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RESEARCH ARTICLE

Understanding the influence of swarming timing on the dispersal of *Ostrea edulis* larvae in the Northern Adriatic Sea

[version 1; peer review: 1 approved with reservations, 1 not approved]

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Abstract

Background

Ostrea edulis, the European Oyster, is a key habitat engineering species, considered "functionally extinct" in much of its native range, however the presence of population patches, large enough to allow the recruitment of juveniles, is likely, at least in the Northern Adriatic Sea. In order to decide which areas to protect or enhance with substratum suitable for settlement, it is necessary to understand larval dispersal dynamics. The main research question was to understand how the settlement areas depends on the timing of swarming and on larvae emission location.

Methods

Larval dispersal modelling tools already exist, and for the purpose of this study the use of an open-source phyton model code 'Opendrift', parametrised for *O. edulis* larvae with specific parameters related to growth and speed of vertical movement, based on existing literature data. Necessary forcing functions (currents, temperature) were taken from Copernicus, and gridded bathymetry data was downloaded from GEBCO repository.

Results

The results of this preliminary model-based study showed that the settling areas depend on the timing of the emission periods, given that different emissions can lead to different time spent as plankton maturing to settlement, therefore potentially reaching further. Initial seeding location can also matter, due to differences in currents that

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could be encountered.

Conclusions

Some experimental validation should follow this modelling approach, including genetic analyses to verify sources, this setup using an open data and an open access existing modelling framework to predict larval settlement is promising in enabling the upscaling and application for restoration and conservation purposes in other areas.

Keywords
European Oysters, Lagrangian modelling, Larval dispersal



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Introduction

Ostrea edulis, the European Oyster, is a key habitat engineering species native to the northeast Atlantic, which could be found from Norway to Morocco, as well as in the Mediterranean and Black Seas (Bromley *et al.*, 2016). However, overfishing and diseases led to a generalized collapse of its population in Europe, to such an extent that it is listed as a threatened/declining species in The Convention for the Protection of the Marine Environment of the North-East Atlantic (the OSPAR Convention) (OSPAR, 2009). The presence and abundance of *O. edulis* in the Mediterranean region is less investigated; historical mapping, based on literature, is currently underway (NORA Europe historical working group) and some data on presence are available for download from the OBIS (Ocean Biodiversity Information System) mapper portal. Concerning the northern Adriatic population, most data are from trawling surveys of the early 1990s (OGS & ISPRA, 2017). Since then, no systematic study aimed at characterizing its presence and abundance, has been undertaken. The presence of population patches, large enough to allow the recruitment of juveniles, is highly likely, as reported by a recent field study (Burioli *et al.*, 2015), by anecdotal evidence (Munari, 2021, Personal Communication) and by the first author (Bertolini) personal observations, who identified *O. edulis* juveniles along the coast of Caorle, Pellestrina and in the Venice Lagoon in the summers of 2022 and 2023.

As is well known in patchy habitats, connectivity plays a major role in population and metapopulation dynamics (Carson *et al.*, 2011; White *et al.*, 2019), however it is not the only factor, as mismatches can occur (Marshall *et al.*, 2010; Staudinger *et al.*, 2019). In this regard, the role of transport processes in connecting *O. edulis* potential larvae sources with settlement sites in the northern Adriatic is still largely unexplored. On the Italian side of the Adriatic, the presence of adult specimen was detected in coastal areas near Trieste, and on the pilings of offshore platforms (Gabellini & Lamberti, 2016; Manoukian *et al.*, 2010; Natura 2000 network in Emilia-Romagna), as well as on bioconstructions ("Tegnùe", Ponti, 2001) and, anecdotally, on wrecks at depths of 18 m.

O. edulis is a swarming species and larvae can cover large distances (Willis *et al.*, 2019). The duration of the larval phase depends largely on water temperature, which affects larvae growth rate (Robert *et al.*, 1988; Rodriguez-Perez, 2019), provided that enough food is available to avoid starvation that would hamper growth ability (Labarta *et al.*, 1999; Millar & Scott, 1967; Robert *et al.*, 1988). Female release $0.1–1.5 \times 10^6$ larvae, with the number being related to the size and condition (Cole, 1941; Jacobs *et al.*, 2020). The amount of larvae found in the water column seems also to be connected to water temperature, specifically to 'degree days' however analysis of data from 1935 to 2011 in the Netherlands showed the peak in number of larvae (70–3,000 L^{-1}) to range between 300 and 1,300 degree days resulting in a time period of around 60 days (Maathuis *et al.*, 2020). Furthermore the actual life cycle could be more complex as two primary emissions were observed in the Adriatic (May and September, Burioli *et al.*, 2015) and during a field experiment in the Venice Lagoon, females ready to release mature eggs ("black sick") were observed from April to December. Given these potential time lags, the main research question was to understand how the settlement areas depends on the timing of swarming and on larvae emission location.

Methods

Ostrea larval dispersal was simulated using the open access software package *Opendrift* (version 1.7.1), which implements a particle tracking algorithm for Lagrangian dispersion using phyton (version 3.9.7) libraries (Dagestad *et al.*, 2018). *Opendrift* includes the '*LarvalFish*' module, which was designed to simulate the dispersion of cod eggs and, after hatching, larvae dispersion (Vikebø *et al.*, 2007). The open-source code was modified as *Ostrea edulis* releases larvae, as eggs hatch within the mantle. The updated code is included as *Extended data* (Bertolini, 2023b). The initial larval size was chosen in accordance with the literature, 0.170 mm (Rico-Villa *et al.*, 2010; Rodriguez-Perez, 2019). Their growth rate and vertical swimming speed were modelled using the allometric equations and the polynomial function given in Table 1, second column. The parameters were estimated based on the data presented in Rodriguez-Perez (2019): plots showing the best-fitting curves are shown in Figure 1.

The forcing functions, *i.e.*, current, salinity and water temperature, were downloaded from the CMEMS global ocean 1/12° physics analysis (x and y water velocities, sea water salinity; 6 hours, https://doi.org/10.48670/moi-00016) and from CMEMS Mediterranean sea physical analysis (temperature, ocean mixed layer thickness, hourly means, https://doi.org/10.25423/CMCC/MEDSEA_ANALYSIS_FORECAST_PHY_006_013_EAS4) for the year 2022 (1 April to 31 December) *via* Copernicus '*my ocean viewer*', using map selection with coordinates spanning (lon: 12.00 to 14.00; lat: 44.00 to 46.00) and all vertical levels. Bathymetry with a 5 arc-second interval grid resolution was downloaded from GEBCO (gebco.net) and transformed the negative values to positives and to allow the recognition as an *Opendrift* bathymetry 'reader'.

Simulations set-ups

O. edulis larvae were released from two areas, which were determined based on the following criteria: i) presence of shipwrecks (http://www.datiopen.it/it/opendata/Mappa_dei_relitti_in_Italia) and ii) presence of the species based on the map of presence/absence of the species available on EMODNET (https://emodnet.ec.europa.eu/geonetwork/srv/eng/catalog.search#/metadata/8e1a8ccc37da27c53c3d2db6bdd5a1efe39db8ea, most of the references for the Northern Adriatic refer to surveys conducted in the early 1990s).

The resulting areas were Wreck 1: 45° 17' 24" N, 12° 59' 24" E ; Wreck 2: 45° 16' 48" N, 12° 34' 48" E. The seeding was set to occur on a radius of 50 m around each wreck to allow for uncertainties in the exact position and seeding was set at 20 cm above seabed (assuming they would be on the wreck, and from observations of adults on raised substrates).

Table 1. Species specific parameters required, equations used and values of coefficients and data source references.

Parameter	Equation	Coefficients	Reference
Growth Rate (%)	$a*e^{b*Tw}$	a=0.475 b=0.149	Data from Rodriguez-Perez (2019)
Growth (µm days^{-1})	$e^{(-a*\ 1/(Tw+273.15)\ +\ b}$.	a=-8354.9 b=30.7	Data from Rodriguez-Perez (2019)
Development time (days)	a / growth	a=110 uM	Data from Rodriguez-Perez (2019)
Length (mm)	L= a * log (W) + b	a= 0.0541 b= 0.6154	Data from Helm & Bourne (2004)
Speed of vertical movement (mm/sec)	Swim speed = $a*L + b*T_w + c*L*T_w + d$	a=0.07 b=0.00009 c= 0.0006 d= 0.0017	Data from Rodriguez-Perez (2019)

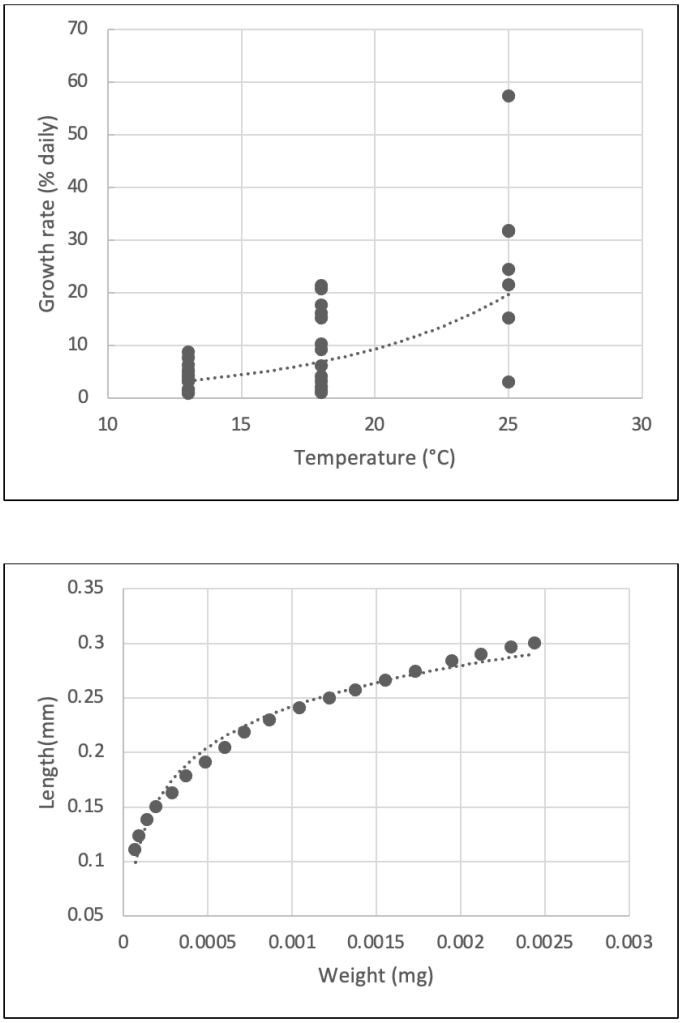

Figure 1. Growth rate and temperature (top) weight and length relationships (bottom) used for model parametrisation.

Since *Opendrift* simulations can be set to last according to time (duration in time, number of calculation steps or final date), larvae were set to retire (reach settlement status) according the development time (the time needed to go from planktonic to settlement stage), which according to Rodriguez-Perez *et al.* (2021) and other previous research (Cole & Jones, 1939; Davis & Calabrese, 1969; Robert *et al.*, 2017), is dependent upon temperature. In this case development time was used as 'expiry date' of the larvae, using it to set the simulation duration in time, and was calculated based on the median water column temperatures at the wreck site, assuming they would be representative of those that a larva would encounter. Simulations were done throughout the period April–December 2022, which was divided in fortnightly periods when simulations were set to end according to the different development times. Within each fortnightly period, 100 larvae were emitted daily at 18:00. Table 2 reports the median temperatures and development times (calculated using the equation in Table 1), for each larval seeding fortnight: these ranged from nearly one month in early spring to approximately one week in the warmest part of summer. Temperatures that were actually encountered by the larvae were quantified a posteriori based on actual trajectories.

Statistical analysis

R (version 4.3) was used to open the .nc output files using '*ncdf4*' (version 1.21) and create plots using '*gtools*' (version 3.94). The code is available as *Extended data* (Bertolini, 2023b).

Results

Table 3 (Bertolini, 2023a) shows the actual temperatures encountered in the trajectories of the larvae and the depths of such trajectories.

In terms of likely settlement areas, as evident from both wrecks, it is highly variable between the different seeding fortnights. Some differences can also be observed in terms of initial seeding locations: while seeding from Wreck 1 larvae go in every direction if the whole reproductive season is cumulated (Figure 2), when seeding from Wreck 2 they do not go to the NE to SE quadrant (Figure 3). This is also evident from the depths (Table 3), where larvae from Wreck 2 tend to occupy also shallower zones in all periods, whereas larvae from Wreck 1 in some fortnight only stays deeper (>10 meters). Generally, however, in both cases the larvae with a longer development time (cooler months, *e.g.*, April and May, November and December) have the potential to settle further away.

Discussion

The results of this preliminary model-based study showed that the settling areas depend on the timing of the emission periods. The spatial distribution of the settling points matches the range of historical distribution from OBIS and observations of spat found in Caorle in summer of 2022 and shallow area of Pellestrina in the summer of 2023 (pers. Obs). Predictions of the settling areas of larvae sourced by Wreck 2 also suggest settlement inside the Venice lagoon, through the Chioggia inlet. Settlement of *O. edulis* was and is recorded on the inlets and the areas facing the inlets (Pellizzato, 1984 and Bertolini personal observation from summer 2022).

Shifts in spawning phenology may be a consequence of climate change (Dijkstra *et al.*, 2011; Thomas & Bacher, 2018), which could, in turn, have consequences for the larvae dispersion. In this area, currents show a marked seasonal pattern, with NAd Gyre (anti-clockwise) being present in autumn (Artegiani *et al.*, 1997). Therefore, the extension of the emission time window leads to a larger dispersion area, which, in turn, favours the genetic mix within the whole northern Adriatic.

The temperature dependence of swarming appears to be dependent by locations. Bromley *et al.* (2016) reports that the onset of spawning of *Ostrea edulis* occurs above > 15°C throughout its range with higher temperatures at the northern end of the range (Norway, Denmark) and lower temperatures (around 12°C), in some part of the Atlantic in the NE of Spain and in the Adriatic. Therefore, even if in our study at the beginning of April median temperatures at the wreck sites in the northern Adriatic were around 11°C it may still be possible that swarming occurred. In this study median temperatures were used for the seeding area and temperatures were not specific to each trajectory, with development time being fixed for each fortnight, which is a limitation of using a pre-existing module. Differences between the temperature used to estimate development time were up to 4°C lower compared to the actual temperatures of the trajectory in spring, equivalent to nearly 10 days of difference. In the period July-October the temperatures were more closely matching, however larvae released at Wreck 1 ended up in deeper water, which in the summer months were colder than median water temperatures expected at the original location. Consideration of depths and potential for temperature stratification at the area studied should therefore be added when determining the temperature to be used in calculation of development time, as this could be over- or under-estimated. An alternative would be to create another function in *Opendrift* that would allow stopping the simulation based on final size attained rather than by time, to allow more fine scale estimates based on single trajectories.

It should be pointed that what is modelled in this study is only the potential dispersal area. The longer the larval phase, the higher the mortality rate due to predation, while growth may also be affected by the actual availability of food resources: to this regard, the latitudinal West-East trophic gradient could decrease the probability the larvae released close to the Italian coast could settle on the other side of the Adriatic. Last but not least, the availability of suitable substrate (*e.g.*, presence of hard substrate, conspecific cues, predator cues, biofilm (Kamermans *et al.*, 2018; Potet *et al.*, 2021; Smyth *et al.*, 2020)), can also affect the outcome of the transition from the larval to the sessile stage of the life cycle.

In combination with this modelling approach scaled up to population, an integrated approach that includes sampling for larvae in the water column, checking settlement on

Table 2. **Median and standard deviation temperatures at the two seeding sites, development days required to reach settlement stage (month and days range considered).**

Period (fortnight)	April 1–14	April 15–30	May 1–14	May 15–31	June 1–14	June 15–31	July 1–14	July 15–31	Aug 1–14	Aug 15–31	Sept 1–14	Sept 15–31	Oct 1–14	Oct 15–31	Nov 1–14	Nov 15–31	Dec 1–14
Median Temperature (°C)	10.9±0.5 10.9±0.5	11.9±0.5 11.9±0.4	14.1±1.6 13.7±1.6	16.3±2.4 15.8±2.4	21.3±2.8 20.7±2.7	22.9±2.8 22.6±2.7	25.3±2.6 25.1±2.6	25.7±2.3 25.4±2.3	26.3±1.9 26±1.9	25.8±1.4 25.7±1.4	25.3±1 25±0.9	23.7±1 23.6±0.9	21.6±0.7 21.5±0.5	21±0.7 21±0.4	20.5±0.9 20.4±0.6	17.7±0.9 17.7±0.8	14.7±1.1 15.2±1
Development time (days)	29.65	26.45	22.65	14.4	11.4	9.11	7.335	6.85	6.55	6.75	7	8.2	9.87	10.66	11.17	14.73	18.4

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Table 3. Temperatures (median ± standard deviation) and Depth (max; min)) of the larvae trajectories for the 100 larvae seeded in each fortnight at the two wrecks location (W1: Wreck 1; W2: Wreck 2).

Period (fortnight)	Site	April 1–14	April 15–30	May 1–14	May 15–31	June 1–14	June 15–31	July 1–14	July 15–31	Aug 1–14	Aug 15–31	Sept 1–14	Sept 15–31	Oct 1–14	Oct 15–31	Nov 1–14	Nov 15–31	Dec 1–14
Temperature (°C)	W1 W2	14.6±0.9 14.7±1.3	13.9±1.9 16.3±1.6	16.5±2.2 20.8±1.6	18±2.7 22.2±1.7	15.8±1.1 24.6±1.1	17.9±3.1 24.3±2.3	23.8±2.2 27±0.6	24.9±1.9 27.6±1	27.2±0.5 25.4±1.8	24.6±1.6 27.1±0.7	24.5±0.8 25.5±0.9	22.1±0.6 22.6±0.5	21.±0.2 21.1±0.6	21.4±1.1 21.7±1	18.2±0.7 17.9±1.6	15.8±0.7 14±0.7	13.3±1.7 13.3±1.9
Depth (m);	W1 W2	31; 0.1 24,1;0.1	48.2;0.1 25.1;0.1	47.2,0.1 27.4;0.1	35;0.1 32;0.1	39.9;14 20;0.1	36;0.1 26.1;0.1	35;1.6 33.6;0.1	34.8;0.1 25;0.1	33.9;2 24;0.1	33;15.2 28.5;0.1	29;14.4 25;0.1	27.8;18 27;0.1	28,6;21 26;0.1	30.5;20 27;0.1	30.4;20 24.4;0.1	33;26 33;0.1	33;25 33;1

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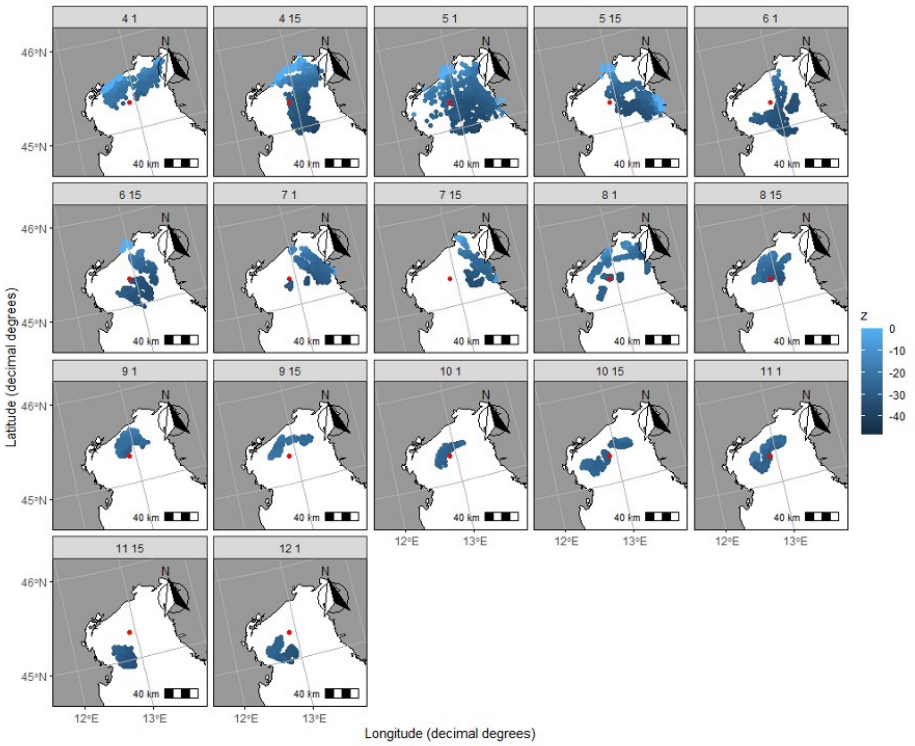

Figure 2. Results from the simulations from Wreck 1. Each facet represents one fortnight (labels: month- day of simulation start). Dots represent potential settling locations and colours represent depth (z).

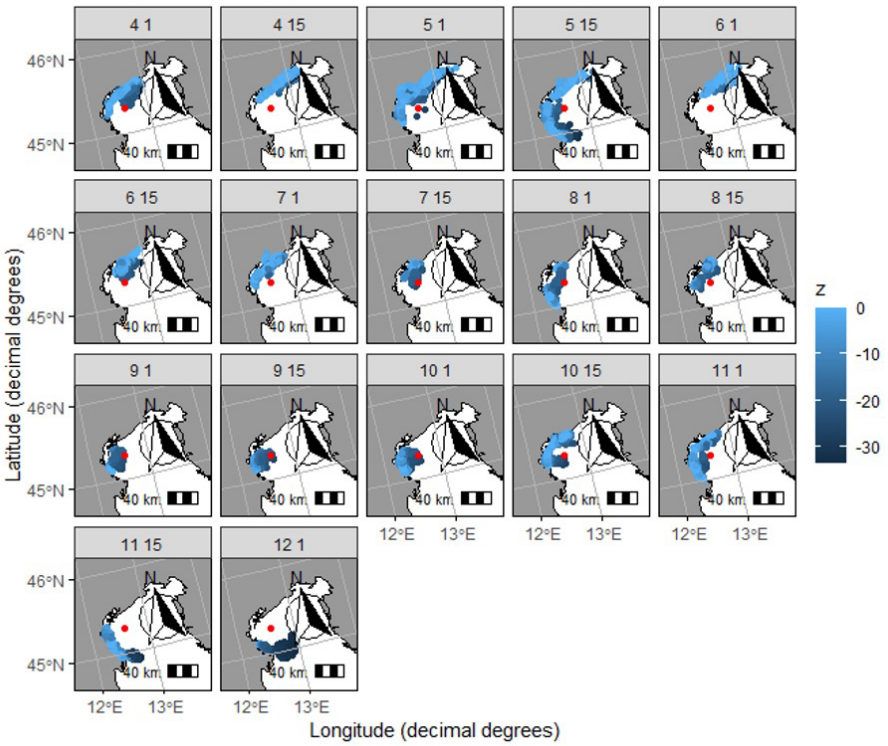

Figure 3. Results from the simulations from Wreck2. Each facet represents one fortnight (labels: month- day of simulation start). Dots represent potential settling locations and colours represent depth (z).

substrates at different times, performing genetic analysis (*e.g.*, paternal reconstruction (Monteiro *et al.*, 2022)) and conducting broad scale surveys of remnant populations in the Adriatic, would be beneficial to better be able to preserve and restore the species–allowing to add suitable substrata in the right places and right time promoting the natural recovery (Kerckhof *et al.*, 2018). While more experimental validation would be necessary, this setup using an open data and an open access existing modelling framework to predict larval settlement is promising and could enable upscaling and application for restoration and conservation purposes in other areas.

Ethics and consent

Ethical approval and consent were not required.

Data availability

Underlying data

Zenodo: Underlying dataset Bertolini and Pastres Understanding the influence of swarming timing on the dispersal of Ostrea edulis larvae in the Northern Adriatic Sea. https://zenodo.org/doi/10.5281/zenodo.10125335 (Bertolini, 2023a).

This project contains the output data files. Other underlying data are from public repositories and links are provided in the text, while the codes developed as part of the study are available at the link in the extended data section.

Data are available under the terms of the Creative Commons Attribution 4.0 International license (CC-BY 4.0).

Extended data

Analysis code available from: https://github.com/camibe90/OstreaOpendrift

Archived analysis code at time of publication: https://zenodo.org/doi/10.5281/zenodo.10149770 (Bertolini, 2023b).

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Publisher Full Text

Open Peer Review

Current Peer Review Status: ? ✗

Version 1

Reviewer Report 11 March 2024

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✗

Ane Pastor Rollan
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The goal of this paper is to understand how the settlement areas of the European Oyster in the Northern Adriatic Sea depend on the timing of swarming and on larvae emission location. This paper does this by using Opendrift software.

The authors have made a nice effort setting up a model for this specific study area. However, there is a lot of information missing in this paper, also shown by its short length. Major flaws in model parameterization, number of larvae, sensitivity analysis needed, wrong terminology used ("statistical analysis") etc. As the authors mention throughout the paper, it is a preliminary model-based study. Therefore, it seems like a preliminary piece of work that could be expanded further in order to produce an impactful and novel paper and story.

I have some concerns regarding the manuscript that I believe need to be addressed before it can be considered for indexing. I have outlined some key points for your consideration:

Introduction:

1. **Missing Major References:** The introduction lacks essential references on connectivity and metapopulations. I suggest including references such as Cowen and Sponaugle (2009[1]) and Cecino and Treml (2021[2]) to provide a more comprehensive background on the topic.

2. **Explanation and Context:** While the paper is easy to read, it lacks sufficient explanation on the role of connectivity and the novelty of this particular study. Providing more context on the value of the study and introducing Opendrift for assessing larval connectivity would enhance the introduction.

3. **Visualization and Citation of Species:** It would be helpful to include a main figure depicting the study area, model boundaries, and the presence of Ostrea edulis for context. Additionally, please refer to the original name and citation of the species as suggested:

(Ostrea edulis L., 1758) (Carlucci *et al.*, 2010[3]).

Methods:

1. **Detailed Model Parameters:** More detailed information on model parameters is needed (e.g., model resolution, number of vertical layers, boundaries). I recommend referring to papers such as Quigley *et al.* (2022[4]), Clavel-Henry *et al.* (2021[5]), and Pastor *et al.* (2023[6]) for proper formulation in this section, they all used Opendrift.

2. **Parameterization Explanation:** Clarify whether multiple parameters were used, if a sensitivity analysis was conducted, or if a single value was chosen for the model parameters mentioned.

3. **Coastal Behaviors and Terminology:** Provide a better explanation of terms such as "larvae were set to retire" and "expiry date of larvae," and discuss the coastal behaviors of Opendrift when larvae reach land boundaries. Incorporating terms like "pelagic larval duration" and "spawning time" would also be beneficial.

4. **Simulation Duration and Number of Larvae:** Explain why only one year was chosen for simulations and why 2022 specifically. Additionally, justify the choice of 100 larvae per day and whether a sensitivity analysis was conducted on this parameter. Please refer to Quigley et al., 2022 for inspiration.

5. **Statistical Analysis Section:** Remove the title "Statistical Analysis" as there was no statistical analysis conducted in the study.

Results and Discussion:

Quantification and Interpretation: The results and discussion sections require more detailed explanations and quantification of results. Consider partitioning the discussion section into subsections for better organization and clarity. Additionally, discuss the impact of the study, its value, and any potential management applications.

The dispersal results need quantification for a more comprehensive understanding. Merely observing dispersal maps may not suffice for drawing conclusions. If the authors aim to assess the extent of dispersal, incorporating probability density functions (PDFs) could be beneficial in this context.

Novelty:

Clear Articulation of Novelty and Significance: Provide a clearer explanation of the novelty of the research and its significance in the introduction. More context on why the study is important would enhance the manuscript.

In conclusion, addressing these issues will significantly improve the quality of your manuscript and its potential contribution to the field. I encourage you to revise the manuscript accordingly. At its present state, I cannot recommend the paper for indexing, but with the necessary revisions, it has the potential to make a valuable contribution to the field.

References

1. Cowen RK, Sponaugle S: Larval dispersal and marine population connectivity.*Ann Rev Mar Sci*. 2009; **1**: 443-66 PubMed Abstract | Publisher Full Text

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4. Quigley C, Roughan M, Chaput R, Jeffs A, et al.: Combined biophysical and genetic modelling approaches reveal new insights into population connectivity of New Zealand green-lipped mussels. *Frontiers in Marine Science*. 2022; **9**. Publisher Full Text
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6. Pastor A, Catalán I, Terrados J, Mourre B, et al.: Connectivity-based approach to guide conservation and restoration of seagrass Posidonia oceanica in the NW Mediterranean. *Biological Conservation*. 2023; **285**. Publisher Full Text

Is the work clearly and accurately presented and does it cite the current literature?
No

Is the study design appropriate and does the work have academic merit?
Yes

Are sufficient details of methods and analysis provided to allow replication by others?
No

If applicable, is the statistical analysis and its interpretation appropriate?
No

Are all the source data underlying the results available to ensure full reproducibility?
Partly

Are the conclusions drawn adequately supported by the results?
No

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: Connectivity, larval dispersal, ecological modelling, network analysis, invertebrates, marine ecology

I confirm that I have read this submission and believe that I have an appropriate level of expertise to state that I do not consider it to be of an acceptable scientific standard, for reasons outlined above.

Reviewer Report 23 February 2024

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?

Tomislav Džoić
Institute of Oceanography and Fisheries, Split, Croatia

The paper is well written, but there are several major objections that would make it a major revision.

I will not answer the above 6 questions individually, but will go through the entire paper and write down all the errors and remarks I have noticed, which, if corrected, will result in all the above questions being answered with yes.

1. Is it necessary for the abstract to be divided into sections? Can it be written in one piece, concise and informative as befits an abstract? I would recommend writing it in one piece.

2. It would be good to make a picture with the locations of the northern Adriatic, the location in the Mediterranean, the Venetian lagoon and all locations important for the topic of this work. This way the reader has to search for locations himself if he is not familiar with the area. It would be good if the bathymetry of this part of the Adriatic could be seen on the map. A sketch of the currents in the northern Adriatic would also be very welcome.

3. Can you clarify the term degree days?

4. Could you write a few more sentences about the dispersion model itself? How does it simulate the spreading, the swimming? A few more details would be nice.

5. Why did you use two oceanographic numerical models with different resolutions? You first used the Operational Mercator Global Ocean Analysis and Forecast System with a resolution of 1/12 degree and then the CMEMS Mediterranean Sea Physical Analysis and Forecast System with a resolution of 1/24 degree. If you are working in the area of the northern Adriatic, it is better to use a model with a more accurate resolution. I see that you used the model resolution of 9 km (1/12) instead of the available 4.5 km. And why?

6. Where was the thickness of the mixed ocean layer used later in the paper, because it is not mentioned anywhere?

7. Python is written with a capital P.

8. Enter the locations of the wrecks on the map as well.

9. As far as Table 1 is concerned, the parameters Tw, L W are not explained anywhere. What do they stand for?

10. In Table 2, the locations w1 and w2 are not labelled, i.e. it is not known which temperature series belongs to which location? The development days were also only calculated for one location, i.e. there are no development times for 2. Or are they very similar? Write this

explanation in the table caption.

11. Redraw figures 2 and 3. Draw them so that they cover the entire page in a 4 x 4 grid. Remove the compass from each figure. It is enough if there is only one. In this old way, the result is barely recognizable. Change the colors on the color bar (let it be a classic color where the differences are easy to see). With these changes, analyzing the result will no longer be so tiring for the eyes.

12. As with the description of Figures 2 and 3, the description of the results of the dispersion simulation can also be better described. In particular, if the spatio-temporal variability of the wind and current regime in this part of the Adriatic at this time of year is taken into account, especially as cold winds (bora) prevail in the colder season, which can also drastically cool the water column.

13. Along with these images, it would be good to draw a map with the monthly averages of the currents at a certain depth (to estimating at which depth the greatest transport took place). This way we would know what drove the particles to the final locations.

14. For future work, it is also better to calculate the particle density (e.g. the number of particles per grid) at the end of the experiment and display it on the map, as this provides a more robust result compared to the particle locations

Is the work clearly and accurately presented and does it cite the current literature?
Yes

Is the study design appropriate and does the work have academic merit?
Yes

Are sufficient details of methods and analysis provided to allow replication by others?
Partly

If applicable, is the statistical analysis and its interpretation appropriate?
Partly

Are all the source data underlying the results available to ensure full reproducibility?
Yes

Are the conclusions drawn adequately supported by the results?
Partly

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: Physical oceanography, Numerical Dispersion, Individual Based Models, Numerical Oceanographic Models

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have

significant reservations, as outlined above.