that

Rhizostoma spp. Gut contents (Hays et al., 2011; Leoni et al., 2022) have a variety of prey types different from the environment where they were caught, supports an active foraging feeding that should be considered when interpreting individuals trajectories.

4.5. The 28-h journey of a jellyfish

Analysis of the environmental data has shown the wind influence on floats and jellyfish trajectories during the 28-h deployment. The wind effect can partly be explained by the geographical configuration of the lagoon. Indeed, the lagoon has a south-eastern opening to the Mediterranean Sea, while mountains surround the rest of the lagoon (Fig. 1). During phases 2 and 4 (Fig. 8), the wind blew in a north-westerly direction, dragging the control float and the jellyfish. However, the wind does not always explain floats trajectories (see phases 1 and 3), suggesting that other environmental variables are involved. Although it is difficult to identify those parameters with certainty, both the trajectories of the jellyfish and the direction of the wind suggest that the local currents in Bages-Sigean lagoon are implicated (see phase 1 in Fig. 8 and Table 1). Wind speed was also studied over the entire period, but its intensity and variations were fairly low (between 4 and 13 km h^{-1}), and did not appear to be related to the different periods of influence on the jellyfish and or the control float. Its average speed was nearly the same for each period (between 6.3 and 7.6 km h^{-1}).

Differences in trajectories between the control float and the tagged jellyfish suggest that the jellyfish was not being towed by the float. The jellyfish displayed a distinct movement pattern, with periods of active swimming perhaps corresponding to periods of predation. Jellyfish direction changes suggest that its attached float did not constraint its movements, allowing the organism to maintain control over its directional changes. Consequently, the GPS tagging system did not seem to have any discernible negative effect on the jellyfish swimming behaviour. In addition, while the control float trajectory covers a wide area, the tagged jellyfish remains in the eastern part of the lagoon where the highest densities of jellyfishes was observed. Therefore, we assume that the jellyfish movements significantly influence its trajectory. Indeed Fossette et al. (2015) suggest that *Rhizostoma pulmo* can change its swimming trajectory according to varying current flows. This active current-oriented movement could be a response to the environment in order to survive and reach/maintain in an advantageous area. In addition, according to Malul et al. (2019), *Rhizostoma pulmo,* despite having constant pulsation frequency, swims faster against the current than with it. This speed variation mechanism could be a sensory reaction to limit the stranding risk.

To go further in the understanding of *Rhizostoma pulmo* movements in the Bages-Sigean lagoon, it would be of interest to combine wind parameters measurements with water current metres. Drone-based video analysis is limited by the short battery life, approximately 30 min. Anyway, the free moving jellyfish movement analysis using drone-based video has demonstrated a great interest for speed analysis. It should be developed by multiplying flights in order to shoot jellyfishes of different sizes with different wind conditions. By having a wider angle (higher altitude), we could increase the duration of analysis by individual. Additional analysis such as pulsation frequency, relative directions between jellyfishes taken simultaneously could also be of interest.

These preliminary results are given for a limited number of tagged jellyfishes and for a still short duration of a maximum of 28 h. Anyway by validating the retrieval of the tagged jellyfish using its transmitted position, this work enables us to consider growth and sexual maturation monitoring and long-term deployments. In addition the in-house development and manufacturing of the tags, using off-the-shelf components and 3D-printing techniques allow the cost to be maintained as low as we can expect to deploy dozens of them.

CRediT authorship contribution statement

Andrea Sauviat: Writing – original draft, Software, Formal analysis, Data curation. **Quentin Ponzo:** Writing – review & editing, Writing – original draft, Software, Formal analysis, Data curation. **Delphine Bonnet:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **Vincent Kerzérho:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Ethical approval

No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with unregulated invertebrate species.

Funding

This study was funded by the scientific support action of Montpellier University (RHITM project: PI DB). AS was supported by the Muse program (Kim Sea & Coast) and the Numev Labex of Montpellier University. QP was supported by a PhD grant from the I2S doctoral school (Montpellier University).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors are grateful to Fabien Gaboyard for the use of his boat. They also acknowledge Gabrielle Pigeon and Marie Meffre for their support during field sampling and tagging.

Data availability

Data will be made available on request.

References

Aubert, A., Antajan, E., Lynam, C., Pitois, S., Pliru, A., Vaz, S., Thibault, D., 2018. No more reason for ignoring gelatinous zooplankton in ecosystem assessment and marine management: concrete cost-effective methodology during routine fishery trawl surveys. Marine Policy Elsevier Ltd 89, 100–108. https://doi.org/10.1016/j.marpol.2017.12.010.

Berline, L., Zakardjian, B., Molcard, A., Ourmières, Y., Guihou, K., 2013. Modeling jellyfish *Pelagia noctiluca* transport and stranding in the Ligurian Sea. Mar. Pollut. Bull. 70, 90–99. https://doi.org/10.1016/j.marpolbul.2013.02.016.

Colin, S.P., Costello, J.H., Klos, E., 2003. *In situ* swimming and feeding behaviour of eight co-occurring hydromedusae. Mar. Ecol. Prog. Ser. 253, 305–309.

Dabiri, J.O., Colin, S.P., Katija, K., Costello, J.H., 2010. A wake-based correlate of swimming performance and foraging behaviour in seven co-occurring jellyfish species. J. Exp. Biol. 213, 1217–1225.

Diamant, R., Alexandri, T., Barak, N., Lotan, T., 2023. A remote sensing approach for exploring the dynamics of jellyfish, relative to the water current. Sci. Rep. 13, 14769. https://doi.org/10.1038/s41598-023-41655-8.

Dunn, F.S., Kenchington, C.G., Parry, L.A., Clark, J.W., Kendall, R.S., Wilby, P.R., 2022. A crown-group cnidarian from the ediacaran of charnwood forest, UK. Nature Ecology & Evolution 6, 1095–1104. https://doi.org/10.1038/s41559-022-01807-x.

Fannjiang, C., Mooney, T.A., Cones, S., Mann, D., Shorter, K.A., Katija, K., 2019. Augmenting biologging with supervised machine learning to study in situ behavior of the medusa *Chrysaora fuscescens*. J. Exp. Biol. 222, jeb207654. https://doi.org/10.1242/jeb.207654.

Fernandez-Alias, A., Marcos, C., Quispe, J.I., Sabah, S., Perez-Ruzafa, A., 2020. Population dynamics and growth in three scyphozoan jellyfishes, and their relationship with environmental conditions in a coastal lagoon. Estuar. Coast Shelf Sci. 243, 106901. https://doi.org/10.1016/j.ecss.2020.106901.

Fiandrino, A., Ouisse, V., Dumas, F., Lagarde, F., Pete, R., Malet, N., Le Noc, S., de Wit, R., 2017. Spatial patterns in coastal lagoons related to the hydrodynamics of seawater intrusion. Mar. Pollut. Bull. 119, 132–144. https://doi.org/10.1016/j.marpolbul.2017.03.006.

Fossette, S., Gleiss, A.C., Chalumeau, J., Bastian, T., Armstrong, C.D., Vandenabeele, S., Karpytchev, M., Hays, G.H., 2015. Current-oriented swimming by jellyfish and its role in bloom maintenance. Curr. Biol. 25, 342–347. https://doi.org/10.1016/j.cub.2014.11.050.

Fossette, S., Katija, K., Goldbogen, J.A., Bograd, S., Patry, W., Howard, M.J., Knowles, T., Haddock, S.H.D., Beddell, L., Hazen, E.L., Robison, B.H., Mooney, T.A., Shorter, K.A., Bastian, T., Gleiss, A.C., 2016. How to tag a jellyfish? A methodological review and guidelines to successful jellyfish tagging. J. Plankton Res. 38, 1347–1363. https://doi.org/10.1093/plankt/fbw073.

Gemmell, B.J., Costello, J.H., Colina, S.P., Stewart, C.J., Dabiri, J.O., Tafti, D., Priyad, S., 2013. Passive energy recapture in jellyfish contributes to propulsive advantage over other metazoans. Proc. Natl. Acad. Sci. USA 110 (44), 17904–17909.

Gogendeau, P., Murad, N.M., Bernard, S., Kerzerho, V., Deknyff, L., Bonhommeau, S., 2018. Oversea Radio Measurements and Channel Characterization with LoRa Technology. IEEE Radio and Antenna Days of the Indian Ocean (RADIO), Wolmar, Mauritius, pp. 1–2. https://doi.org/10.23919/RADIO.2018.8572461, 2018.

Graham, W.M., Pages, F., Hamner, W.M., 2001. A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia 451, 199–212.

Hays, G.C., Doyle, T.K., Houghton, J.D.R., Lilley, M.K.S., Metcalfe, D.J., Righton, D., 2008. Diving behaviour of jellyfish equipped with electronic tags. J. Plankton Res. 30, 325–333. https://doi.org/10.1093/plankt/fbn003.

Hays, G.C., Bastian, T., Doyle, T.K., Fossette, S., Gleiss, A.C., Gravenor, M.B., Hobson, V.J., Humphries, N.E., Lilley, M.K.S., Pade, N.G., Sims, D.W., 2011. High activity and Lévy searches: jellyfish can search the water column like fish. Proc. Biol. Sci. 279, 465–473. https://doi.org/10.1098/rspb.2011.0978.

Holton, M.D., Wilson, R.P., Teilmann, J., Siebert, U., 2021. Animal tag technology keeps coming of age: an engineering perspective. Philosophical Transactions of the Royal Society B 376, 20200229. https://doi.org/10.1098/rstb.2020.0229.

Houghton, J.D.R., Doyle, T.K., Davenport, J., Hays, J.C., 2006. Developing a simple, rapid method for identifying and monitoring jellyfish aggregations from the air. Mar. Ecol. Prog. Ser. 314, 159–170.

Jarms, G., Morandini, A.C., 2019. World atlas of jellyfish. Dölling und Galitz Verlag.

Jepsen, N., Thorstad, E.B., Havn, T., Lucas, M.C., 2015. The use of external electronic tags on fish: an evaluation of tag retention and tagging effects. Animal Biotelemetry 3, 49. https://doi.org/10.1186/s40317-015-0086-z.

Jovalekic, N., Drndarevic, V., Pietrosemoli, E., Darby, I., Zennaro, M., 2018. Experimental study of LoRa transmission over seawater. Sensors 18, 2853. https://doi.org/10.3390/s18092853.

Larson, R.J., 1987. Costs of transport for the scyphomedusa *Stomolophus meleagris* L. Agassiz. Can. J. Zool. 65 (11), 2690–2695. https://doi.org/10.1139/z87-408.

Lee, S.H., Marco Scotti, M., Jung, S., Hwang, J.S., Molinero, J.C., 2023. Jellyfish blooms challenge the provisioning of ecosystem services in the Korean coastal waters. Hydrobiologia 850, 2855–2870. https://doi.org/10.1007/s10750-022-05076-4.

Leoni, V., Bonnet, D., Ramírez Romero, E., Molinero, J.C., 2020. Biogeography and phenology of the jellyfish *Rhizostoma pulmo* (Cnidaria: scyphozoa) in southern European seas. Journal of Global Ecology and Biogeography 30, 622–639. https://doi.org/10.1111/geb.13241.

Leoni, V., Molinero, J.C., Meffre, M., Bonnet, D., 2021. Variability of growth rates and thermohaline niches of *Rhizostoma pulmo*'s pelagic stages (Cnidaria: scyphozoa). Mar. Biol. 168, 107. https://doi.org/10.1007/s00227-021-03914-y.

Leoni, V., Molinero, J.C., Crochemore, S., Meffre, M., Bonnet, D., 2022. Ontogenetic dietary shifts of the medusa *Rhizostoma pulmo* (Cnidaria: scyphozoa). Hydrobiologia 849, 2933–2948. https://doi.org/10.1007/s10750-022-04903-y.

Malul, D., Lotan, T., Makovsky, Y., Holzman, R., Shavit, U., 2019. The Levantine jellyfish *Rhopilema nomadica* and *Rhizostoma pulmo* swim faster against the flow than with the flow. Sci. Rep. 9, 20337. https://doi.org/10.1038/s41598-019-56311-3.

Marques, R., Albouy-Boyer, S., Delpy, F., Carré, C., Le Floc'h, E., Roques, C., Molinero, J.C., Bonnet, D., 2015. Pelagic population dynamics of Aurelia sp. in French Mediterranean lagoons. J. Plankton Res. 37, 1019–1035. https://doi.org/10.1093/plankt/fbv059.

Mooney, T.A., Katija, K., Shorter, K.A., Hurst, T., Fontes, J., Afonso, P., 2015. ITAG: an eco-sensor for fine-scale behavioural measurements of soft-bodied marine invertebrates. Animal Biotelemetry 3, 31. https://doi.org/10.1186/s40317-015-0076-1.

Moriarty, P., Andrews, K., Harvey, C., Kawase, M., 2012. Vertical and horizontal movement patterns of scyphozoan jellyfish in a fjord-like estuary. Mar. Ecol. Prog. Ser. 455, 1–12. https://doi.org/10.3354/meps09783.

Ramírez-Romero, E., Molinero, J.C., Paulsen, M., Javidpour, J., Clemmesen, C., Sommer, U., 2018. Quantifying top-down control and ecological traits of the scyphozoan *Aurelia aurita* through a dynamic plankton model. J. Plankton Res. 40 (6), 1–15. https://doi.org/10.1093/plankt/fby04.

Ramírez-Romero, E., Amores, A., Diaz, D., Muñoz, A., Catalan, I.A., Molinero, J.C., Ospina-Alvarez, A., 2023. Atmospheric–ocean coupling drives prevailing and synchronic dispersal patterns of marine species with long pelagic durations. Sci. Rep. 13, 2366. https://doi.org/10.1038/s41598-023-29543-7.

Rouyer, T., Bernard, S., Kerzerho, V., Giordano, N., Giordano, F., Ellul, S., Ellul, G., Derridj, O., Canet, R., Deguara, S., Wendling, B., Bonhommeau, S., 2022. Electronic tagging of Bluefin Tunas from the Maltese spawning ground suggests size-dependent migration dynamics. Environ. Biol. Fish. 105 (5), 635–644. https://doi.org/10.1007/s10641-022-01262-4.

Rouyer, T., Bonhommeau, S., Bernard, S., Kerzerho, V., Derridj, O., Bjarnason, Á., Allal, H., Steffensen, J.F., Deguara, S., Wendling, B., Bal, G., Thambithurai, D., Mckenzie, D.J., 2023. A novel protocol for rapid deployment of heart rate data storage tags in Atlantic bluefin tuna *Thunnus thynnus* reveals cardiac responses to temperature and feeding. J. Fish. Biol. https://doi.org/10.1111/jfb.15507.

Yang, P.Y., Lemons, M., Hu, D.L., 2018. Rowing jellyfish contract to maintain neutral buoyancy. Theoretical and Applied Mechanics Letters 8 (3), 147–152. https://doi.org/10.1016/j.taml.2018.03.001.