Counter-wave jellyfish swimming

The scyphozoan *Rhopilema nomadica* actively swims away from the coast in a synchronized directional manner

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Abstract

Having a profound influence on marine and coastal environments worldwide, jelly-
fish hold significant scientific, economic, and public interest. The predictability
of outbreaks 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 jelly-
fish 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 surface grav-
ity waves. Taking a Lagrangian viewpoint from drone videos that allows tracking
of multiple adjacent jellyfish and focusing on the scyphozoan *Rhopilema nomadica* as a model
organism, we show that the behavior of individual jellyfish translates into
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 move-
ment, and open the way for a more accurate representation in model studies, thus
improving the predictability of jellyfish outbreaks and their dispersion, and contribut-
ing 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

Jellyfish outbreaks exert a profound influence on marine and coastal envi-
ronments worldwide, impacting ecosystem structure and functioning, biogeochemical
cycles, and human well-being [1-5]. Despite their broad impact, our understanding
and ability to predict jellyfish outbreaks and their subsequent dispersion, are charac-
terized 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 is evidence
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 ecol-
ogy 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]. In the case of jellyfish, motion capacity has been
thoroughly addressed in a large number of laboratory experiments and numerical mod-
els, providing a mechanistic understanding of jellyfish swimming abilities, energetics,
modes of swimming, turning mechanics, and the unique flow structures that are cre-
ated [16-18]. Here we strive to achieve a fundamental understanding on the nature of
jellyfish movement, by unveiling the interrelationships between the three last com-
ponents. 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 pre-
dominantly found in proximity to the coastline [19]. We hypothesize that due to the
critical need of jellyfish to reduce the risk of stranding, both their internal state (i.e.,
the intrinsic factors affecting the motivation of jellyfish to move) and navigation capac-
ity are linked to external factors associated with the threat of stranding, jointly acting
to reduce this threat.

Evidence in regard to the importance of directional movement in reducing jellyfish strand-
ing was provided by Fossette et al. [9], who attributed swimming directionality to the strong tidal
currents characterizing their study area in the Bay of Biscay. Here we elu-
cidate the nature of jellyfish movement in the context of surface currents that are not
dominated by a coastward component, such that current-oriented swimming wouldnot necessarily reduce the risk of stranding. We focus on the southeastern
Mediterranean Sea, where circulation is characterized by relatively weak tidal cur-
rents and strong along-shore currents [20, 21]. Our model organism is the scyphozoan
*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 provides synoptic non-intrusive observations of large numbers of adjacent indi-
viduals [24-28]. 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 eight experiments during summertime jellyfish blooms
in 2020–2022 (Fig. SI). 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 ± sd* ) was recorded by a drone
hovering at a fixed height, location, and orientation above the aggregation. The videos
were analyzed in a Lagrangian framework, which tracked jellyfish along their trajectories
(Fig. 1). At constant intervals along the trajectory of each jellyfish, we obtained the
instantaneous swimming orientation (a), defined as the direction in which the head was
pointing, based on the observed body positioning (see top insert in Fig. 1).



**Fig. 1 An exemplary drone-based Lagrangian view of the movement of aggregated
jellyfish.** The dotted lines show Lagrangian jellyfish trajectories extracted from a 5-minute 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 indicate locations of jellyfish in that frame. The
upper insert shows an enlargement of a single frame, focusing on an individual jellyfish, with a black arrow
indicating swimming orientation, *a.* Lower insert shows the distribution of *a* 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. SI).

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 an average standard deviation
(SD) of *a* along individual trajectories of 26.8 ± 18.5° (Fig. 2A).Out of the 4240 jellyfish examined, 4143 (> 97%) consistently 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
*(a)* and found that the individual instantaneous orientations deviated from it by only
±62° (shaded area in Fig. 2B). In agreement with this, aggregated jellyfish were found
to collectively orient their swimming in the same direction (Rayleigh’s test *p* < 0.001).
Notably, in all cases, *a* had a strong westward component, with a mean azimuth of
262 ± 44.7° (north defined as 0° and clockwise is the positive direction; Fig. 2C).
In our study area, this westward orientation coincided with swimming away from the
general direction of the coast (Fig. SI).

The directional nature of the swimming behavior indicates the use of an external
cue [32]. Consistent 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 *a* differing from the direction of
short waves and long waves by 174 ± 83° and 155 ± 50°, respectively (Fig. 2C and
Table 1). Moreover, a statistical analysis revealed that *a* 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 jellyfish swimming behavior.** (A) The standard deviation of *a*along the trajectories of 4,240 jellyfish. The median standard deviation of *a* is 21°, which indicates
that jellyfish maintained relatively straight paths. (B) The deviation of *a* from *a* in all 90,429 instances
of measurement (4,240 jellyfish), with the shaded area showing 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 *a* (orange) in each of the 57 movies examined.

Further investigation of the linkage between the different components of jellyfish
movement was conducted through numerical modeling of jellyfish swimming behav-
ior. We first reconstructed the observed jellyfish movement trajectories (e.g. Fig. 1).
Jellyfish swimming speeds *(vjs)* were taken from a previous analysis of the drone

**Table 1** Circular statistics between *a* and possible environmental cues

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | *P* | *P — value* | Difference in direction1 | *N* | Source |
| Short surface waves | -0.658 | *P‘* | < 0.001 | 174 ± 83° | 57 | Drone video |
| Long surface waves | -0.6731 | *p<* | < 0.001 | 155 ± 50° | 53 | Reference to model - Aviv |
| Surface currents | 0.1363 | *P'* | < 0.25 | 115 ±77° | 57 | Drone video |
| Sun azimuth | 0.4146 | *p<* | < 0.01 | 61 ± 38° | 53 | Reference - Dror |
| Magnetic field declination | 0.4755 | *p<* | < 0.025 | 103 ± 40° | 53 | Reference - Dror |

1 Absolute values

data used here, showing that *R. nomadica* in the region swim at a mean velocity of
0.1±0.03 ms-1 (Tai 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
0.02 s-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 simu-
lated 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
compared the latter, defined here as the percentage of jellyfish whose net propagation
was towards the coast, for varying levels of directionality (manifested by changes in *B,*going from 0 s for fully directional swimming away from the coast, to 200 s for simple
random-walk behavior) (Fig. 3b). The comparison was performed for coastward current
speeds that were half, similar and double the mean *Vjs,* which were representative of the
summertime surface currents measured in the region (Fig. S ??). For the case of *Vjs*equal to the percentage of stranded jellyfish, it was 40% when the swimming was fully
directional (i.e., *B* —> 0 s), and it reached 100% when *B* approached 150 s. For the case of

- 0.5, the percentage of stranded jellyfish went from 7% when swimming was
fully directional to 88% when *B* increased to 200 s. In the extreme case when *vcc* was very
high compared with *Vjs (ycc* — 2vJS), the directionality became negligible for jellyfish
survival, as jellyfish swimming was too slow to counteract the flow (90% stranding
when *B* —> 0 s).

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 direction-
ality and significant negative correlation between the wave and swimming directions
suggest that an 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 aggregar
tions are commonly found [19], the direction of surface waves most often indicates
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 (black) and modeled (red) jellyfish trajectories, for July 6, 2020.
The model was run for 100 s under a constant current, *vcc,* of 0.04 ms-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) and modeled (red) aggregated jellyfish. (B) Percentage of jellyfish with net
coastward propagation under varying model parameters, *B* (an increase in *B* manifests a decrease in
*Vja*

in swimming directionality, with *B* —> 0 representing fully directional swimming away from the coast,
and 200 s 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 coast-
line. In agreement with this, in our observations, *a* 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 in 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. Therefore, efficient avoidance of stranding requires coun-
teracting the effect of waves, rather than that of the currents, which can only transport
the jellyfish to the vicinity of the shoreline.

Evidence for animals orienting their swimming against surface waves is limited
to a small number of animals [33, 37-40]. A wave-induced directional perception mech-
anism was identified in sea turtles, who were found to detect wave direction from
the sequence of accelerations occurring within wave orbits below the water surface

1. . In jellyfish, while such a sensory mechanism has not been identified, counter-wave
orientation was suggested as a possible explanation to the observed correlation between
the direction of jellyfish swimming and that of surface wind [6]. As for the observa
tions 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 compo-
nents of the flow field. These may include shear flows, local turbulence, and orbital
currents produced by surface waves [42, 43], as suggested here.

By providing a unique Lagrangian viewpoint on multiple adjacent jellyfish, our drone-
based observations provide new insights on jellyfish swimming behavior and their resulting
movements in their natural environment. By focusing on aggregations of *R. nomadica,*we found that individual jellyfish consistently maintained a constant swimming direc-
tion oriented against surface gravity waves and away from 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 advan-
tage 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 representa
tion of jellyfish movement in model studies, thereby improving our ability to understand and
predict dynamical, ecological, biogeochemical and societal aspects of jellyfish outbreaks.

**Supplementary information.** Supplementary files are found at the end of the
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* Funding
* Conflict of interest/Competing interests (check journal-specific guidelines for which
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* Ethics approval
* Consent to participate
* Consent for publication
* Availability of data and materials
* Code availability
* Authors’ contributions

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