

Report

Current Biology

Current-Oriented Swimming by Jellyfish and Its Role in Bloom Maintenance

Highlights

- Wild *Rhizostoma* jellyfish were equipped for the first time with accelerometers
- These jellyfish can orientate their movements with respect to currents
- They can actively swim countercurrent in response to current drift
- This behavior is adaptive for jellyfish bloom maintenance and survival

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In Brief

Current drift can have major and potentially negative effects on the lives of weakly swimming species in particular. Fossette et al. show that jellyfish modulate their swimming behavior in relation to current. Such oriented swimming has significant life-history benefits, such as increased bloom formation and a reduction of probability of stranding.

Current-Oriented Swimming by Jellyfish and Its Role in Bloom Maintenance

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Summary

Cross-flows (winds or currents) affect animal movements [1–3]. Animals can temporarily be carried off course or permanently carried away from their preferred habitat by drift depending on their own traveling speed in relation to that of the flow [1]. Animals able to only weakly fly or swim will be the most impacted (e.g., [4]). To circumvent this problem, animals must be able to detect the effects of flow on their movements and respond to it [1, 2]. Here, we show that a weakly swimming organism, the jellyfish *Rhizostoma octopus*, can orientate its movements with respect to currents and that this behavior is key to the maintenance of blooms and essential to reduce the probability of stranding. We combined in situ observations with first-time deployment of accelerometers on free-ranging jellyfish and simulated the behavior observed in wild jellyfish within a high-resolution hydrodynamic model. Our results show that jellyfish can actively swim counter-current in response to current drift, leading to significant life-history benefits, i.e., increased chance of survival and facilitated bloom formation. Current-oriented swimming may be achieved by jellyfish either directly detecting current shear across their body surface [5] or indirectly assessing drift direction using other cues (e.g., magnetic, infrasound). Our coupled behavioral-hydrodynamic model provides new evidence that current-oriented swimming contributes to jellyfish being able to form aggregations of hundreds to millions of individuals for up to several months, which may have substantial ecosystem and socioeconomic consequences [6, 7]. It also contributes to improve predictions of jellyfish blooms' magnitude and movements in coastal waters.

Results

Scyphozoan jellyfish form aggregations of hundreds to millions of individuals mostly in coastal areas [8], where they

face the risk of stranding if carried onshore by currents. Aggregations play a critical role in the ecology of jellyfish by facilitating reproduction and reducing predation [9]. Aggregations may be caused by the combination of the drifting action of a current and the active swimming behavior of the jellyfish themselves [10], but the fine-scale mechanism is not well understood. Previous studies have suggested that jellyfish might change their swimming direction with respect to current orientation [11–17]; however, in most cases, currents were not measured in situ but were simply inferred, making any reported relationship ambiguous. Directional swimming against vertical shears has only been demonstrated in the jellyfish *Aurelia aurita* [5], but the benefits of such oriented swimming in jellyfish are unknown. Here we tackled both of these issues: for the first time, jellyfish swimming direction in changing horizontal flows and the adaptive value of this behavior were assessed. Massive aggregations of the jellyfish *Rhizostoma octopus* are observed every summer in the Pertuis Breton, Bay of Biscay, France (Figure 1) [19]. Eighteen of these jellyfish were captured at sea and equipped with acceleration data loggers recording diving behavior, activity, and body orientation for a maximum of 6.6 hr (Figure 1 and Table S1 available online; see the Supplemental Experimental Procedures). Jellyfish spent on average 14.0% (SD = 20.6%, range = 0%–73%) of their time performing V-shaped dives and 82.9% (SD = 21.6%, range = 19.8%–100%) swimming horizontally between 0 and 2 m, independently of the state of the tide (Table S1). Accordingly, we found no significant difference in jellyfish depth in relation to sea state (generalized additive model [GAM], $t_{\text{Seasate}} = 1.750$, $P_{\text{Seasate}} = 0.083$) or flow index (product of magnitude of the current and the amplitude of the present tide; GAM, $F_{\text{FlowIndex}} = 1.447$, $P_{\text{FlowIndex}} = 0.223$). During these periods of shallow horizontal swimming, the mean bell pulse frequency of the jellyfish was 0.80 pulses/s (SD = 0.23 pulses/s; range = 0.43–1.39 pulses/s). The routine swimming speed (see the Supplemental Experimental Procedures) was 0.05 m/s (SD = 0.02 m/s; range 0.03–0.08 m/s; Figure S1 and Table S2), i.e., an order of magnitude slower than the tidal currents in the Pertuis (~20–50 cm/s). All tracked jellyfish were active almost continuously (mean partial dynamic body acceleration = 0.03 g, SD = 0.02 g, range = 0.019–0.107 g; Table S2) without significant effect of sea state ($p = 0.0584$). However, state of the tide significantly impacted mean activity level, which peaked during slack waters (i.e., lowest flow index values; GAM, $F_{\text{FlowIndex}} = 2.933$, $P_{\text{FlowIndex}} = 0.008$; Figure S2).

As jellyfish spent most of their time swimming horizontally close to the surface, we measured the instantaneous compass headings of their longitudinal body axis and compared these with the direction of local currents (measured with surface drifting buoys). Nineteen 30 min transects were performed during slack water ($n = 7$), ebb ($n = 6$), and flood ($n = 6$) tides, during which two observers used hand-held compasses to record the swimming direction of 844 jellyfish passing within 3 m of the boat (mean = 44 jellyfish/transect, SD = 14; Table S3; see the Supplemental Experimental Procedures). In all transects, the distribution of the jellyfish swimming directions was significantly different from random (Rayleigh test, $p < 0.05$ in all cases), and in five cases the distribution was bimodal (Table S3). The correlation between the mean swimming direction

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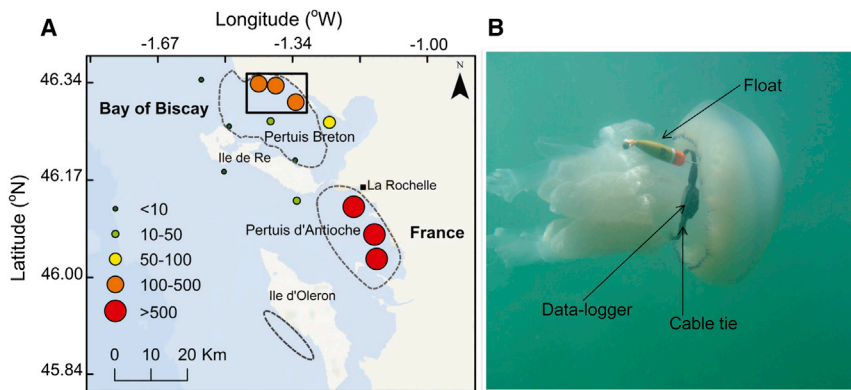


Figure 1. *Rhizostoma octopus*, Distribution and Abundance

(A) Distribution and abundance of scyphozoan jellyfish *Rhizostoma octopus* in the Pertuis Breton and Pertuis d'Antioche, Bay of Biscay, France, estimated during an aerial survey performed on August 22, 2011. The size of the color-coded dots is proportional to the number of jellyfish observed within 5 min survey periods. The dotted gray areas indicate areas where jellyfish aggregations were observed during boat surveys from April to September 1983 (data modified from [18]). The solid black box shows the area where the boat transects were performed in August and September 2011.

(B) Picture of a scyphozoan jellyfish, *Rhizostoma octopus*, equipped with a triaxial acceleration data logger recording diving behavior, activity, and body orientation. The float allows the whole package to be close to neutral buoyancy. See also Tables S1 and S2.

of the jellyfish and the mean current heading along each transect was statistically significant on the ebb tide (circular-circular correlation, $r = 0.463$, $p < 0.05$, $n = 5$ paired measures; Table S3) and on the flood tide ($r = 0.508$, $p < 0.05$, $n = 7$ paired measures, Table S3), but not during slack water ($r = 0.108$, $p > 0.05$, $n = 9$ paired measures; Table S3).

On the ebb tide, the mean jellyfish swimming direction was countercurrent (mean jellyfish direction = 89.2° , $SD = 61.8^\circ$; $n = 241$ individuals, $r = 0.559$, Rayleigh test, $p < 0.01$; versus mean current direction = 268.2° , $SD = 11.9^\circ$; $n = 4$ buoys, $r = 0.979$, $p < 0.01$; Figure 2A). On the flood tide, the jellyfish were either swimming with (80.6° , $SD = 38.8^\circ$, $n = 118$ individuals, $r = 0.795$, $p < 0.01$) or against (273.0° , $SD = 34.8^\circ$, $n = 155$, $r = 0.832$, $p < 0.01$) the current (106.2° , $SD = 15.1^\circ$; $n = 6$ buoys, $r = 0.966$, $p < 0.01$; Figure 2B). Jellyfish swimming against the current were observed in areas significantly shallower (mean bottom depth = 5.87 m, $SD = 0.41$ m) than areas where jellyfish were swimming with the current (8.06 m, $SD = 1.72$ m, Mann-Whitney test, $p = 0.0259$, $n = 7$ transects). During slack water, mean current direction (115.9° , $SD = 68.2^\circ$, $n = 7$ buoys, $r = 0.492$, $p > 0.05$) and mean jellyfish direction (96.9° , $SD = 79.8^\circ$, $r = 0.379$, $n = 330$ individuals, $p < 0.05$) were more variable (Figure 2C). Therefore, jellyfish orientation seems to be modulated by tidal currents.

The impact of this current-oriented swimming behavior by the jellyfish on bloom maintenance, spatial dynamics, and individual survival was investigated by running a particle-tracking model simulating the movements of virtual jellyfish within a modeled velocity field [20]. The hydrodynamic circulation in the Pertuis is well studied ([21] and references therein), resulting in accurate models for the area. A total of 4,800 virtual particles were released in the area (Figure 3) and tracked for 90 days (see the Supplemental Experimental Procedures). Our goal was to understand how, once a bloom has formed, it can remain in an area, disappear from this area, and/or spread toward other areas (i.e., “apparent” blooms [10]) via transport by currents and jellyfish’s behavior. Accordingly, we assumed that jellyfish dispersed from the north of the Pertuis Breton, where blooms were observed during the aerial survey preceding our fieldwork and where the boat transects were performed (Figures 1 and 3).

We ran two scenarios: (1) the virtual jellyfish were passive and (2) the virtual jellyfish swam against the current at a swimming speed of 0.05 m/s on both the flood and ebb tides and in

random directions during slack water (see the Supplemental Experimental Procedures). In both scenarios, the spatial distribution of the virtual jellyfish was relatively similar, but passive virtual jellyfish dispersed further south ($\sim 45.8^\circ N$) than active virtual jellyfish ($\sim 46.2^\circ N$). The distribution pattern of active virtual jellyfish matched more closely historical and current distributional patterns of real *R. octopus* as documented by boat and/or aerial surveys (Figures 1 and 3). An aerial survey preceding our fieldwork revealed a total of 12 jellyfish blooms in the Pertuis (Figures 1 and 3). During the 3-month simulation, active virtual jellyfish aggregated in seven of these 12 areas, compared to five for passive virtual jellyfish (Figure S3A).

To quantitatively compare dispersal, we computed an index of aggregation following [22]. This index varied throughout the simulation for both scenarios with peaks, suggesting the formation of large, transient aggregations (Figure 4A). It was higher for active jellyfish than for passive jellyfish on 81% of the days, indicating that active virtual jellyfish were more often aggregated than passive virtual jellyfish. Finally, we found a significant difference in the incidence of jellyfish stranding (Figure 4B). After 1 month, $\sim 4\%$ of passive particles were stranded compared to zero active particles. At the end of the 3-month simulation, 43.2% of passive particles were stranded compared to 3.7% of active particles (see the Supplemental Experimental Procedures for results from models under different wind forcing conditions and Figures S3 and S4).

Discussion

In situ observations and first-time deployment of accelerometers on free-ranging jellyfish reveal that the jellyfish *Rhizostoma octopus* can actively change its swimming direction in response to current drift and changing current flows. Therefore, jellyfish orientation seems to be modulated by tidal currents, with a likely scenario of direct current detection. This result corroborates previous studies that described directional swimming in other jellyfish species [11–17], suggesting that this ability may be widespread in bloom-forming jellyfish. Behavioral simulations within a high-resolution hydrodynamic model also demonstrate that there may be a strong adaptive benefit to this current-oriented swimming behavior by keeping bloom-forming species in particular areas rather than dispersed or washed ashore.

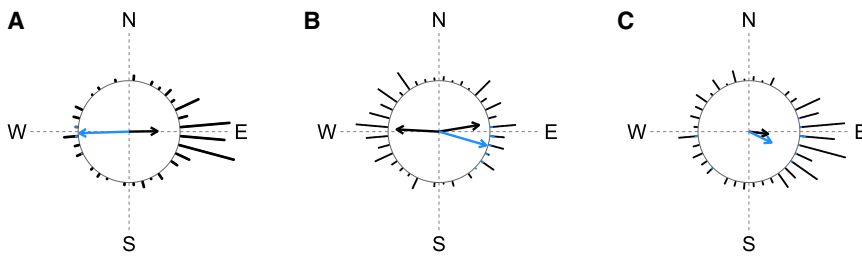


Figure 2. Jellyfish Swimming Directions in Relation to Current Directions

Circular diagrams of the swimming directions of jellyfish *Rhizostoma octopus* (black) and the current direction (blue) measured on the ebb tide (n = 6 transects, n = 4 buoys, and n = 241 jellyfish; A), the flood tide (n = 6 transects, n = 6 buoys, and n = 273 jellyfish; B) and the slack water (n = 7 transects, n = 7 buoys, and n = 330 jellyfish; C) in the Pertuis Breton, Bay of Biscay, France. Directions are shown by individual dots stacked in 10° intervals of total circular range. In each figure, the

mean swimming direction of the jellyfish and the mean current direction are depicted as black and blue arrows, respectively. On the flood tide, the distribution of the jellyfish swimming directions was bimodal, hence the two black arrows. The arrow length is proportional to the magnitude of the mean vector r (i.e., a measure of the variation around the mean value), with the radius of the circle corresponding to $r = 1$. See also Table S3.

There is significant interest in understanding the ecosystem impacts of jellyfish blooms, which are being reported more frequently around the world [7, 23, 24]. Our results show that current-oriented swimming is key to the maintenance of these blooms, as hypothesized by [10, 17], and will allow blooms to persist even in high-flow areas. For larger jellyfish, not only do individuals actively swim, but this behavior is consistent across individuals and hence influences the distribution of blooms as a whole.

A similar mechanism has been described for the accumulation of smaller zooplankton species, e.g., copepods and mollusks, at frontal zones in coastal waters. These animals maintain their depth in the water column by detecting and swimming against upwelling and downwelling currents [25], but not horizontal flows like the jellyfish in our study. How depth and current direction are sensed is currently unknown for most of these species. Copepods may detect flow direction as a fluid velocity difference between their sensory setae positioned along their antennae and the ambient water [26–28] and can exhibit positive rheotaxis (i.e., countercurrent swimming) in other contexts [29]. This behavior may reduce passive drift to help maintain position in a river, for instance [29]. Some fish can also perform positive rheotaxis by using visual, olfactory, and sometimes tactile cues [30–32].

A possible mechanism for the jellyfish's ability to orientate their movements with respect to currents may thus be the direct detection of current shears at the air-water interface across the body surface (see also [10]). The jellyfish in our study spent >80% of their time swimming horizontally at the surface, a position that may allow them to sense these shears. Evidence for this mechanism exists in the jellyfish *Aurelia aurita* [5]; under laboratory conditions, individual jellyfish orient directionally against vertical velocity shears via asymmetric bell pulsing. In a similar way, high-flying nocturnal insects may use microturbulences within the airstream as a mechanism for direct wind detection [33]. In addition, these insects are better at orientating in the downwind direction when migrating in layers and flying at the altitude of maximum wind speed [34], suggesting that flight altitude, or swimming depth in our case, may affect the ability of animals to detect these cues.

Several other mechanisms could help jellyfish indirectly assess their drift and current direction. They may detect the orbital motion of waves, which can be linked with the direction of water flow at the surface layer, as previously described in hatchling turtles (e.g., [35]). Relative changes in the magnetic field could also provide jellyfish with an indication of their drift direction as described in other species (e.g., [36, 37]). Whether jellyfish can detect such changes over half a tidal cycle and a

horizontal displacement of a few kilometers remains to be tested. Jellyfish may also use infrasounds to orientate themselves, as shown in birds (e.g., [38]) and several marine species (review in [39]). The statocysts, organs located at the margin of the jellyfish's bell, enable jellyfish to detect gravity [40], sense vibrations [41], and potentially sense pressure variations [42] and may therefore contribute to the ability of jellyfish to directly or indirectly detect current flow. *Rhizostomae* jellyfish do not possess ocelli (i.e., photoreception organs [43]) and are therefore unlikely to use the sunlight as a visual cue as suggested in other scyphozoan and cubozoan species (e.g., [44, 45]).

Our results show that current-oriented swimming as a response to current drift may have important life-history consequences for jellyfish. Such a response to current drift also exists in fish and crustacean larvae or juveniles, where it may also have consequences in terms of population dynamics influencing survival, connectivity, and recruitment (e.g., [46–50]). Oriented swimming in hatchling turtles, using geomagnetic cues [36] and/or by direct detection of current drift [51], may also allow them to remain within warm-water currents favorable for growth and survival and avoid drifting into areas where thermal conditions may pose threats to their survival [52, 53]. It seems, therefore, that diverse weakly swimming animals (i.e., swimming speed varying between a few millimeters per second to tens of centimeters per second), but also weakly flying animals such as insects [33, 34], whose movements have often been assumed to be dictated exclusively by flows may, in fact, employ similar strategies, i.e., active flow-oriented movements and potentially direct flow sensing, to mitigate flow drift and improve their chance of survival and/or of reaching favorable habitat. In contrast, animals that can outswim or outfly the flow, such as migrating adult sea turtles or migrating birds, may not show strong and/or immediate response to current drift as their traveling speed may allow them to compensate for drift and/or reorientate later in their journey. For instance, loggerhead turtles may use a goal-oriented strategy while crossing the Mediterranean Sea. They do not seem to detect current flow, and consequently drift off course, reorienting later in the journey [3]. Birds migrating across oceans may also follow a constant compass bearing and do not compensate for wind drift until nearer to the goal (e.g., [1, 2, 54]). In both cases, these strategies do not prevent migrants from eventually reaching their goal, nor do they directly impact their survival, as would be the case for slow-moving species. Even though many different strategies exist among fast-moving species [1], having continuous access to navigational cues to be able to head toward their goal may be more important than being

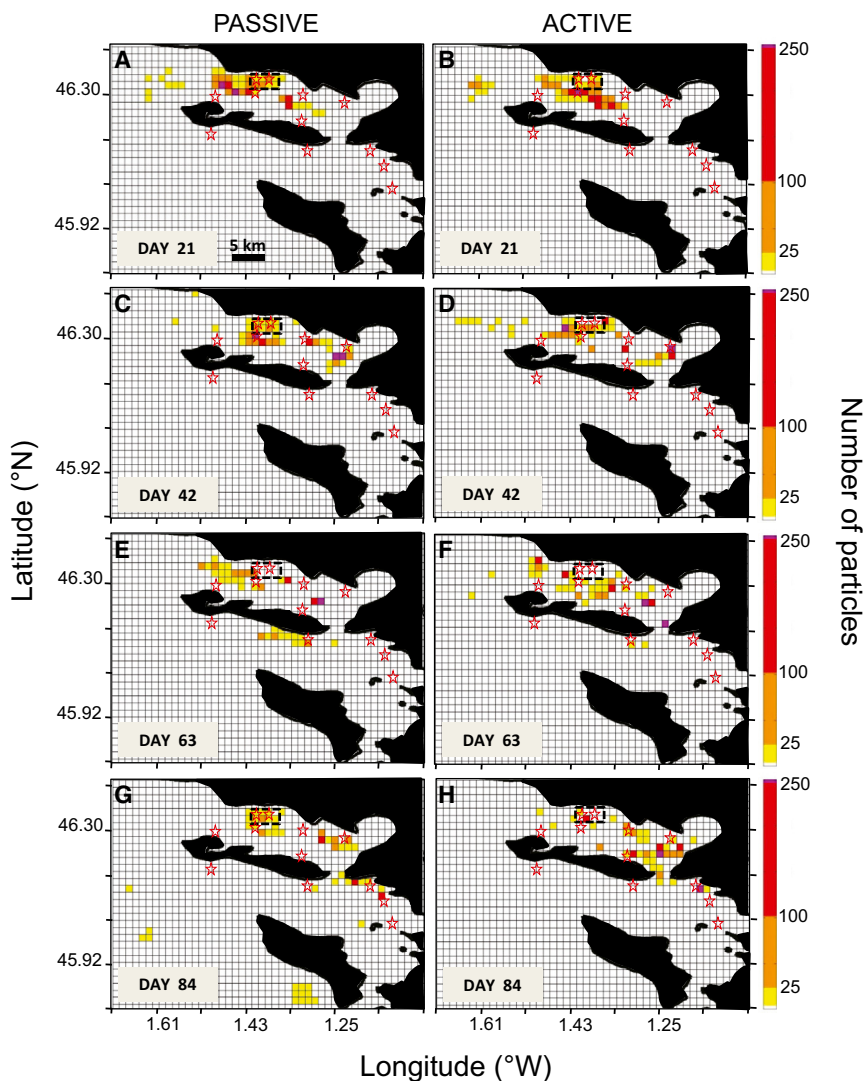


Figure 3. Computer Simulations of Active versus Passive Virtual Jellyfish Movements

Distribution of 4,800 particles (i.e., virtual jellyfish) with either a passive, non-oriented swimming behavior (A, C, E, and G) or an active, oriented swimming behavior (B, D, F, and H) tracked for 90 days in the Pertuis Breton and Pertuis d'Antioche, Bay of Biscay, France. The particles were initially released within the black dotted box at a rate of 40 particles every 3 hr for the first 15 days. The colors indicate the number of particles within each 1×1 km cell throughout the simulation. The purple cells indicate a bloom (i.e., >250 particles/cell in one day). The red stars indicate the location of the 12 major jellyfish blooms observed during an aerial survey at the start of this study's fieldwork in the Pertuis Breton and Pertuis d'Antioche (cf. Figure 1). A purple cell overlapping a red star indicates that the model correctly predicted the location of one of the 12 observed blooms. The model was forced with tides and a west wind of 4 m/s (see the Supplemental Experimental Procedures for details). See also Figure S3.

arrival or the magnitude of harmful jellyfish blooms near major tourist areas [56], aquaculture facilities [58], or power plants [6]. Understanding the swimming and orientation behavior of these organisms is therefore imperative if negative socioeconomic impacts are to be reduced.

To conclude, our results show that jellyfish exhibit complex current-modulated orientation strategies that play important roles in bloom maintenance. The fact that free-living jellyfish can actively change their swimming direction in response to current drift and changing current flows poses questions of how widespread this ability is

among other slow-moving taxa and what the adaptive significance of this strategy might be for each taxon. Such questions are essential for understanding the evolution of animal orientation strategies.

able to continuously detect flow drift throughout their journey [2]. The impact of flow drift, and ultimately the costs or benefits associated with it, may thus largely depend on the ratio of animal speed to flow speed [1]. Selective pressure on animals to adopt strategies to detect and respond to flow drift may be stronger in slow-moving than in fast-moving species [2, 4].

The predicted distribution of the active virtual jellyfish in the Pertuis was in good agreement with historical and current distributional patterns. To date, the three other attempts to model the formation and dispersal of jellyfish blooms have assumed that jellyfish drift passively [19, 55, 56]. These models have provided useful information about jellyfish ecology and patterns of connectivity between populations, but our study has revealed that including the empirically derived behavior of jellyfish in particle-tracking models can significantly modify predicted patterns of distribution and abundance. Similarly, including the behavior of small flying animals (insects) in particle-tracking models may have very substantial effects on the distance and direction of movement of these animals, and thus on their population dynamics (e.g., [57]). Achieving more realistic predictions of jellyfish dispersal would improve our ability to forecast the time of

among other slow-moving taxa and what the adaptive significance of this strategy might be for each taxon. Such questions are essential for understanding the evolution of animal orientation strategies.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, four figures, and three tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.11.050>.

Author Contributions

G.C.H., S.F., and A.C.G. conceived the study; S.F., G.C.H., T.B., and S.V. completed the fieldwork; J.C. and M.K. ran the particle tracking models; S.F., G.C.H., A.C.G., and C.D.A. led the data analysis and interpretation; and S.F., A.C.G., and G.C.H. led the writing with contributions from all authors.

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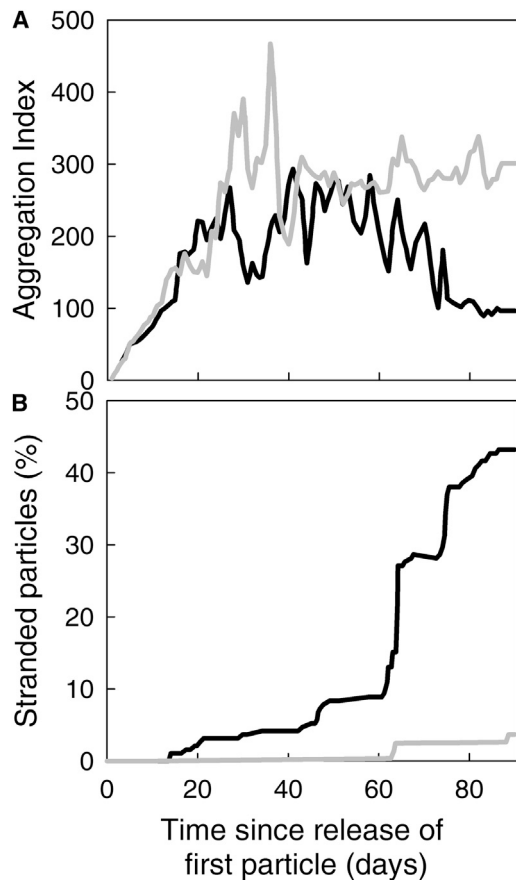


Figure 4. Aggregation Index and Stranding Rate of Active versus Passive Virtual Jellyfish

(A) Aggregation index of 4,800 particles (i.e., virtual jellyfish) tracked for 90 days in the Pertuis Breton and Pertuis d'Antioche, Bay of Biscay, France. The aggregation index is defined as the ratio between the variance of the number of particles per cell and the average number of particles per cell. A total of 2,538 grid cells were considered for the calculation of the index. The size of the grid was based on the maximum extent of the jellyfish dispersion across all simulations. When the index is high, the particles are aggregated. When the index is low, the particles are dispersed. At the beginning of the simulation, the index is close to zero and steadily increases as particles are gradually released in the model at a rate of 40 particles every 3 hr over the first 15 days. The index starts fluctuating after the 15th day, when all particles have been released in the model. Black line, aggregation index of particles with a passive, non-oriented swimming behavior; gray line, aggregation index of particles with an active oriented swimming behavior. The model was forced with tides and a west wind of 4 m/s (see the [Supplemental Experimental Procedures](#) for details).

(B) Number of stranded particles (i.e., virtual jellyfish) in percentage throughout the simulation. A total of 4,800 particles were tracked for 90 days in the Pertuis Breton and Pertuis d'Antioche, Bay of Biscay, France. The number of stranded particles was counted at every time step. Black line, number of stranded particles with a passive, non-oriented swimming behavior; gray line, number of stranded particles with an active oriented swimming behavior. In both simulations, the model was forced with tides and a west wind of 4 m/s (see the [Supplemental Experimental Procedures](#) for details). See also [Figure S4](#).

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