

Swimming ability of the *Carybdea marsupialis* (Cnidaria: Cubozoa: Carybdeidae): implications for its spatial distribution

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Summary statement: The analysis of the swimming ability of *C. marsupialis* elucidates its key role in the spatial distribution of a northwestern Mediterranean population.

Keywords. *Carybdea marsupialis*, Advection, box jellyfish, Effective Displacement Index, surface currents, swimming speed.

ABSTRACT

Although usually considered part of the plankton, cubozoans are strong swimmers. The aim of this study was to determine the influence of the active swimming ability of the box jellyfish *Carybdea marsupialis* on the spatial distribution of a well-studied population off Dénia (NW Mediterranean) where adults and juveniles do not overlap geographically. To achieve this aim, we analyzed the swimming speed, proficiency, effective velocity, and effective displacement index (EDI) of 27 individuals with diagonal bell widths (DBW) ranging from 1.1 to 36 mm. The laboratory analysis utilized conventional video recordings and the video analysis tool Tracker. Mean swimming speed for small juveniles ($DBW \leq 5$ mm), medium juveniles ($5 \text{ mm} < DBW < 15$ mm) and adults ($DBW \geq 15$ mm) were $9.65 \pm 0.76 \text{ mm}^{-1}$, $21.91 \pm 2.29 \text{ mm}^{-1}$ and $43.10 \pm 1.78 \text{ mm}^{-1}$ (mean \pm s.e.m.), respectively. Comparing these results with the local currents obtained from drifting buoys analyzed in the area over the course of three years, adults would be able to swim strongly enough to overcome almost 70% of the currents, whereas the small juveniles would not reach 17%. This allows larger individuals to select their habitat, while smaller individuals are left dependent on advection. Although experiments adding currents in aquaria would be necessary to confirm these theoretical results, the data obtained would be useful in improving the performance of bio-mathematical models used to predict jellyfish blooms since, even though the sting of *C. marsupialis* is non-fatal, it may produce systemic effects in sensitive swimmers.

INTRODUCTION

The word “plankton” is a collective term for pelagic organisms adapted to life in suspension, which have in common the passive entrainment by water currents (Reynolds and Padisák, 2013). Historically, jellyfish of the classes Scyphozoa and Cubozoa have been classified in this category, but some studies indicate otherwise. Studies have demonstrated that the scyphozoans *Aurelia* sp., *Cyanea capillata*, *Phacellophora camtschatica*, *Rhizostoma octopus*, *Rhizostoma pulmo* and *Rhopilema nomadica* can actively swim against a current and exhibit positive rheotaxis (Fossette et al., 2015; Malul et al., 2019; Moriarty et al., 2012; Rakow and Graham, 2006). In

addition, other movements such as vertical migrations or sun-compass horizontal migrations have also been reported (Albert, 2007; Hamner and Hauri, 1981; Hamner et al., 1994; Hays et al., 2012). Cubozoans even go a step further. In addition to swim at counter-current (described for *Tripedalia cystophora* and *Chiropsella bronzie* (Garm et al., 2007), *Chironex fleckeri* (Schlaefer et al., 2018) and *Copula sivickisi* (Schlaefer et al., 2020)), their unique visual system, which comprises a total of 24 eyes (Garm and Bielecki, 2008), allows them to direct their swimming in response to external stimuli (Kingsford et al., 2021). Obstacle avoidance has been reported for *C. fleckeri* (Hamner et al., 1995; Schlaefer et al., 2018) and *T. cystophora* and *C. bronzie* (Garm et al., 2007). Positive phototaxis, the tendency to move towards a light source, has also been observed in *T. cystophora* (Buskey, 2003) and *C. sivickisi* (Garm et al., 2012), which is a common trait among cubozoans and is often used to collect them during nocturnal samplings (Acevedo, 2016; Bolte et al., 2021; Morandini et al., 2014). All these findings suggest that, at least for adult specimens, it may be more appropriate to classify them as part of the nekton, a term that includes pelagic organisms that swim freely independently of currents.

In the Mediterranean Sea, *Carybdea marsupialis* (Linnaeus, 1758) is the sole reported species of the Class Cubozoa (Acevedo et al., 2019). Usually observed in low densities, over recent decades it has been massively detected in some Italian (mainly in the Adriatic Sea), Tunisian and Spanish coastal zones (Boero, 2013; Bordehore et al., 2011; Gueroun et al., 2015). Like other cubozoan jellyfish, *C. marsupialis* has a biphasic life cycle with a benthic polyp and a free-swimming medusa. Recently detached medusae measure less than 2 mm DBW (Diagonal Bell Width, distance between opposite pedalia at level of pedalia joining bell) while adults can grow up to 40 mm (Acevedo et al., 2019). On the Spanish coast of Dénia, where it has been detected in higher abundance and where a population is maintained year after year, *C. marsupialis* shows a clear seasonality. Polyp metamorphosis occurs in spring (Acevedo et al., 2019), resulting in the appearance of small juveniles from May to July (DBW <5mm), medium-size juveniles ($5 \leq \text{DBW} < 15\text{mm}$) from July to August and adults (DBW >15mm, up to 40 mm) approximately from August to October or early November (Acevedo, 2016; Bordehore et al., 2015a; Bordehore et al., 2020a; Canepa et al., 2017). *C. marsupialis* shows a clear coastal distribution at all stages (e.g. 90.8 % of the total catches of the samplings carried out in the period 2013-2015 correspond to the strip located between 0

and 15 m from the coast (Bordehore et al., 2020b), however, adults tend to concentrate in areas with high food availability (high levels of primary and secondary production), while small-juveniles can be found in other locations (Bordehore et al., 2020a; Canepa et al., 2017). The limited dispersal of *C. marsupialis* may be attributed to coastal dynamics and/or its ability to actively maintain itself in a chosen area by swimming. Thus, studying the swimming ability and current resistance across different developmental stages is crucial in understanding the species' spatial distribution.

To obtain swimming behavioral data on jellyfish within their habitats, electronic tags (acoustic transmitters and acceleration data loggers) have been used (Fossette et al., 2015; Gordon and Seymour, 2009; Moriarty et al., 2012). Nevertheless, the use of these tags is limited by the size of the species, among other constraints (Fossette et al., 2016). In our case, adults of *C. marsupialis* reach a maximum of 40 mm in DBW (half the size recommended by Gordon and Seymour 2009 to reduce potential confounding effects due to tag weight), making it necessary to develop smaller transmitters, which would be impossible to place in the case of early (5 mm) or late (15 mm) juveniles.

The main objective of this study was to elucidate the influence of active swimming ability on the spatial distribution of *C. marsupialis*. The specific goals include: i) To determine the ontogenic swimming speed and the effective displacement of *C. marsupialis* in the laboratory using video recordings and free tracking software, and ii) To provide data on their theoretical ability to overcome currents.

MATERIALS AND METHODS

***Carybdea marsupialis* collection and care**

Cubomedusae were collected between June and October 2016 on the coasts of Dénia and El Campello (Spain, Western Mediterranean Sea) by day (for juveniles and adults specimens) and night (only for adults) samplings (Fig. 1). Diurnal samplings were performed on foot, walking for a duration of 15 min parallel to the coastline within 15 m from the shoreline at 0.4 m/s using hand plankton nets (length 1.5 m, mouth area 0.15 m², mesh size 500)(Bordehore et al., 2020a). At night, waterproof LED lights (50W, 12 V) were used. Two lights were mounted at dusk, 15 meters from the shoreline and 1 meter deep. After 1 hour of light exposure, the first cubozoans appeared and they were gathered using plastic beakers (Bordehore et al., 2020b). In both types of samplings,

once collected, *C. marsupialis* individuals were placed into 50 L plastic containers filled with clean seawater and transported to the Dénia Montgó Scientific Station, where they were maintained in aquaria with filtered seawater at 24.5 °C and a salinity of 37.4. They were fed daily with *Artemia salina* nauplii.

In the laboratory, the DBW of each specimen was measured using a stereoscopic microscope (LEICA S8APO) for medusae that were ≤ 10 mm wide and with calipers for larger ones. Afterwards, cubozoans were grouped into three categories that represented different developmental stages based on their DBW: small (≤ 5 mm), medium (between 5 and 15 mm) and large (≥ 15 mm) individuals (Acevedo et al., 2013).

Surface currents speed

Within the framework of the LIFE CUBOMED project (www.cubomed.eu), periodic samplings were carried out between 2013 and 2015 along the 17 km of the coast of Dénia at 0, 250, and 500 meters from the shoreline. Surface currents speeds were obtained by deploying two drift buoys at different sampling locations (11 points at 0 m and 4 points at 250 and 500 meters) and recording their initial and final waypoints (5 min after release) with a GPS device (Garmin 72H)(Bordehore et al., 2020a; Canepa et al., 2017). The speed of the buoys were calculated from geographic coordinates and using the Haversine mathematical formula and the deployed time.

***Carybdea marsupialis* swimming experiments**

A total of 27 specimens (12 small juveniles, 7 medium-size juveniles and 8 adults) were evaluated. The DBW ranges for the three classes were: 1.1 to 3.9 mm for small, 5.4 to 14.2 mm for juveniles and 29.8 to 36.0 mm for adults. Individuals were video recorded within 48 h of collection while freely swimming in different recipients significantly larger than their body size. A minimum aquarium volume to jellyfish volume ratio of >3000 was ensured for all classes to avoid wall effects or other artifacts of the laboratory environment (Dabiri et al., 2010).

The small juveniles were analyzed in a Petri dish of 8.6 cm in diameter (equivalent to a range of $1/78.2 - 1/22.1$ DBW/petri dish) and 1.2 cm in height filled with 44 mL of filtered seawater at 50 μM . Lateral face was covered with black tape to avoid the

incidence of lateral light and the possible positive phototropism effects that *C. marsupialis* exhibits even in small sizes (Bordehore, 2014). Medium-sized specimens were divided into two subgroups (DBW >10 mm and DBW <10mm) and studied in two different cylindrical aquaria, the larger one of 29.5 cm diameter x 19.1 cm height, with 10 L of filtered seawater, and the smaller one of 17.3 cm diameter and 19.9 cm height, with 1.2 L. The minimum ratio between the DBW of the specimens and the diameter of the container was 1/28.6 and 1/32.0, respectively. Adults (>1.5 cm DBW) were placed in a rectangular aquarium (26 cm width x 29.5 cm height x 58 cm length) with 25L of filtered seawater. In this case, the length was 19.5 times larger than the diameter of the smallest adult tested (DBW=29.8 mm), respectively.

The Petri dish and 1.2 L aquarium were recorded using a Hercules Dualpix Infinite Camara in zenith position, and fixed on a tripod. For the 10 L and 25 L aquariums a Sony Handycam DCR-SR32 was used in the same position. To ensure that perpendicular trajectories to the main camera were recorded, an auxiliary camera (GoPro Hero3+) on the side of the aquariums was utilized. In all cases, a grid was included as a reference in the background, including the Petri dish.

Video image processing

The GoPro Hero+3 images were analyzed using GoPro Studio software (goo.gl/DiruZY) to eliminate the fisheye effect that alters the trajectory.

In the adult recordings, sections where the jellyfish remained in the corners of the aquarium or where their movement was not horizontal (i.e. perpendicular to the main camera) were eliminated using editing software Movie Maker and Sony Vegas Pro 13 (goo.gl/xLpB9n).

Swimming kinematics

We analyzed swimming speed (distance/time), displacement and effective velocity (defined here as total displacement/time) for each individual using the free software video analysis and modeling tool Tracker (<https://physlets.org/tracker/>).

Considering speed as the time rate at which an object is moving along a path, swimming speeds of *C. marsupialis* were calculated from the position-time data of the reference

point in the apex of the bell (Rubio-Tortosa et al., 2016). Tracker's software uses the finite algorithm shown below (eqn 1 and 2), which defines the parameter evaluated for a step as the average value over 2-step intervals. Subscripts refer to step numbers, and dt is the time between steps in seconds.

$$s_{xi} = \frac{(x_{i+1} - x_{i-1})}{(2 \times dt)} \quad (1).$$

$$s_{yi} = \frac{(y_{i+1} - y_{i-1})}{(2 \times dt)} \quad (2).$$

A minimum of 50 intervals were analyzed per specimen (with a maximum of 438 and a mean \pm s.e.m., standard error of the mean, of 200 ± 20), with a 4-5 step size (number of frames per interval).

To determine displacement and effective velocity, 5 segments were selected randomly for each specimen. Displacement was measured as the linear difference between the final position and its starting position, using the Tracker's tape measure. Knowing the time elapsed between the two points, effective velocity was calculated.

To represent the relationship between effective velocity and swimming speed, we created an index called "Effective Displacement Index" (EDI), obtained by dividing the velocity by the speed. It can range from 0 to 1. When EDI = 1, speed and velocity have the same value meaning that the jellyfish traveled in a straight line (distance and displacement are equal). Values of EDI close to 0 indicate that the jellyfish do not follow a linear path, but a more complex trajectory (in this case distance is greater than the displacement)(Fig. 2).

The proficiency of swimming was quantified as the diameter-normalized swimming speed, as follows (Eqn 3):

$$Proficiency = \frac{Swimming\ speed}{Diameter\ Bell\ Width} \quad (3).$$

RESULTS

Swimming speeds and effective velocities

In the laboratory conditions specified, the average swimming speed of all *C. marsupialis* specimens (N=27) was $22.74 \pm 2.89 \text{ mm s}^{-1}$ (mean \pm s.e.m.). It increased proportionally to DBW (Fig. 3). Per groups, the smaller ones ($1.1 \leq \text{DBW} \leq 3.9 \text{ mm}$) swam at $9.65 \pm 0.76 \text{ mm s}^{-1}$ (mean \pm s.e.m., n=12), whereas the medium ones ($5.4 \leq \text{DBW} \leq 14.2 \text{ mm}$) did it at $21.91 \pm 2.29 \text{ mm s}^{-1}$ (mean \pm s.e.m., n=7), and the adults ($29.8 \leq \text{DBW} \leq 36 \text{ mm}$) at $43.10 \pm 1.78 \text{ mm s}^{-1}$ (mean \pm s.e.m., n=8).

Regarding the average maximum velocity, it also varies with the size (Fig. 4), being $41.23 \pm 4.93 \text{ mm s}^{-1}$ (mean \pm s.e.m.) when all the medusae were grouped together, and $18.64 \pm 1.34 \text{ mm s}^{-1}$, $40.98 \pm 4.34 \text{ mm s}^{-1}$ and $75.35 \pm 3.17 \text{ mm s}^{-1}$ when divided by size class, from smallest to largest, respectively (mean \pm s.e.m., same N per group as previous analysis). The range of maximum and minimum individual velocities was as follows: $0.04\text{-}29.75 \text{ mm s}^{-1}$ for smaller jellyfish, $0.67\text{-}54.27 \text{ mm s}^{-1}$ for medium-size specimens and $5.72\text{-}87.23 \text{ mm s}^{-1}$ for adults.

The effective velocity was also proportional to the DBW (Fig. 5). It was $+5.04 \pm 0.68 \text{ mm s}^{-1}$ for juvenile 1, $+18.83 \pm 2.54 \text{ mm s}^{-1}$ for juvenile 2 and $+38.83 \pm 3.13 \text{ mm s}^{-1}$ for adults (mean \pm s.e.m.). The calculated EDI for each group was 0.51 ± 0.05 , 0.84 ± 0.06 and 0.90 ± 0.05 (mean \pm s.e.m.), respectively. The trajectory of small juveniles tends to be spiral-shaped, while medium-size specimens and adults tend to have a straighter trajectory.

Proficiency

The calculated proficiency decreased following a potential function, with the highest values observed for the smallest juvenile stage (up to 9.47), and reaching a plateau in adults (1.37 ± 0.13 , mean \pm s.d., N=8)(Fig. 6).

Surface current velocities and capability of *C. marsupialis* to overcome them

We analyzed a total of 850 short tracks of drifting buoys (X-Y m of track). The velocity of the currents in the study area varied depending on the month and the distance from the coast. At shoreline (0 m) the lowest values were obtained, ranging between $31.87 \pm 3.82 \text{ mm s}^{-1}$ in November and $58.01 \pm 11.79 \text{ mm s}^{-1}$ in May (mean \pm s.e.m., N=32 and N=39, respectively). Grouping all months, the average current speed at this distance was $44.32 \pm 3.05 \text{ mm s}^{-1}$ (mean \pm s.e.m., N=510). At 250 and 500 m, the values were higher

and similar to each other, with mean values of $94.72 \pm 10.82 \text{ mm s}^{-1}$ and $107.71 \pm 14.93 \text{ mm s}^{-1}$, respectively, when considering all months. In both distances, the minimum values were obtained in November, while the maximum ones were recorded in July ($41.18\text{-}42.47 \text{ mm s}^{-1}$ and $120.09\text{-}159.24 \text{ mm s}^{-1}$, at 250 and 500 m, respectively).

Taking into account these differences, we calculated the theoretical percentage of currents overcome by each stage, considering the months in which they are present. Specifically, we used May-July for the smaller specimens, July-August for the medium-sized specimens, and August-November for adults (see Fig. 7). We then compared the average speed of each specimen in each group with the calculated velocities of the buoys assigned to each period and distance. The number of buoys used for calculating current speeds at 0, 250 and 500 meters, were: 250, 81 and 87 for the period May-July, 191, 48 and 60 for July-August and 260, 90 and 82 for August-November months, respectively.

While the adults are able to swim strongly enough to overcome almost 70% of currents at 0 m, this percentage decreases to below 27% at farther distances. For medium-size juvenile percentages are lower, not even reaching 40% on the shoreline. Small ones can practically not overcome currents at any distance (in fact its percentage is 0 at 250 m and the highest value, at 0 m, does not even reach 17%).

DISCUSSION

Carbydea marsupialis is a strong swimmer. We analyzed 27 specimens from 1.1 mm to 36 mm DBW, which showed an average swim speed of $22.74 \pm 2.89 \text{ mm s}^{-1}$ (mean \pm s.e.m.), with higher speeds for larger individuals. This increase in swimming performance with size is a common trait among laboratory-tested cubozoans (Colin et al., 2013; Garm et al., 2007; Schlaefter et al., 2020; Shorten et al., 2005), but differs from the study of Schlaefter et al. on *C. fleckeri* in the field where the opposite relationship was found (Schlaefter et al., 2018). The authors suggested that this discrepancy may be due to the fact that the observed jellyfish in the wild were not swimming at their full capacity.

The average maximum speed recorded ranged from 18.64 mm s^{-1} for small juveniles (DBW $\leq 5\text{mm}$) to 75.35 mm s^{-1} for adults (DBW $\geq 15 \text{ mm}$), with a speed of 40.98 mm

s^{-1} for the medium-size class ($5 \leq DBW \leq 15$ mm). These velocities are comparable to those observed in other cubozoans of similar size range. For example, in trials performed in the laboratory, *T. cystophora* of 8-12 mm bell diameter (BD) and *C. bronzie* of 30-50 mm BD swam at maximum speeds of 3-4 cm s^{-1} and 7-8 cm s^{-1} against a 1-1.5 cm s^{-1} current, respectively (Garm et al., 2007). Meanwhile *C. sivickisi* with IPD (inter pedial diameter, a distance between opposite pedalia at the level of the bell turn-over, a measure slightly larger than DBW, Acevedo et al., 2019) ranging from 4 to 11 mm 4.9 cm against currents of 3-18 cm s^{-1} (Schlaefer et al., 2020). For *C. fleckeri*, Schlaefer et al. 2018 reported a maximum speed of 6.5 cm s^{-1} for a specimen of 4 cm IPD and Hamner (1995) described speeds about 8 cm s^{-1} for jellyfish of 30-100 mm BD.

The calculated EDI per size groups varied from 0.51 in small specimens to 0.90 in adults. Although based on speeds and velocities rather than distances and displacements, our EDI would be comparable to the NGDR (net to gross displacement ratio, i.e. displacement/distance)(Buskey et al., 1993; Vidal et al., 2018). In Buskey et al., the crustacean *Artemia salina* showed a variation in its NGDR from 0.11 to 0.55 with increasing nauplius stage, and initial nauplius stages of different copepod species presented low NGDR values (0.12-0.35) that increased up to 0.65 for second nauplius stage copepods. On the contrary, Vidal et al. (2018) registered decreasing NGDR values for the paralarvae of the squid *Doryteuthis opalescens* (from 0.63 to 0.36 for individuals of 2.65 to 9.81 mm mantle lengths, respectively). However, in their study, they applied a current of 1 cm s^{-1} that smaller individuals were not able to overcome, so they showed relatively long horizontal displacements due to the drift. The bigger squids, on the other hand, spent most of the time hovering (when doing so in the wild they remain in the same area, e.g. areas of high food availability), which makes the relative path displacement considerably reduced. To the best of our knowledge, there are no studies that determine the NGDR of cubozoan species.

The observed proficiency trend in *C. marsupialis* according to size is also consistent with those obtained in other box jellyfish such as *C. fleckeri* and *C. bronzie* (Colin et al., 2013), as well as the hydromedusa *Sarsia tubulosa* (Katija et al., 2015). As the bell diameter increased, the swimming proficiency decreased. Proficiency is related to foraging strategies. Species that forage as cruising predators have associated a lower swimming proficiency whereas ambush foraging species swim more proficiently

(Dabiri et al., 2010). Adults of *C. marsupialis* showed a proficiency value of 1.37 ± 0.13 (mean \pm s.d., N=8), which would be consistent with a cruising foraging strategy (Colin et al., 2013; Kiørboe, 2011) as previously stated (Acevedo et al., 2013).

Regarding the surface currents present in the study area and a comparison with the average speeds calculated for the different size groups, only adults could –theoretically– overcome them in a remarkable way. This result could be key to understanding their spatiotemporal distribution. On the coast of Dénia (Western Mediterranean) juveniles and adults are usually found in different areas some kilometers apart. Whereas adults are present in high productivity areas, juveniles have a more dispersed distribution (Bordehore et al., 2020a; Canepa et al., 2017), far from these highly productive areas. These results support the hypothesis that adults have strong enough swimming abilities to select their habitat, whereas juveniles rely on drifting currents and thus reflect the advection pattern caused by these currents. Nevertheless, it would be necessary to conduct experiments using currents to verify it completely.

The methodology developed in this paper allows the acquisition of high-quality swimming speed measurements for specimens of size ≥ 1 mm with conventional video recordings. In addition, it allows the animal to swim freely and, therefore, represents a good approximation of its behavior in the wild. This information is increasingly valuable because including empirically derived jellyfish behavior in particle tracking models that are used to forecast the timing and magnitude of jellyfish proliferation near major tourist areas, aquaculture facilities or power plants, makes them more realistic (Fossette et al., 2016). It should be noted, that the last months of the bathing season in the Mediterranean (August-September) overlaps with the months when *C. marsupialis* reaches its adult stage (Boero and Minelli, 1986; Bordehore et al., 2020a; Canepa et al., 2017) so knowing its presence in advance can be very useful. Although its sting can be considered of moderate intensity (Kokelj et al., 1992; Peca et al., 1997) with cutaneous affection mainly, it can further generate systemic effects in an unknown percentage of the population (Bordehore et al., 2015b).

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Competing interests

No competing interests declared.

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References

- Acevedo, M. J.** (2016). Biology, ecology and ecophysiology of the box jellyfish *Carybdea marsupialis* (Cnidaria: cubozoa). *PhD thesis*, Polytechnic University of Catalonia.
- Acevedo, M. J., Fuentes, V. L., Olariaga, A., Canepa, A., Belmar, M. B., Bordehore, C. and Calbet, A.** (2013). Maintenance, feeding and growth of *Carybdea marsupialis* (Cnidaria: Cubozoa) in the laboratory. *J. Exp. Mar. Bio. Ecol.* **439**, 84–91.
- Acevedo, M. J., Straehler-Pohl, I., Morandini, A. C., Stampar, S. N., Bentlage, B., Matsumoto, G. I., Yanagihara, A. A., Toshino, S., Bordehore, C. and Fuentes, V. L.** (2019). Revision of the genus *Carybdea* (Cnidaria: Cubozoa: Carybdeidae):

clarifying the identity of its type species *Carybdea marsupialis*. *Zootaxa* **4534**, 515–548.

- Albert, D. J.** (2007). Aurelia labiata medusae (Scyphozoa) in Roscoe Bay avoid tidal dispersion by vertical migration. *J. Sea Res.* **57**, 281–287.
- Boero, F.** (2013). Review of Jellyfish Blooms in the Mediterranean and Black Sea. Studies and Reviews. In *General Fisheries Commission for the Mediterranean*, p. 93.
- Boero, F. and Minelli, A.** (1986). First record of carybdea-marsupialis new-record cnidaria cubozoa from the adriatic sea. *Boll. del Mus. Civ. di Stor. Nat. di Venezia* **35**, 179–180.
- Bolte, B., Goldsbury, J., Huerlimann, R., Jerry, D. and Kingsford, M.** (2021). Validation of eDNA as a viable method of detection for dangerous cubozoan jellyfish. *Environ. DNA* **3**, 769–779.
- Bordehore, C.** (2014). Studies on the ecology of Carybdea marsupialis and jellyfish sting risk management. *PhD thesis*, University of Alicante.
- Bordehore, C., Fuentes, V. L., Atienza, D., Barberá, C., Fernandez-Jover, D., Roig, M., Acevedo-Dudley, M. J., Canepa, A. J. and Gili, J. M.** (2011). Detection of an unusual presence of the cubozoan *Carybdea marsupialis* at shallow beaches located near Denia, Spain (south-western Mediterranean). *Mar. Biodivers. Rec.* **4**,.
- Bordehore, C., Fuentes, V. L., Segarra, J. G., Acevedo, M., Canepa, A. and Raventós, J.** (2015a). Use of an inverse method for time series to estimate the dynamics of and management strategies for the box jellyfish *Carybdea marsupialis*. *PLoS One* **10**, e0137272.
- Bordehore, C., Nogué, S., Gili, J. M., Acevedo, M. J. and Fuentes, V. L.** (2015b). *Carybdea marsupialis* (Cubozoa) in the mediterranean sea: The first case of a sting causing cutaneous and systemic manifestations. *J. Travel Med.* **22**, 61–63.
- Bordehore, C., Fonfría, E. S., Alonso, C., Rubio-Tortosa, B., Acevedo, M. J., Canepa, A., Falcó, S., Rodilla, M. and Fuentes, V.** (2020a). Effects of environmental variables on the distribution of juvenile cubomedusae *Carybdea marsupialis* in the coastal Western Mediterranean. *PLoS One* **15**,.
- Bordehore, C., Fuentes, V. L., Alonso, C., Fonfría, E. S., Acevedo, M. J., Canepa,**

- A. and Bosch-Belmar, M.** (2020b). *Estudios de biología y ecología de la cubomedusa Carybdea marsupialis (Cubozoa)*. (ed. Universidad de Alicante).
- Buskey, E.** (2003). Behavioral adaptations of the cubozoan medusa *Tripedalia cystophora* for feeding on copepod (*Dioithona oculata*) swarms. *Mar. Biol.* **142**, 225–232.
- Buskey, E. J., Coulter, C. and Strom, S.** (1993). Locomotory patterns of microzooplankton: potential effects on food selectivity of larval fish. *Bull. Mar. Sci.* **53**, 29–43.
- Canepa, A., Fuentes, V., Bosch-Belmar, M., Acevedo, M., Toledo-Guedes, K., Ortiz, A., Durá, E., Bordehore, C. and Gili, J. M.** (2017). Environmental factors influencing the spatio-temporal distribution of *Carybdea marsupialis* (Lineo, 1978, Cubozoa) in South-Western Mediterranean coasts. *PLoS One* **12**, e0181611.
- Colin, S. P., Costello, J. H., Katija, K., Seymour, J. and Kiefer, K.** (2013). Propulsion in Cubomedusae: Mechanisms and Utility. *PLoS One* **8**.
- Dabiri, J. O., Colin, S. P., Katija, K. and Costello, J. H.** (2010). A wake-based correlate of swimming performance and foraging behavior in seven co-occurring jellyfish species. *J. Exp. Biol.* **213**, 1217–1225.
- Fossette, S., Gleiss, A. C., Chalumeau, J., Bastian, T., Armstrong, C. D., Vandenabeele, S., Karpytchev, M. and Hays, G. C.** (2015). Current-oriented swimming by jellyfish and its role in bloom maintenance. *Curr. Biol.* **25**, 342–347.
- Fossette, S., Katija, K., Goldbogen, J. A., Bograd, S., Patry, W., Howard, M. J., Knowles, T., Haddock, S. H. D., Bedell, L., Hazen, E. L., et al.** (2016). How to tag a jellyfish? A methodological review and guidelines to successful jellyfish tagging. *J. Plankton Res.*
- Garm, A. and Bielecki, J.** (2008). Swim pacemakers in box jellyfish are modulated by the visual input. *J. Comp. Physiol. A* **194**, 641–51.
- Garm, A., O'Connor, M., Parkefelt, L. and Nilsson, D. E.** (2007). Visually guided obstacle avoidance in the box jellyfish *Tripedalia cystophora* and *Chiropsella bronzie*. *J. Exp. Biol.* **210**, 3616–3623.
- Garm, A., Bielecki, J., Petie, R. and Nilsson, D. E.** (2012). Opposite patterns of diurnal activity in the box jellyfish *Tripedalia cystophora* and *Copula sivickisi*.

Biol. Bull. **222**, 35–45.

Gordon, M. R. and Seymour, J. E. (2009). Quantifying movement of the tropical Australian cubozoan *Chironex fleckeri* using acoustic telemetry. In *Hydrobiologia*, pp. 87–97.

Gueroun, S. K. M., Acevedo, M. J., Kefi-Daly Yahia, O., Deidun, A., Fuentes, V. L., Piraino, S. and Daly Yahia, M. N. (2015). First records of *Carybdea marsupialis* proliferation (Cnidaria: Cubozoa) along the eastern Tunisian coast (Central Mediterranean). *Ital. J. Zool.* 1–6.

Hamner, W. M. and Hauri, I. R. (1981). Long-distance horizontal migrations of zooplankton (Scyphomedusae: Mastigias). *Limnol. Oceanogr.* **26**, 414–423.

Hamner, W. M., Hamner, P. P. and Strand, S. W. (1994). Sun-compass migration by *Aurelia aurita* (Scyphozoa): population retention and reproduction in Saanich Inlet, British Columbia. *Mar. Biol.* **119**, 347–356.

Hamner, W. M., Jones, M. S. and Hamner, P. P. (1995). Swimming, feeding, circulation and vision in the Australian box jellyfish, *Chironex fleckeri* (Cnidaria: Cubozoa). *Mar. Freshw. Res.* **46**, 985–990.

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., et al. (2012). High activity and lévy searches: Jellyfish can search the water column like fish. *Proc. R. Soc. B Biol. Sci.* **279**, 465–473.

Katija, K., Colin, S. P., Costello, J. H. and Houshuo, J. (2015). Ontogenic propulsive transitions by *Sarsia tubulosa* medusae. *J. Exp. Biol.* **218**, 2333–2343.

Kingsford, M. J., Schlaefer, J. A. and Morrissey, S. J. (2021). Population structures and levels of connectivity for scyphozoan and cubozoan jellyfish. *Diversity* **13**.

Kjørboe, T. (2011). How zooplankton feed: Mechanisms, traits and trade-offs. *Biol. Rev.* **86**, 311–339.

Kokelj, F., Del Negro, F. and Montanari, G. (1992). Dermatitis due to *Carybdea marsupialis*. *Contact Dermatitis* **27**, 195.

Linnaeus, C. (1758). *Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.* Tomus

I. Editio decima, reformata, Holmiae, Impensis L. Salvii. 824.

- Malul, D., Lotan, T., Makovsky, Y., Holzman, R. and Shavit, U.** (2019). The Levantine jellyfish *Rhopilema nomadica* and *Rhizostoma pulmo* swim faster against the flow than with the flow. *Sci. Rep.* **9**,.
- Morandini, A. C., Stampar, S. N. and Kubota, S.** (2014). Mass occurrence of the cubomedusa *Copula sivickisi* (Cnidaria: Cubozoa) at Seto Harbor, Shirahama, Wakayama, Japan in summer of 2013; a possible recent example of global warming. *Publ. Seto Mar. Biol. Lab* **42**, 108–111.
- Moriarty, P. E., Andrews, K. S., Harvey, C. J. and Kawase, M.** (2012). Vertical and horizontal movement patterns of scyphozoan jellyfish in a fjord-like estuary. *Mar. Ecol. Prog. Ser.* **455**, 1–12.
- Peca, G., Rafanelli, S., Galassi, G., Di Bartolo, P., Bertini, S., Alberani, M. and Beccari, G.** (1997). Contact reactions to the jellyfish *Carybdea marsupialis*: Observation of 40 cases. *Contact Dermatitis* **36**, 124–126.
- Rakow, K. C. and Graham, W. M.** (2006). Orientation and swimming mechanics by the scyphomedusa *Aurelia* sp. in shear flow. *Limnol. Oceanogr.* **51**, 1097–1106.
- Reynolds, C. S. and Padisák, J.** (2013). Plankton, Status and Role of. In *Encyclopedia of Biodiversity: Second Edition*, pp. 24–38.
- Rubio-Tortosa, B., Parra, L., Sendra, S., Bordehore, C. and Lloret, J.** (2016). Preliminary results on the effect of electromagnetic fields on swimming patterns and the umbrella contraction of two scyphozoans: *Rhizostoma pulmo* and *Pelagia noctiluca*. In *5th International Jellyfish Bloom Symposium*, p. 235. Barcelona, Spain.
- Schlaefer, J. A., Wolanski, E. and Kingsford, M. J.** (2018). Swimming behaviour can maintain localised jellyfish (*Chironex fleckeri*: Cubozoa) populations. *Mar. Ecol. Prog. Ser.* **591**, 287–302.
- Schlaefer, J. A., Wolanski, E., Yadav, S. and Kingsford, M. J.** (2020). Behavioural maintenance of highly localised jellyfish (*Copula sivickisi*, class Cubozoa) populations. *Mar. Biol.* **167**,.
- Shorten, M., Davenport, J., Seymour, J. E., Cross, M. C., Carrette, T. J., Woodward, G. and Cross, T. F.** (2005). Kinematic analysis of swimming in

Australian box jellyfish, *Chiropsalmus* sp. and *Chironex fleckeri* (Cubozoa, Cnidaria: Chiropsodidae). *J. Zool.* **267**, 371–380.

Vidal, E. A. G., Zeidberg, L. D. and Buskey, E. J. (2018). Development of swimming abilities in squid paralarvae: Behavioral and ecological implications for dispersal. *Front. Physiol.* **9**,.

Figures legends

Fig. 1. Sampling areas (Dénia and El Campello) on the Spanish coast (Western Mediterranean Sea).

Fig. 2. Difference between distance and displacement (and, consequently, for the same elapsed time, speed and velocity) of a moving object.

Fig. 3. Mean swimming speed of *C. marsupialis* with increasing size (mean \pm s.e.m.) (n=27).

Fig. 4. Maximum swimming speed of *C. marsupialis* with increasing size (n=27).

Fig. 5. Effective velocity of *C. marsupialis* with increasing size (n=27).

Fig. 6. Swimming proficiency of *C. marsupialis* with increasing size (n=27).

Fig. 7. Percentage of current overcome of each size group of *C. marsupialis* in relation to their periods of presence and distance from the coast (mean \pm s.e.m.)(n=12 for small juveniles, n=7 for medium juveniles and n=8 for adults).

Fig. 1.

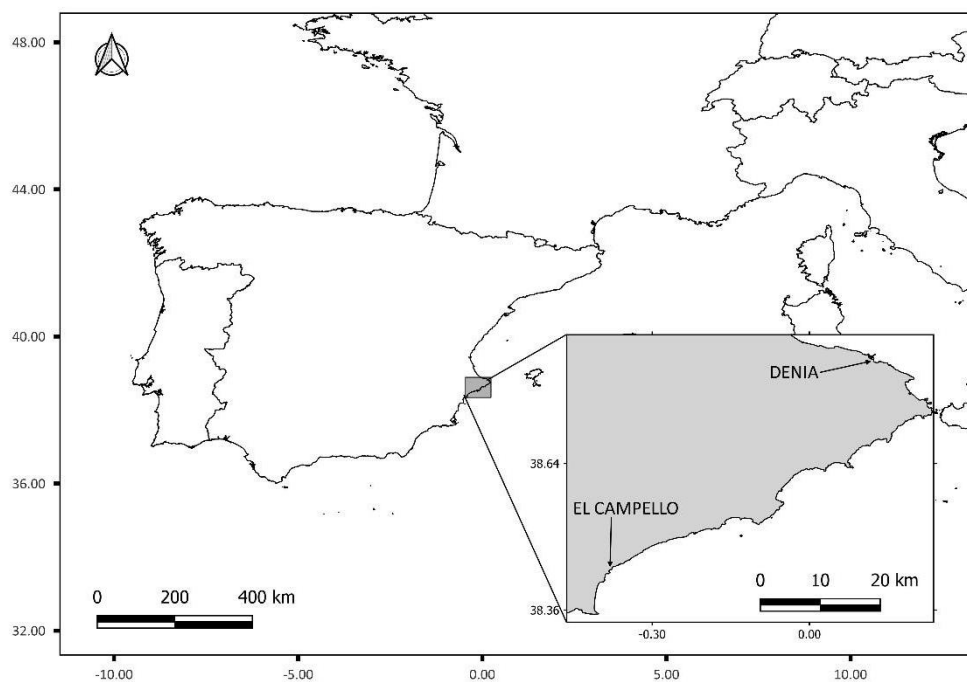


Fig. 2.

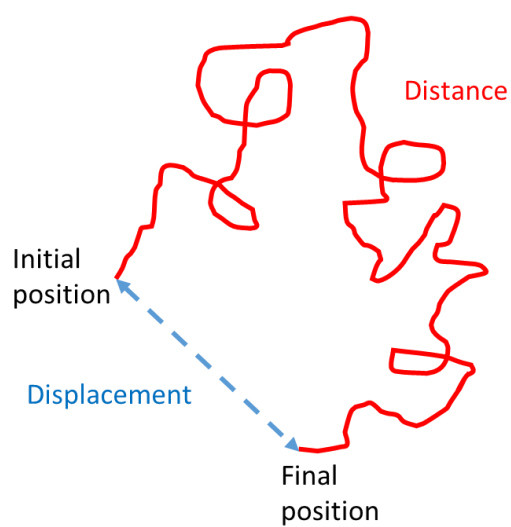


Fig. 3.

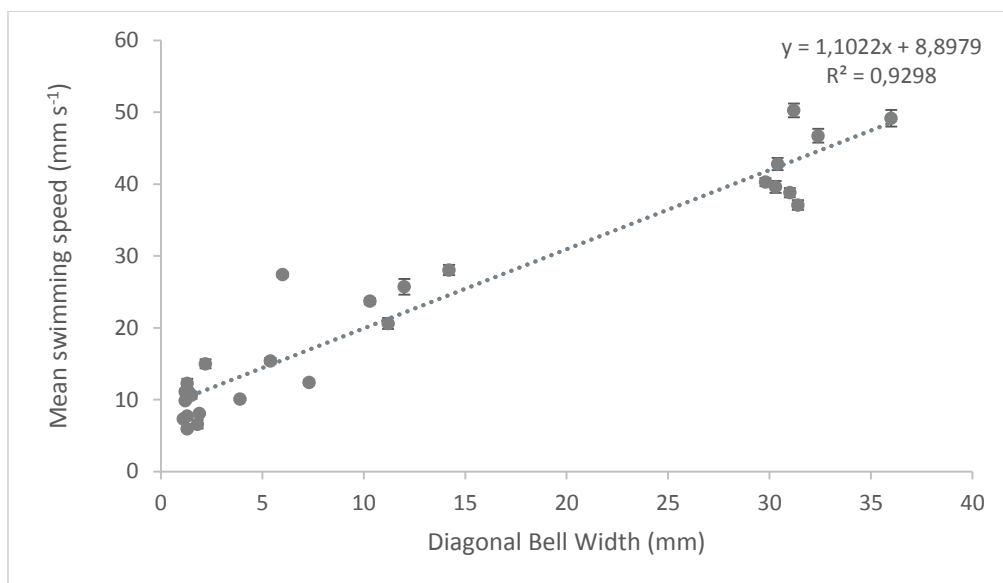


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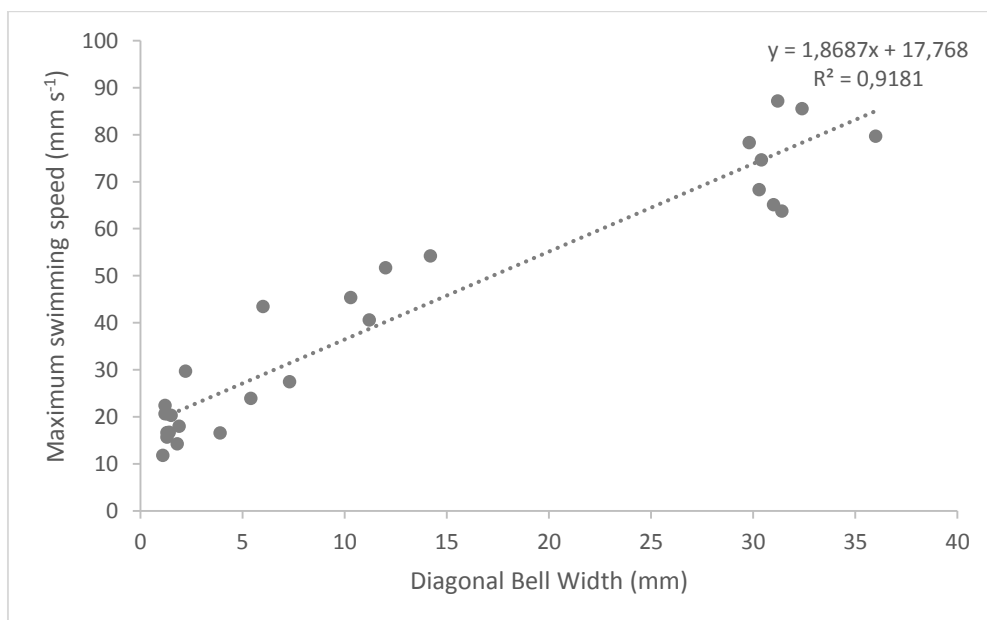


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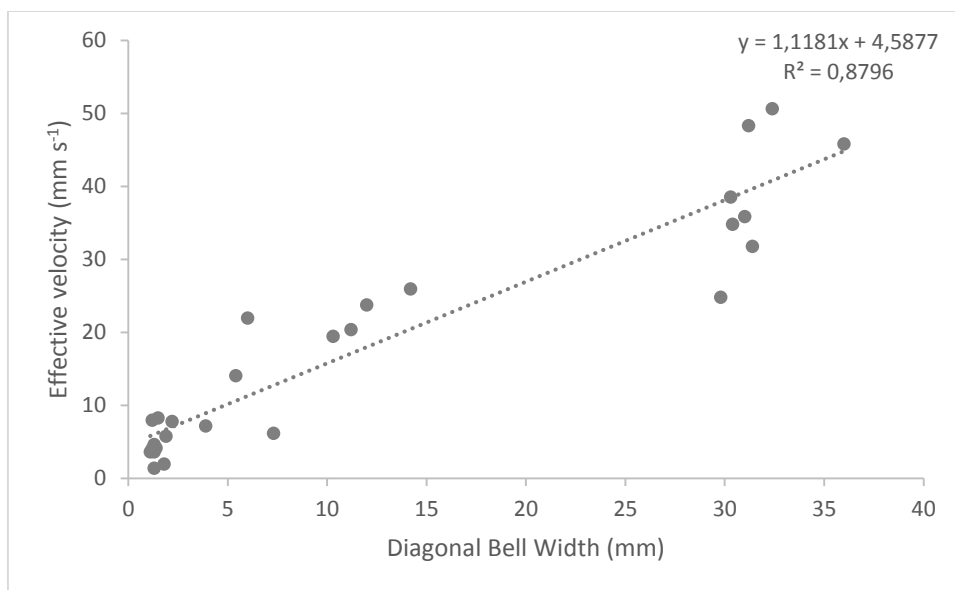


Fig. 6.

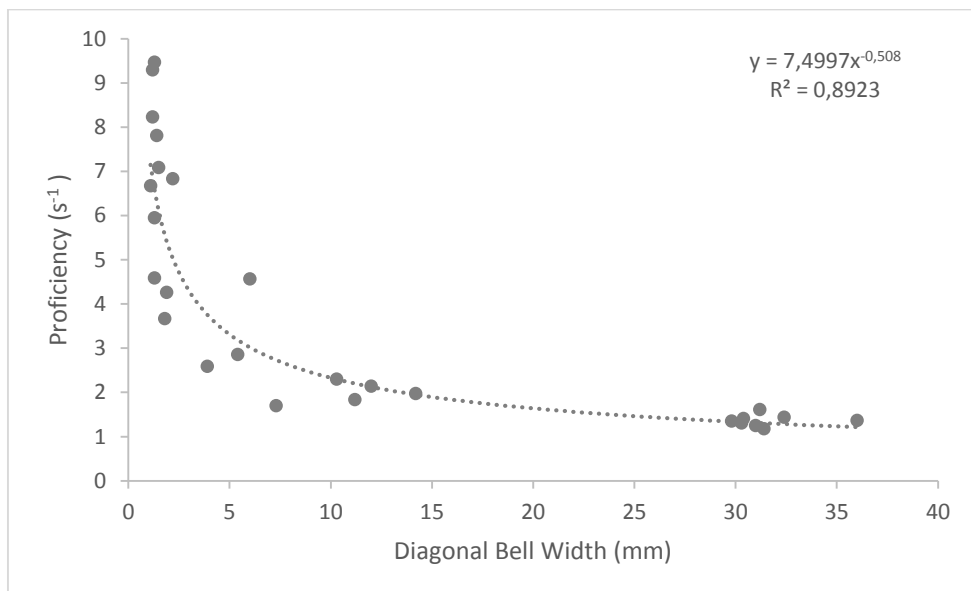


Fig. 7.

