Counter-wave jellyfish swimming

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Abstract

Having a profound influence on marine and coastal environments worldwide, jellyfish hold a significant scientific, economic, and public interest. The predictability of outbreak and dispersion of jellyfish is limited by a fundamental gap in our understanding of their movement. Although there is evidence that jellyfish may actively affect their position, the role of active swimming in controlling jellyfish movement, and the characteristics of jellyfish swimming behavior, are not well understood. Consequently, jellyfish are often regarded as passively-drifting or randomly-moving organisms, both conceptually and in process studies. Here we show that the movement of jellyfish is controlled by distinctly directional swimming patterns, which are oriented against the direction of the surface gravity waves. Taking a Lagrangian viewpoint from drone videos that allows tracking of multiple adjacent jellyfish, and focusing on *Rhopilema Nomadica* as a model organism, it is shown that the behavior of the individual jellyfish translates into a synchronized directional swimming of the aggregation as a whole. Numerical simulations show that this counter-wave swimming behavior results in biased correlated random walk movement patterns that reduce the risk of stranding, thus providing jellyfish with an adaptive advantage critical to their survival. Our results emphasize the importance of active swimming in regulating jellyfish movement, and open the way for a more accurate representation in model studies, thus improving the predictability of jellyfish outbreak and dispersion, and contributing to our ability to mitigate their possible impact on coastal infrastructure and populations.

Keywords: Jellyfish movement, directional swimming, surface gravity waves, Lagrangian analysis, drone-based remote sensing

Main text

The outbreak of jellyfish exerts a profound influence on marine and coastal environments worldwide, impacting ecosystem structure and functioning, biogeochemical cycles, and human well being [1–5]. Despite their broad impact, our understanding and ability to predict the jellyfish outbreak and subsequent dispersion, are characterized by a high level of uncertainty. A major source of this uncertainty is lack of sufficient knowledge on the nature of jellyfish movement. Although there are evidences that jellyfish may actively affect their position [6–9], the role of active swimming in controlling jellyfish movement, and the environmental cues triggering and directing it, are not clear. Consequently, jellyfish are often regarded as passively-drifting or randomly-moving organisms, both conceptually [2, 10] and in environmental studies [11–13].

A natural framework to study jellyfish movement is rooted in the movement ecology paradigm, which attributes the temporal change in the position of an organism to four basic components, namely motion capacity, navigation capacity, internal state and external factors [14, 15]. For the case of jellyfish, the motion capacity has been thoroughly addressed in a large number of laboratory experiments and numerical models, providing a mechanistic understanding of jellyfish swimming abilities, energetics, modes of swimming, turning mechanics, and the unique flow structures that are created [16–18]). Here we look to achieve a fundamental understanding on the nature of jellyfish movement, by unveiling the interrelationships between the three latter components. As a conceptual framework, we center our analysis around the eminent risk of stranding, whose severity is intensified by the fact that jellyfish swarms are predominantly found in proximity to the coastline [19]. We hypothesize that due to the critical need of jellyfish to reduce the risk of stranding, both the internal state (i.e. the intrinsic factors affecting jellyfish motivation to move), and the navigation capacity are linked to external factors associated with the stranding threat, jointly acting to reduce it.

Evidence to the importance of directional movement in reducing jellyfish stranding was provided by [9], who attributed swimming directionality to the strong tidal currents characterizing their study area in the Bay of Biscay. Here we look to elucidate the nature of jellyfish movement in the context of surface currents not being dominated by a coastward component, such that current-oriented swimming would not necessarily reduce the risk of stranding. For that we focus on the Southeastern Mediterranean Sea, where the circulation is characterized by relatively weak tidal currents and strong along-shore currents [20, 21]. Our model organism is the Scyphozoan jellyfish *Rhopilema nomadica*, which forms massive seasonal regional blooms [22, 23].

A useful tool in the study of jellyfish is aerial imaging from airplanes and drones, which provide synoptic non-intrusive observations of large numbers of adjacent individuals [24–28]. Here we expand the common utilization of aerial imaging in jellyfish research, and collect the required information using drone videos, which provide the time-varying perspective necessary for investigating organismal movement.

Drone data were collected in 8 experiments during the summertime jellyfish blooms of the years 2020 - 2022 (Fig. S1). In each experiment, a research vessel was directed to the heart of a spatially-dense jellyfish aggregation that was detected in real-time by an observer on a small aircraft flying simultaneously above. Upon arrival to the experiment site, a series of videos (mean duration $XX \pm sd$) were recorded by a drone hovering at a fixed height, location, and orientation, above the aggregation. The videos were analyzed in a Lagrangian framework, which tracks jellyfish along their trajectories (Fig. 1). At constant intervals along the trajectory of each jellyfish, we obtained the instantaneous swimming orientation (α), defined as the direction to which the head is pointing, based on the observed body positioning (see top insert in Fig. 1).

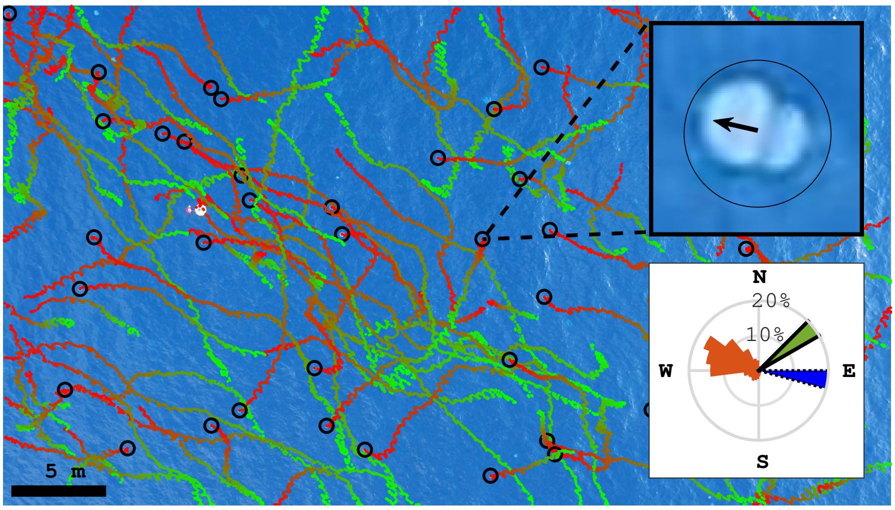

Fig. 1 An exemplary drone-based Lagrangian view on the movement of aggregated jellyfish. The dotted lines show Lagrangian jellyfish trajectories extracted from a 5 minutes video. The trajectories are overlaid on the last frame of the video, with the colors gradually changing from green to red during the trajectory. Black circles indicating locations of jellyfish in that frame. The upper insert shows a blow up of a single frame, focusing on an individual jellyfish, with the black arrow pointing to its swimming orientation, α. Lower insert shows the distribution of α for all instances measured in this video (2589 instances of 117 jellyfish in total, orange), and mean direction of surface gravity waves (blue, dotted edge) and currents (green, solid edge). The video was taken at 7:45 AM on July 6, 2020 (Fig. S1)

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A key behavioral trait in aquatic locomotion is directional movement, defined as the tendency of an individual to move along a straight path [29, 30].The observed jellyfish maintained a constant swimming orientation, with the standard deviation (SD) of α along individual trajectories being, on average, $26.8 \pm 18.5°$ (Fig. 2A). Consistently, out of the 4240 jellyfish examined, 4143 ($> 97\%$) exhibited statistically significant directional swimming (Rayleigh's test $p < 0.05$ [31]).

Expanding the analysis, we tested swimming directionality at the scale of the jellyfish aggregation. For each video we calculated the mean swimming orientation ($\overline{\alpha}$) and found that the individual instantaneous orientations deviated from it by only $\pm 62°$ (shaded area in Fig. 2B). In agreement with that, aggregated jellyfish were found to collectively orient their swimming in the same direction (Rayleigh's test $p < 0.001$). Notably, in all cases $\overline{\alpha}$ had a strong westward component, with a mean azimuth of $262 \pm 44.7°$, (north defined as 0° and clockwise is the positive direction; Fig. 2C). In our study area, this westward orientation coincides with swimming away from the general direction of the coast (Fig. S1).

The directional nature of the swimming behavior indicates the use of an external cue [32]. Consistently with the hypothesized importance of stranding avoidance in modulating jellyfish movement, jellyfish swimming was distinctly oriented opposite to the direction of surface gravity waves, which in coastal areas provide a reliable indicator to the general direction of the shoreline [33], with $\overline{\alpha}$ differing from the direction of short-waves and long-waves by $174 \pm 83°$ and $155 \pm 50°$, respectively (Fig. 2C and Table 1). Moreover, a statistical analysis revealed that $\overline{\alpha}$ was significantly negatively correlated with the direction of long and short surface gravity waves ($p < 0.001$; circular-circular correlation; Table 1).

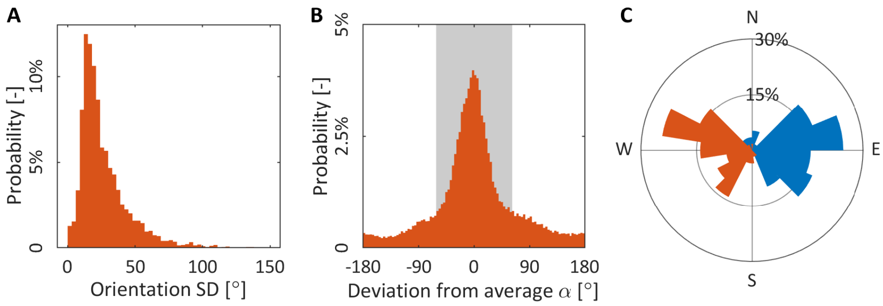

Fig. 2 Characteristics of the jellyfish swimming behavior. (A) The standard deviation of α along the trajectories of 4,240 jellyfish. The median standard deviation of α is 21°, which indicates that jellyfish maintained relatively straight paths; (B) The deviation of α from $\overline{\alpha}$ in all 90,429 instances of measurement (4,240 jellyfish), with the shaded area showing the standard deviation. The narrow distribution indicated that aggregated jellyfish tend to swim in the same direction; (C) Mean direction of short surface gravity waves (blue) and $\overline{\alpha}$ (orange) in each of the 57 movies examined.

Further investigation of the linkage between the different components of jellyfish movement was done through numerical modeling of the jellyfish swimming behavior. We first reconstructed the observed jellyfish movement trajectories (e.g. Fig. 1). Jellyfish swimming speeds (v_{js}) were taken from previous analysis of the drone

Table 1 Circular statistics between $\overline{\alpha}$ and possible environmental cues

	ρ	$P-value$	Difference in direction[1]	N	Source
Short surface waves	-0.658	$p < 0.001$	$174 \pm 83°$	57	Drone video
Long surface waves	-0.6731	$p < 0.001$	$155 \pm 50°$	53	Reference to model - Aviv
Surface currents	0.1363	$p < 0.25$	$115 \pm 77°$	57	Drone video
Sun azimuth	0.4146	$p < 0.01$	$61 \pm 38°$	53	Reference - Dror
Magnetic field delenation	0.4755	$p < 0.025$	$103 \pm 40°$	53	Reference - Dror

[1]Absolute values

data used here, showing that *R. Nomadica* in the region swim at a mean velocity $0.1 \pm 0.03ms^{-1}$ Tal et al.. The simulated jellyfish trajectories exhibited distinct Biased Correlated Random Walk (BCRW, [34]) movement patterns. To optimize the BCRW parameters we employed a genetic algorithm, which yielded an angular diffusivity of $0.02s^{-1}$, a preferred angle of 287.4° and an average reorientation time to the preferred angle (B) of $32.2°s$. When subject to constant velocity current conditions, the simulated Lagrangian particle tracking produced trajectories similar to the drone-captured jellyfish trajectories (Fig. 3a).

To test the importance of directional swimming in reducing stranding risk, we compare the latter, defined here as the percentage of jellyfish whose net propagation is towards coats, for varying levels of directionality (manifested by changes in B, going from $0s$ for fully directional swimming away from the coast, to $200s$ for simple random walk behavior)(Fig. 3b). The comparison is performed for coastward current speeds that are half, similar and double the mean v_{js}, which are representative of the summertime surface currents in measured in the region (Fig. S **??**). For the case of v_{js} equal to v_{cc}, the percentage of stranded jellyfish is 40% when the swimming is fully directional (i.e. $B \rightarrow 0s$), and reaches 100% when B approaches $150s$. For the case of $\frac{v_{js}}{v_{cc}} = 0.5$, the percentage of stranded jellyfish goes from 7% when the swimming is fully directional to 88% when B increases to 200s. In the extreme case when v_{cc} is very high compared with v_{js} ($v_{cc} = 2v_{js}$), the directionality becomes negligible for jellyfish survival, as the jellyfish swimming is too slow to counteract the flow (90% stranding when $B \rightarrow 0s$).

The westward (i.e. away from the coast) counter-wave swimming, and its role in reducing the risk of stranding, manifest a distinct relationship between the internal state and external forcing components of jellyfish movement. The opposite directionality and significant negative correlation between the wave and swimming directions suggests that interrelationship also exists with the navigation capacity component, such that the jellyfish orient their swimming by perception of the surface gravity waves. This hypothesis is supported by the fact that in coastal areas, where jellyfish aggregations are commonly found [19], the direction of surface waves is most often indicative to the direction of the coastline [33], making the applicability of a wave-perception mechanism for swimming away from the coast a universal feature. This is in contrast to other environmental cues that were previously found to be associated with jellyfish swimming directionality, such as the magnetic field [35], sun position [7], and current

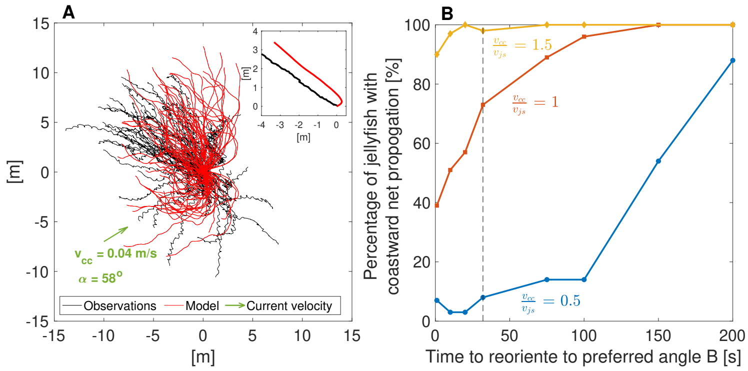

Fig. 3 Numerical simulation of jellyfish swimming behavior and its impact on stranding. (A) Comparison between observed (blacked) and modeled (red) jellyfish trajectories, for July 6, 2020. The model was run for $100s$ under a constant current, v_{cc}, of $0.04ms^{-1}$ at an azimuth of $58°$ (indicated by the green arrow in the lower left corner). The upper right insert displays the trajectories of center-of-mass of the observed (black) modeled (red) aggregated jellyfish. (B) Percentage of jellyfish with net coastward propgation under varying model-parameters B and $\frac{v_{cc}}{v_{js}}$. Increase in B manifest decrease in swimming directionality, with $B \to 0$ representing fully directional swimming away from the coast, and $200s$ represents simple random walk behavior). Vertical line marks the value of B found here.

direction [9], which require a-priori knowledge on the relative location of the coastline. In agreement with that, in our observations $\overline{\alpha}$ was found to be less correlated with the sun azimuth and magnetic field inclination, and not significantly correlated with surface currents (circular-circular correlation $p > 0.2$) (Table 1). In addition, as was recently shown for the case of oil pollution transport [36], the actual process of beaching is driven by waves that, via stokes drift, produce the only mechanism for substantial cross-shore flows. Therefor, efficient avoidance of stranding requires counteracting the effect of waves, rather than that of the currents, which can only bring the jellyfish to the vicinity of the shoreline.

Evidences for animals orienting their swimming against surface waves are limited to a small number of animals [33, 37–40]. A wave-induced directional perception mechanism was identified in sea turtles, who were found to detect the wave direction from the sequence of accelerations occurring within wave orbits below the water surface [41]. In jellyfish, while such sensory mechanism has not been identified, counter-wave orientation was suggested as a possible explanation to observed correlation between the direction of jellyfish swimming and that of surface wind [6]. As for the observations reported here, this explanation is supported by the fact that in the context of moving fluids, it is likely that any mechanoreceptor sensitive to fluid motion would not be sensitive to constant unidirectional flow, but rather to time-dependent components of the flow field. These may include shear flows, local turbulence, and orbital currents produced by surface waves [42, 43], as suggested here.

Providing a unique Lagrangian viewpoint on multiple adjacent jellyfish, our drone-based observations bring new insights on jellyfish swimming behavior, and resulted movement, in their natural environment. Focusing on aggregations of *R. Nomadica*, we found that individual jellyfish consistently maintained constant swimming direction, oriented against the surface gravity waves and away the shoreline. This behavior translates into synchronized directional swimming of the aggregation as a whole, which reduces the eminent risk of stranding, and provides jellyfish with an adaptive advantage critical to their survival. In addition to shedding light on jellyfish swimming behavior and its importance, our results open the way for a more accurate representation of jellyfish movement in model studies, improving our ability to understand and predict dynamical, ecological, biogeochemical and societal aspects of jellyfish outbreak.

Supplementary information. Supplementary files are found at the end of the document

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Declarations

- Funding
- Conflict of interest/Competing interests (check journal-specific guidelines for which heading to use)
- Ethics approval
- Consent to participate
- Consent for publication
- Availability of data and materials
- Code availability
- Authors' contributions

References

[1] Purcell, J. E., Uye, S.-i. & Lo, W.-T. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series* **350**, 153–174 (2007).

[2] Richardson, A. J., Bakun, A., Hays, G. C. & Gibbons, M. J. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in ecology & evolution* **24**, 312–322 (2009).

[3] Condon, R. H. *et al.* Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. *Proceedings of the National Academy of Sciences* **108**, 10225–10230 (2011).

[4] Hays, G. C., Doyle, T. K. & Houghton, J. D. A paradigm shift in the trophic importance of jellyfish? *Trends in ecology & evolution* **33**, 874–884 (2018).

[5] Wright, R. M., Le Quéré, C., Buitenhuis, E., Pitois, S. & Gibbons, M. J. Role of jellyfish in the plankton ecosystem revealed using a global ocean biogeochemical model. *Biogeosciences* **18**, 1291–1320 (2021).

[6] Shanks, A. L. & Graham, W. M. Orientated swimming in the jellyfish stomolopus meleagris l. agassiz (scyphozoan: Rhizostomida). *Journal of Experimental Marine Biology and Ecology* **108**, 159–169 (1987).

[7] Hamner, W., Hamner, P. & Strand, S. Sun-compass migration by aurelia aurita (scyphozoa): population retention and reproduction in saanich inlet, british columbia. *Marine Biology* **119**, 347–356 (1994).

[8] Graham, W. M., Pagès, F. & Hamner, W. M. *A physical context for gelatinous zooplankton aggregations: a review*, 199–212 (Springer, 2001).

[9] Fossette, S. *et al.* Current-oriented swimming by jellyfish and its role in bloom maintenance. *Current Biology* **25**, 342–347 (2015).

[10] Chapman, J. W. *et al.* Animal orientation strategies for movement in flows. *Current Biology* **21**, R861–R870 (2011).

[11] Moon, J.-H., Pang, I.-C., Yang, J.-Y. & Yoon, W. D. Behavior of the giant jellyfish nemopilema nomurai in the east china sea and east/japan sea during the summer of 2005: A numerical model approach using a particle-tracking experiment. *Journal of Marine Systems* **80**, 101–114 (2010).

[12] Vodopivec, M., Peliz, Á. J. & Malej, A. Offshore marine constructions as propagators of moon jellyfish dispersal. *Environmental Research Letters* **12**, 084003 (2017).

[13] Edelist, D. *et al.* Tracking jellyfish swarm origins using a combined oceanographic-genetic-citizen science approach. *Frontiers in Marine Science* 486 (2022).

[14] Nathan, R. *et al.* A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences* **105**, 19052–19059 (2008).

[15] Allen, R. M., Metaxas, A. & Snelgrove, P. V. Applying movement ecology to marine animals with complex life cycles. *Annual Review of Marine Science* **10**, 19–42 (2018).

[16] Costello, J. H., Colin, S. P. & Dabiri, J. O. Medusan morphospace: phylogenetic constraints, biomechanical solutions, and ecological consequences. *Invertebrate Biology* **127**, 265–290 (2008).

[17] Gemmell, B. J. *et al.* Passive energy recapture in jellyfish contributes to propulsive advantage over other metazoans. *Proceedings of the National Academy of Sciences*

110, 17904–17909 (2013).

[18] Costello, J. H. *et al.* The hydrodynamics of jellyfish swimming. *Annual Review of Marine Science* **13**, 375–396 (2021).

[19] Lilley, M. *et al.* Global patterns of epipelagic gelatinous zooplankton biomass. *Marine Biology* **158**, 2429–2436 (2011).

[20] Ferrarin, C., Bellafiore, D., Sannino, G., Bajo, M. & Umgiesser, G. Tidal dynamics in the inter-connected mediterranean, marmara, black and azov seas. *Progress in Oceanography* **161**, 102–115 (2018).

[21] Solodoch, A. *et al.* Basin scale to submesoscale variability of the east-mediterranean sea upper circulation. *Journal of Physical Oceanography* (2023).

[22] Galil, B., Spanier, E. & Ferguson, W. The scyphomedusae of the mediterranean coast of israel, including two lessepsian migrants new to the mediterranean. *Zoologische mededelingen* **64**, 95–105 (1990).

[23] Edelist, D. *et al.* Phenological shift in swarming patterns of rhopilema nomadica in the eastern mediterranean sea. *Journal of Plankton Research* **42**, 211–219 (2020).

[24] Magome, S. *et al.* Jellyfish patch formation investigated by aerial photography and drifter experiment. *Journal of Oceanography* **63**, 761–773 (2007).

[25] Kim, H. *et al.* *Development of a uav-type jellyfish monitoring system using deep learning*, 495–497 (IEEE, 2015).

[26] Schaub, J. *et al.* Using unmanned aerial vehicles (uavs) to measure jellyfish aggregations. *Marine Ecology Progress Series* **591**, 29–36 (2018).

[27] Hamel, H., Lhoumeau, S., Wahlberg, M. & Javidpour, J. Using drones to measure jellyfish density in shallow estuaries. *Journal of Marine Science and Engineering* **9**, 659 (2021).

[28] Raoult, V. *et al.* Operational protocols for the use of drones in marine animal research. *Drones* **4**, 64 (2020).

[29] Cheung, A., Zhang, S., Stricker, C. & Srinivasan, M. V. Animal navigation: the difficulty of moving in a straight line. *Biological cybernetics* **97**, 47–61 (2007).

[30] Berenshtein, I. *et al.* Evidence for a consistent use of external cues by marine fish larvae for orientation. *Communications biology* **5**, 1307 (2022).

[31] Batschelet, E. Circular statistics in biology. *ACADEMIC PRESS, 111 FIFTH AVE., NEW YORK, NY 10003, 1981, 388* (1981).

[32] Dusenbery, D. B. Sensory ecology: how organisms acquire and respond to information. *(No Title)* (1992).

[33] Lohmann, K. J., Lohmann, C. M. & Endres, C. S. The sensory ecology of ocean navigation. *Journal of Experimental Biology* **211**, 1719–1728 (2008).

[34] Codling, E. A., Plank, M. J. & Benhamou, S. Random walk models in biology. *Journal of the Royal society interface* **5**, 813–834 (2008).

[35] Cresci, A. *et al.* Glass eels (anguilla anguilla) have a magnetic compass linked to the tidal cycle. *Science advances* **3**, e1602007 (2017).

[36] Weisberg, R. H., Lianyuan, Z. & Liu, Y. On the movement of deepwater horizon oil to northern gulf beaches. *Ocean Modelling* **111**, 81–97 (2017).

[37] Nishimoto, R. T. & Herrnkind, W. F. Directional orientation in blue crabs, callinectes sapidusrathbun: Escape responses and influence of wave direction. *Journal of Experimental Marine Biology and Ecology* **33**, 93–112 (1978).

[38] Rudloe, A. E. & Herrnkind, W. F. Orientation by horseshoe crabs, limulus polyphemus, in a wave tank. *Marine & Freshwater Behaviour & Phy* **7**, 199–211 (1980).

[39] Hamilton, P. & Russell, B. Field experiments on the sense organs and directional cues involved in offshore-oriented swimming by aplysia brasiliana rang (mollusca: Gastropoda). *Journal of Experimental Marine Biology and Ecology* **56**, 123–143 (1981).

[40] Wang, J. H., Jackson, J. K. & Lohmann, K. J. Perception of wave surge motion by hatchling sea turtles. *Journal of Experimental Marine Biology and Ecology* **229**, 177–186 (1998).

[41] Lohmann, K. J., Swartz, A. W. & Lohmann, C. M. Perception of ocean wave direction by sea turtles. *Journal of Experimental Biology* **198**, 1079–1085 (1995).

[42] Arkett, S., Mackie, G. & Meech, R. Hair cell mechanoreception in the jellyfish aglantha digitale. *Journal of experimental biology* **135**, 329–342 (1988).

[43] Watson, G. M. & Hessinger, D. A. Cnidocyte mechanoreceptors are tuned to the movements of swimming prey by chemoreceptors. *Science* **243**, 1589–1591 (1989).