21/09/2021

Dear editor,

We thank you for the opportunity to revise manuscript ID PONE-D-21-06875 entitled "Driving the blue fleet: Temporal variability and drivers behind bluebottle *Physalia physalis* beachings off Sydney, Australia" which was submitted for consideration for publication in PLOS ONE.

We thank the reviewers for their thoughtful suggestions to our study. We have addressed our responses to the reviewers' comments below and identified where changes have been made in the revised manuscript using track changes and here with green text. We hope that the study is now suitable for publication. It would be an honour to be published in PLOS ONE.

Yours sincerely,

Natacha Bourg and co-authors

REVIEWER 1:

Comments on:
"Driving the blue fleet: Temporal variability and drivers behind bluebottle Physalia
physalis beachings off Sydney, Australia."

Abstract

Reviewer comment: The usage of "Jellyfish-like colonial organism" is not required since the formal
definition of Jellyfish encompasses the order Siphonophorae.
Author response: We have changed to "are colonial siphonophores that live at the surface of the
ocean" (Line 1 of Abstract).

The are other datasets of Physalia strandings covering comparable temporal coverage, so the use of
the words "unprecedented dataset".
We did not come across such a daily presence / absence dataset for 4 years (please provide the
reference) but "unprecedented" was removed.

Classical presence/absence related with the higher sampling effort in summer?, in abstract must
include the avoidance to this factor.
The two sites focused on in this study (Maroubra and Coogee) have the same sampling rate (daily)
for presence / absence (lifeguard observations) in summer and throughout the year.

Introduction

Line 7: Reference #2 must be updated since the provided reference link to the pre-print version, but
now the work from Munro et al., can be found here (https://doi.org/10.1038/s41598-019-51842-1).
Thank you, the reference has been updated line 7.

Line 8: A reference must be given to this statement.
References have been added line 9 regarding the predatory behaviours and diet of *P. physalis*.
Specifically, Purcell (1984) and Munro et al. (2019) have been added.

Line 12: The cited reference (Prieto et al., 2015) doesn't account for any Fatal encounter with *P.
physalis*. The proper citation must be given.
We have added proper citation: Burnett et al (1989) line 13.

Line 20: You must provided already available (and listed in your reference list) information dealing
with spatio-temporal distribution and drivers of massive stranding, for this species in other places.
Line 20-21: There isn't such a gap of information. Proper references must be given (see work from
Pontin et al., Canepa, et al, etc). You can refine the knowledge to some specific location and/or
analytical process; but the meaning of a gap isn't what we have today.
We have completely re-written and organised the introduction, including a paragraph on the spatio-
temporal context and previous studies. We had missed the study from Canepa et al. (2020) and are
grateful for the mention of this great study. The new paragraph read (Lines 40-71):

"Previous studies have linked P. physalis beach stranding to environmental conditions and model
their arrival to the coast, but have usually focused on unusual events (e.g. swarms). Ferrer and
Pastor (2017); Prieto et al. (2015) studied massive beaching events that occurred in summer 2010

off the Basque coast (Spain) and the Mediterranean Basin using lagrangian particle tracking. Ferrer and Pastor (2017) proposed that offshore origin of these beached P. physalis was strongly dependent on the wind parametrisation used in the lagrangian tracking model. They therefore concluded these beaches P. physalis, were likely to have originated from the northern part of the North Atlantic Subtropical Gyre, thousands of kilometers away. They proposed wind as a dominant driver of P. physalis transport both off and on the coast. Prieto et al. (2015) suggested that the massive arrival of P. physalis to the coast had been strongly influenced by zonal winds. Since then, massive beachings of P. physalis off the coast of Ireland in autumn 2016 (August and October) prompted further research (Headlam, 2020) to identify source populations of P. physalis. Results suggested that the population of P. physalis may have originated from the North Atlantic Current, supporting the findings of Ferrer and Pastor (2017). Using sting reports from five summers across eight locations in New Zealand, Pontin et al. (2009) developed a neural network-based model to simulate the arrival of P. physalis towards the shore while assessing the contribution of large-scale winds and waves. They show that wave direction far from the shore can transport swarms to the studied region, while wind direction and speed one day before sting reports, in cells close to the shore strongly influence the strandings of P. physalis. A more recent and similar study by Pontin et al. (2011) extended the analysis to different regions all around New-Zealand. They validate results found by Pontin et al. (2009) that both wind and wave influence the occurrence of P. Physalis strandings, while highlighting that different oceanographic regimes driving the beachings occur in different study areas. Unlike previous studies, a recent survey from Canepa et al. (2020) recorded nearly continuous strandings of P. Physalisin Chile for three years, with the highest densities in the winter seasons two years in a row. These massive events coincided with an El Niño Southern Oscillation (ENSO) perturbation, with warmer ocean temperature conditions, and positive zonal wind anomalies (westerlies) transporting P. physalis to the coast, further highlighting wind as the major driver of P. physalis movements and variability
"

Line 28-30: You use a moon's phase effect over monthly aggregation of a box jellyfish which is totally different from a "pleustonic drifter" as *Physalia physalis* is. Beside this, you don't provide any reference and/or data that supports this statement. Please modify.
Thank you for this comment. However, the moon phase has been suggested to be relevant for *P. physalis* in Hawaii. Even so, we have removed all analyses and mentions to the moon cycle in the manuscript since we observed no association.

Line 30-31: You suggest a physiologic response of *P. physalis* to the moon cycle, based in one statement which hasn't any support. Remove this phrase.
The sentence has been removed.

Line 69: The Basque coast as cited in the proposed reference ("individuals of this species arrived at the Basque coast (southeastern Bay of Biscay)") refers to Spain and not France.
Our apologies, this has been rectified, line 42, and now reads:
"Prieto et al., 2015 and Ferrer and Pastor, 2017 studied massive beaching events that occurred in summer 2010 off the Basque coast (Spain) and the Mediterranean Basin using lagrangian particle tracking."

Line 88: The reference here (Pontin et al.) must have the number 14 and not the number 21. Beside this, there is another report from the same author which is much conclusive and required to be incorporated into the document (refer to this: https://doi.org/10.1016/j.ecolmodel.2011.03.002).
Thank you for this information, we have updated these references as suggested see line 61.

Methods

Fig. 1: The satellite image isn't clear enough where comes from. A dashed square highlighting the area (or something similar) will be required.
Thank you, the image has been modified to illustrate this (see image below).
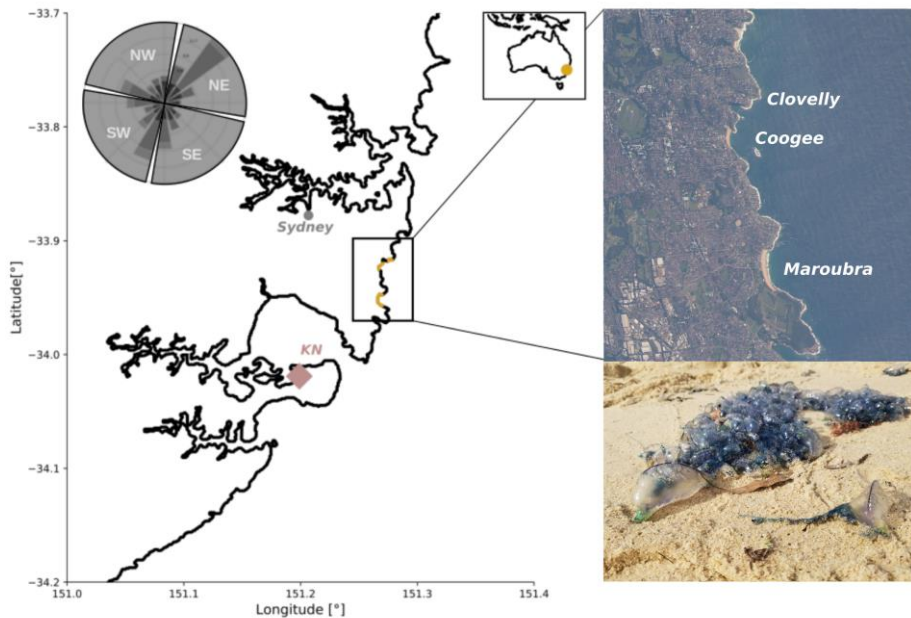
Line 137-138: Provide the statistical summary of the no-correlation between number of sting and beach-goers' statement.
Nothing is said about how author's will analyze the effects of environmental variables over the stranded data. A full section of Data Analysis is highly recommended, since this step is crucial in the development of the objectives.
Thank you for highlighting this, there is now a full section with the heading Statistical Analyses in the revised manuscript (lines 162-180) where a new statistical analysis is presented, and the methods are described in detail.

Results

Line 193 and general: When highlighting comparisons about the number and/or percentage the statistical result must be given.
The Results section has almost been entirely re-written including new statistical analyses. Please see details below.

Line 196: There is no enough evidence along the section to infer a collective death in winter, since some colonies can be washed offshore by the change in wind conditions. Also the life span of colonies is highly unknown.
This statement has been modified, and now reads (lines 202-206):
"Interestingly, there are still instances of winter beaching for Coogee and Maroubra, up to 10% of annual sightings in Coogee. This suggests that despite the seasonal cycle to their strandings, *P. physalis* survive wintertime and cold temperatures and can still be advected to the coast."

Drivers of beaching events

Line 202-203: No formal statistical approach is given to give support to that statement.
Line 204: Just for the wave height condition the usage of the Pearson's correlation coefficient is showed but considering the literature that authors have read, they should know that a direct correlation coefficient isn't enough to explain complex spatio-temporal process.
Line 210-225: The association between environmental variables and stranded jellyfish are analyzed individually and mostly based on visual inspection of the environmental and biological process, without the usage of proper statistical approaches.
The revised manuscript now includes a whole new set of statistical analysis. We have added lagged correlations, and results from Generalized Estimating Equations (GEE) models for the two all-yearlong beaching sites, and different timescales (daily and weekly), that support our previous findings. Please see Data & Methods (lines 163-180) and Results (lines 220 and lines 252).

Seasonality of environmental variables

Line 230: There is no prove to sustain that statement
In the new GEE analysis, we investigate a possible relationship between the different environmental variables and beaching events, supporting the statistical relationship between zonal (I.e., cross-shore) wind and beaching events, see Section Results lines 270-278 and Table 2.

Line 308: Put a comma after "Interestingly"
Done, line 315.

Discussion

Lines 319-321: You cannot sustain this statement "Our results demonstrate a strong relationship between this spatio-temporal variability and wind direction at the daily timescale", since you haven't provided an analytical framework where statistical-based conclusions have arise. This requires much more than image (visual) inspection.
We agree with the reviewer, and hope that the new statistical analysis mentioned above will convince them.

Lines 323-325: You have not inspect the proportion of left/right-handed stranded *Physalia physalis* colonies in your study; so you cannot conclude a direct effect from the wind, avoiding local surface currents in complex coastal areas as you have signaled.
The reviewer is right, this was only a supposition which needs to be tested when the relevant observations are available. This is what we meant by "It is possible that" at the beginning of the sentence.

Conclusion
In general conclusions must be re-written after the proper analytical method have been given and executed.
The whole manuscript has been re-written including a better organized introduction, new analytical methods and results, which provide additional support to our conclusion.

REVIEWER 2:

SOME COMMENTS ABOUT THE PAPER:
After reading the article, I write down some recommendations and some thoughts that could help the authors to tweak some comments made throughout the article.

We are thankful for the constructive comments which helped to improve the manuscript. Please find details below.

The authors use some apostrophes in grammatical structures where their use at the scientific article level may not be necessary or these structures can be rewritten. It is recommended to review its use with a native speaker, such as in:

…*P.physalis*'s morphology
…*P. physalis*'s course

Updated to *P. physalis*, thanks.

Line 67:
"For validation, these models were compared to massive beaching events that occurred in summer 2010 off the Basque coast (France) and the Mediterranean Basin."
The Basque coast is in Spain, in the autonomous community of the Basque Country. This community ends at the border between Spain and France. In the summer of 2010, the presence of *Physalia* occurred at several beaches along the coast. But on some important beaches, such as La Concha Beach (in the city of Donostia-San Sebastián), small fishing boats were transformed into cleaning boats and left the beach area to meet the Portuguese man-of-war and collect them before their arrival along the beach.

Our apologies, this has been rectified (line 43). Thanks for sharing the background for this event, it is nice to see that this was a shared effort between different communities.

Line 194:
"The few number of sightings in winter as well as P. physalis supposed lifecycle could be explained by a collective death in winter."
For me, a low or no number of winter sightings in the coastal area does not mean that there are a large number of deaths in the open sea. It is to be expected that there are always Portuguese man-of-war of different ages drifting for months in the great oceanic gyres (using the wind as main driver) with a peak of reproduction that could occur at the end of summer-beginning of autumn. On the European coast of the North Atlantic Ocean, it is typical that during the winter (not only in the months of summer) there is also a notable presence of small *Physalia* (3-5 cm long float, 3-4 months old) that due to the very strong southerly winds of successive storms (favourable to dragging towards the Bay of Biscay) have caused the appearance of *Physalia* on the coast to be anticipated. Therefore, the highest mortality possibly occurs when these organisms reach the dry beach, where they no longer leave and end up dying. These organisms do not appear to die from the severe winter conditions, at least in the North Atlantic Ocean. These conditions can make it possible for them to reach the coast at a time other than summer. It is for this reason that it is important to monitor the beaches outside of the time that the beaches are patrolled and during the lifetime of the organisms.

We have removed this statement and thank the reviewer for the additional examples. We have also observed *P. physalis* in winter, but much less than in summer, even during favourable wind conditions. We are planning a survey of *P. physalis* ' size to investigate the link between size and seasonality in the area, all year-round. We would be interested in following up this comment directly if possible.

Line 348:
"[11] similarly suggest that wind is a dominant driver of P. physalis transport, but propose wind to be more relevant offshore and ocean circulation becoming the main driver in nearshore areas."

[11] suggests that the wind is the most relevant mechanism both off and on the coast for this peculiar organism. The very superficial ocean circulation (considering this as the one that exists in the first 5 centimetres of the water column, where *Physalia* lives) in the great gyres of ocean circulation is greatly influenced by the wind, as shown by very low-weight drift buoys floating on the surface. The data of these buoys shows that the surface ocean circulation is far from following the Ekman theory (that is, generating a surface current at 45 degrees from the wind). It is for this reason that possibly the best solution to explain the drift of *Physalia* is to use the wind, because also the wind is the generator of local waves and the circulation at the upper centimetres of the water column.

We have removed the sentence and agree with the reviewer, as mentioned in the Discussion: "It is important to highlight that the wind is a major contributor to the ageostrophic component of the surface current (influencing circulation and generating local waves) and stokes drift and wind-induced currents are known to be highly relevant in regard to the transport of passive tracers, especially in the first centimeters of the ocean. Then, this relationship between beaching events and cross-shore wind can be explained by the wind drag on P. physalis outside of water, but also by the action of wind-induced current on its transport". (Lines 357-363)

Line 358:
"In addition, there was a high frequency of beaching events in spring recorded during weeks that were dominated by south-westerly winds, as can be observed during September and May in Fig 5. This result is surprising since beachings would not be expected when wind is coming from land, if wind were the only driving variable."

To study the arrival of these organisms, it would be necessary to analyse not only the winds of the days prior to arrival, but also the evolution of winds throughout the life of these organisms, which could be from a few months to a year (more or less), depending on the size of the organism. Prevailing southwesterly winds could probably bring many *Physalia* located in the open sea below Australia. And winds from the northeast, east or southeast (in the days prior to arrival), even if they were of short duration, could cause these organisms to end up in the study beaches. Therefore, it is highly recommended to analyse the annual evolution of the wind in a very large area (several degrees in longitude and latitude) around the study area. Surely these organisms have been able to travel more than 10,000 kilometres on their journey to reach the beach.

We agree that the environmental conditions during *P. physalis* journey will determinate its trajectory, including how likely it will be close to the coast. However, to reach and strand on the beach, we show that the last 24 hours are key. While the long-term large-scale drivers are definitely of interest, we would need to know where *P. physalis* comes from and how long it has been floating in the ocean, which is still largely unknown. This will be the topic of further investigation in the future.

Line 371:
"Observations of ocean currents closer to the surface and of higher resolution (e.g. coastal High-Frequency RADAR) may be necessary to expose any dependence of beaching events on these variables."

The fundamental problem with using high-frequency radar observations to explain caravel drifts is that they provide information on currents at 1-3 meters above the surface. This information is quite different from that existing in the same ocean-atmosphere interface, that is, in the first centimeters

of the water column. So to speak, the Portuguese caravel is a very light balloon (a caravel of 10 centimeters of float can weigh around 25 grams) that has tentacles that act as an anchor so that it does not fly. So it seems unlikely that trying to explain their drift with currents below 5-10 centimeters from the sea surface will not do much.

The reviewer is right, the significant vertical shear at the surface makes HF radars not optimal. We have removed this statement.

EDITOR :

Thank you for submitting your manuscript to PLOS ONE. After careful consideration, we feel that it has merit but does not fully meet PLOS ONE's publication criteria as it currently stands. Therefore, we invite you to submit a revised version of the manuscript
that addresses the points raised during the review process.
Before this ms can be published, substantial changes need to be implemented to augment the analyses and strengthen the main lessons of the paper.
We thank the editor for their time and effort to provide additional comments which helped us improving the manuscript. We hope that the editor will agree that the revised manuscript provides the statistical evidence to support our conclusion. We also made substantial changes to the writing and organization of the manuscript.

The introduction needs to be streamlined. For instance, the second paragraph (lines 17 to 46) is very lengthy and could be split into smaller focused sections.   The next two paragraphs (lines 47 to 94) could also be streamlined, and some of the material could be moved to the discussion, where it would be placed in context of the project's findings.
The Introduction as well as most other sections of the manuscript have been re-written, taking into consideration all comments.

As stated by one reviewer, the authors have not performed the proper statistical analysis to sustain their conclusions. Even though several papers dealing with the analytical approach required to understand environmental forcing are cited, the authors have only used person correlations in their analysis. The authors have to improve this section (by including a whole Data Analysis section in the methods) and undertake a more comprehensive analysis of the data at hand.to determine the influence of these factors (and potentially their interactions) on the beachings (and the summer stings). The current piece-meal approach, where a single variable is considered at a time need to be augmented and strengthened.
New analyses are proposed in the revised manuscript. We chose to use a Generalised Estimating Equations (GEE) model, taking into account multiple explanatory variables and using the daily beaching dataset as the response. We used an autoregressive AR(1) structure for the GEE model to consider strong auto-correlations in the daily time-series. The data at the two sites which have observations all year-round were considered, not the site which is only patrolled in summer. See Data & Methods (lines 163-180) and Results (lines 220 and lines 252).

To facilitate the understanding of the patterns, I would also suggest focusing on the two sites with year-long data and removing the third site (rocky shore with only summer-time data).   Limiting the analysis to the two sites with year-long data (Clovelly and Maroubra) provides a more comprehensive and comparable perspective. The ms already explains that this site is inherently different: "Note that Coogee has a small rocky outcrop (known as the Wedding Cake Island) 740 m from the beach, which limits wave action on the beach. Clovelly beach is more South-oriented and is at the end of a narrow bay, hence more protected than the two other beaches (Fig 1)."
There is a misunderstanding between Coogee and Clovelly here. Coogee and Maroubra cover all seasons and were the focus of statistical analysis. Still, we mostly use Maroubra as it seems to be the most "neutral" (fewer missing data, largest beach with a quite neutral orientation, no island located in front of the beach). Clovelly data, which is patrolled only in summer, is only shown when focusing on summer.

Additionally, the Physalia physalis datasets need to be analyzed in a more quantitative fashion. In particular, I would suggest the following analyses:

* Number of beachings:
Compare the number of beaching observations versus the number of survey days from a beach to beach. There are 38 and 132 beaching reports for Clovelly and Maroubra respectively, even though the two beaches were surveyed on 94% and 93% of the days. Is this difference significant? Is there an overall higher beaching rate in Maroubra? Despite the data gaps, I would suggest you perform a cross-correlation to quantify how well the beachings data at the two beaches cross-correlate with each other.

We have added the information in the manuscript. It now read lines 192-195: "Simultaneous beaching in Maroubra and Coogee occurs only 10-20% of the beaching days, and the correlation between the timeseries of beaching presence at the daily timescale is r = 0.1, increasing to r = 0.3 when considering the weekly number of beachings."

* Number of stings:
I would suggest focusing this analysis on the same two beaches used in the beachings analysis, and discarding the data from Coogee. Despite the data gaps, I would suggest you perform a cross-correlation to quantify how well the beachings data at the two beaches cross-correlate with each other.
You state that "More than 10 stings have been reported 6, 9 and 10% of all patrolled days for Clovelly, Coogee and Maroubra".
Why did you not consider days where less than 10 stings have been recorded? You could use values above and below this threshold as two separate categories (low and high), or you could take the log10-transform of the data.
How was this threshold number selected? Seems like anomalous events should be determined on a beach-basis, not using the same threshold across all beaches. I would suggest you provide a data summary of the number of stings reported per day, and then attempt to model these distributions to figure out "outlier days" for each beach.

* Number of beachings VS Number of stings:
It would be very useful to investigate whether these two datasets are correlated. Using the summer-period only, when stings are reported, can you perform a correlation for each beach, to see if there are more stings on days with more beachings. This would be a very informative analysis.

We have now included more information on the comparison between beaching and stings (lines 118-122): "Comparing the beaching and sting datasets for matching days and locations (although different authors), only 7.9 %, 15.8%, and 32.3% of the stings corresponded to a day when beaching was also at Clovelly, Coogee, and Maroubra, respectively. The daily match between these two datasets needs more investigation (see Discussion) and longer time-series."
The threshold of 10 stings have been chosen to remove outliers, since we suspect that the lifeguards do not report the presence of *P. physalis* when they only see one specimen. We have performed a sensitivity study to this threshold, but the correspondence does not change much.

For your interest, the two figures below provide additional details, including the beach attendance, and the ratio between stings/beach attendance (size of the symbols). The association between stings and beach attendance might exist in Coogee, but is not clear in Maroubra. Furthermore, even days with high numbers of stings do not necessarily correspond to a beaching observation (see the colours).
We discuss the potential reasons for the discrepancy between stings and beaching in the manuscript, but this will need further investigation (lines 373-375):
"Differences between the two datasets could be explained by the difference in the timing of the reports but also by the nature of the reports (stings happen in the water, while beachings are reported only when *P. physalis* are stranded on the shore)."
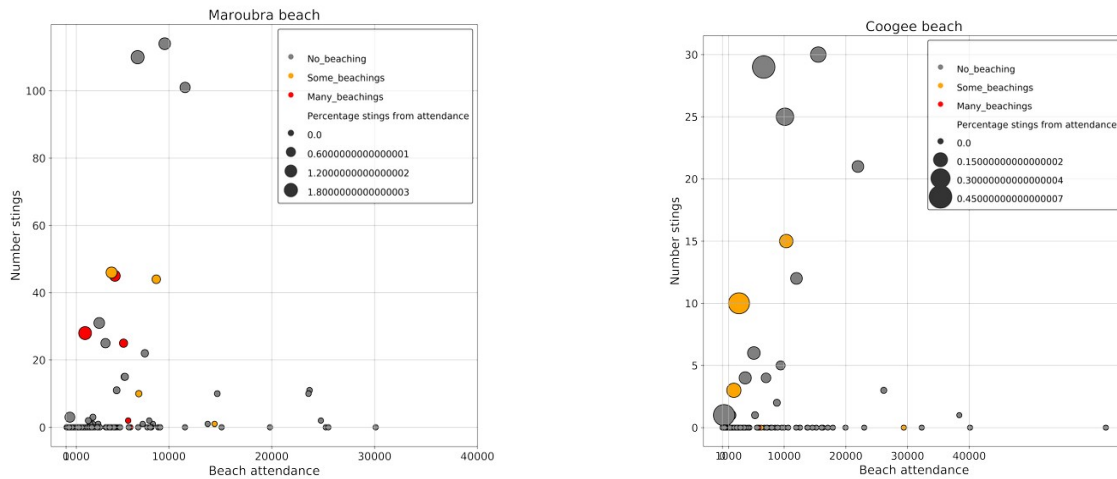
Figure caption: Scatter plot showing beach attendance against number of stings, with the colours displaying wether the beaching was reported by lifesavers or not for the same day. The size of the markers show the percentage of stings compared to the beach attendance.

* Wind Data:
Can you please define the wind sectors and provide some summaries of wind speed / direction for the different seasons? The ms currently states "predominant winds in this area are north-easterly, westerly and southerly, as shown on the windrose in Fig 1."
The analyses of beachings per wind direction also need to involve statistical tests, using either chi-square tests or logistic regressions. Reporting mere proportions is not enough. You need to provide a sense of the variability (SD for the proportions) and the associated p values.
Instead of a logistic regression, we included a GEE model (see comment above), which takes into account the variability of the wind. We also refer to Wood et al (2016) which details the monthly mean and variance of the same wind dataset (see line 144).

* Ocean Currents:
Can you please report how well the near-surface and the integrated currents correlate with each other? And report how well they match the wind speeds?   Currently, the ms states: "Here, we used daily averages at the shallowest bins (11 m and 12 m, respectively) and the depth integrated flow".
Unfortunately, the shallowest surface current estimates we have in the region are at 11m and 12m, which we expect to be less wind-driven than the top few centimeters of the ocean.
For your information, the figure below shows the correlation matrix the zonal (u) and meridional (v) components of the 11m-depth and depth-averaged currents, and the wind velocity. It shows that depth-integrated ocean currents are strongly correlated to the wind, but less so for the 11m depth current.
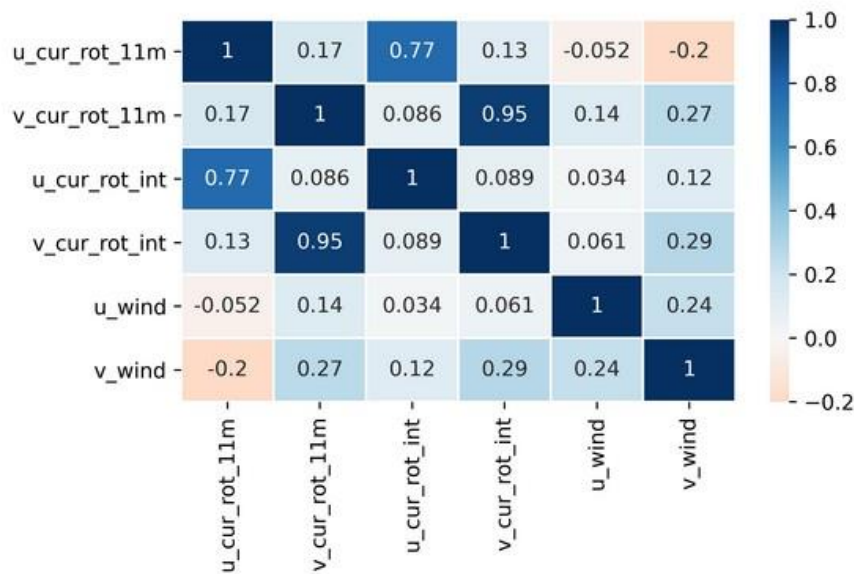
* Seasonality:
The proportion of beachings needs to be statistically related to the different seasons. This could be done with a chi-square test or using a logistic regression model, with the response variable of presence / absence of beachings. The latter approach would be better, because it would allow you to assess the influence of other variables at once, including inter-annual variability. Currently, the ms merely reports the %s of summer / winter days with beachings, and a metric of variability (SD for the proportions) is needed Moreover, these proportions need to be compared statistically, using p values and measures of effect size (like the odds ratio).

The variability of beaching is shown in Figure 6, as a shading around the weekly means.
The inter-annual variability of the presence/absence of beaching is included in the GEE model as the response variable, and the p-values reported take into account the auto-correlation of the time-series. See comments above.

* Lags and Multiple Temporal Scales:
While the paper mentions a "zero" lag and provides results at daily and weekly time scales, it is unclear how many lags were tested and how the weekly data were averaged and analyzed. I would suggest you provide a summary table, showing what analyses were done, listing the lags that were attempted and the different temporal scales that were considered.

Thank you for the remark, we have added Figure 3 in the manuscript to show correlations at different lags, supporting the choice of investigating the wind with a 24h lag.
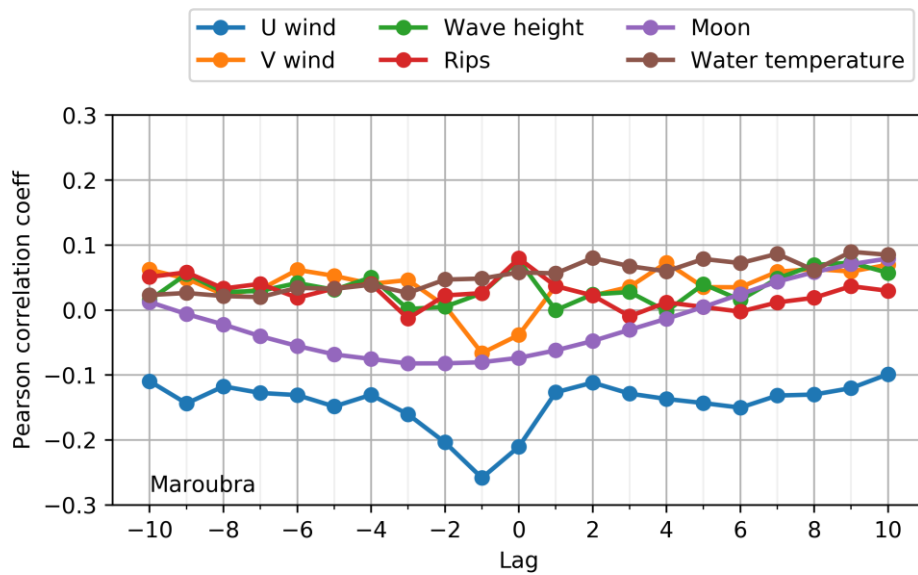
* Multi-variate Analyses:
These environmental factors are likely cross-correlated: wind speed / direction, currents, water temperature. I would ask the authors to explore these cross-correlations and to provide a supplementary table where these results are summarized. If there are significant cross-correlations, I would urge the authors to use partial correlations to explore the influence of the drivers, after accounting for other cross-correlated variables.
New analyses answer to this as GEE is multivariate.

Moreover, it would be useful to know whether these environmental drivers differed seasonally and from year-to-year (within seasons). This would provide the readers with a broader oceanographic background of the study area and the potential drivers.
We have not considered inter-annual variability in this study since four years is a relatively short time-scale. We have however shown how ocean temperature, wind speed, and cross-shore winds vary with seasons in Figure 6. For broader background, we refer to Wood et al. (2016), in particular their Figure 5 which shows how winds and currents in the region vary month to month.

Finally, I would also suggest you summarize the weather (wind / current) and water temperature conditions measured during periods of unusually high and unusually low beaching (and stringing) periods. This would provide a complementary perspective to the previous modeling approach, which would give readers a more in-depth understanding of the drivers of unusual "events".
We agree that understanding unusual events is of great interest. This is discussed in the discussion in a whole paragraph, lines 377-394.
Unfortunately, we do not have the right observational dataset to investigate properly the influence of these parameters, hence cannot provide more than an educated guess for these events.