



Predicting the export of retention-oriented larvae from their natal population using coastal features: a modelling study on the Pacific oyster

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ABSTRACT: Larvae from many marine coastal species deploy ecological strategies that promote their arrival to geographically close or distant populations. Some larvae adjust their vertical positions in response to the tidal cycle, which, in combination with coastal features, helps keep them relatively close to their natal population instead of being advected offshore (retention-oriented larvae). However, a few of these larvae are transported away from their natal population and spread further afield. In this study, we aimed to better understand the environmental mechanisms that influence the export of retention-oriented larvae by modelling the transport of tidal larvae and using a species distribution model to predict that export rate. The larval transport model was parametrised with ecological data about the Pacific oyster *Magallana gigas* and tidal larval behaviour from 2 Irish coastal regions. The simulated dispersal of retention-oriented larvae showed that 55–60% of larvae were exported from the 2 regions. This export rate decreased to below 40% if the release occurred in protected and shallow coastal areas. The exportation of larvae occurred relatively early in a larva's simulated pelagic life (when the larva began to have an active behaviour). When export rate was associated with the coastal features in the 2 Irish regions, wave exposure at the release sites was an important predictor for low (below 20%) and high (above 90%) export rates. The study has implications for the management of coastal grounds since export rates of retention-oriented larvae can be predicted based on knowledge of local hydrodynamics. Our approach could be applied to predict the export rate of other coastal larvae with retention-oriented behaviour.

KEY WORDS: Particle transport modelling · Larval dispersal · Larval transport · Larval export · Coastal habitats · Pacific oyster

1. INTRODUCTION

Analyses of larval dispersal help to underpin our understanding of habitat colonisation, population dynamics and connectivity, and species' life cycle strategies (Cowen & Sponaugle 2009, Wilson et al. 2018). Eggs and larvae are the first stages in the life

cycle of many marine species. These stages are often pelagic drifters within the 3-dimensional (3D) oceanic circulation. For species with little or no motile ability (e.g. many benthic species), drifting in pelagic waters likely improves the spread away from their natal population. Larval dispersal is directly and indirectly conditioned by hydrodynam-

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ics and environmental conditions during the adult reproductive cycle and during pelagic life (Gaine & Lafferty 1995, Shima et al. 2018, Wilson et al. 2018). During their pelagic life, larvae develop an adaptive behaviour and modulate their exposure to oceanographic conditions (e.g. water temperature, main and mesoscale circulation), which results in a diversity of dispersal amplitudes in time and space. Controlling the vertical positioning in the water column is one of the most significant behaviours (Leis 2021). Larvae migrate to favourable depths in response to environmental cues and phenotypic needs such as pressure, light, and feeding activity (e.g. Fobert et al. 2019). For coastal and estuarine species, vertical migration of larvae can be associated with strategies favouring offshore transport or near-shore retention (Satterthwaite et al. 2021), often related to cyclic tidal currents (Knights et al. 2006) or to upwellings (Morgan & Fisher 2010).

Mechanisms of near-shore larval retention are well described in studies focusing on retention-oriented larval behaviour (Sponaugle et al. 2002). These larvae can recruit in their native populations thanks to their retentive behaviour (Cowen et al. 2003, Paris & Cowen 2004) and the synergy of adult reproduction with local conditions. Nonetheless, a few of these retention-oriented larvae are exported away from their natal population and can greatly contribute to their population dynamics (Strathmann et al. 2002). This larval export often explains a species' colonisation at significantly distant and suitable habitats (Mari et al. 2017, Vic et al. 2018) even for larvae of coastal species (Gaines & Bertness 1992, Burgess et al. 2022) and facilitates marine species invasion after the species is introduced to a region (Geburzi & McCarthy 2018). For example, the Pacific oyster *Magallana gigas* (Thunberg, 1793) is one very well-studied invasive species in European waters. The species was introduced for aquaculture but escaped the farm facilities through larval dispersal and established in the coastal ecosystem as wild populations (Lallias et al. 2015). Pacific oyster larvae move deeper in the water column during the ebb tide and thus avoid the offshore currents, which presumably favours their near-shore retention (Hill 1991, Knights et al. 2006). The export of Pacific oyster larvae, despite a retention-oriented behaviour, has been estimated (Robins et al. 2017) and assumed in Irish coastal waters after observing new wild populations at locations without aquaculture facilities (Kochmann 2012, Kochmann et al. 2012).

As much as knowledge of retention processes is an asset, it is also helpful to know about the factors driv-

ing the transport of larvae with retention-oriented behaviour away from their natal sources. Knowledge of factors driving larval export can be beneficial for spatial conservation management. Specifically, understanding the invasion processes and monitoring the establishment of marine invasive species in coastal waters are features claimed by international conventions and directives (e.g. Convention on Biological Diversity 2014, Tsiamis et al. 2021). Some studies, without specifically focusing on retention-oriented larval behaviour or invasive species, highlight habitat topology and coastal morphology as external forces impacting the chances of long and distant dispersal (Jessopp & McAllen 2008, Grober-Dunsmore et al. 2009, Treml et al. 2012, 2015, Anadón et al. 2013). Habitat topology, coastal morphology, and associated environmental features such as water temperature and mixing have been scarcely related to the export of larvae with retention-oriented behaviour or used for spatially predicting the export of larvae at given sites.

In the present study, our main objective is to quantitatively predict the export of retention-oriented larvae through the relationship between the coastal features at a larva's natal population and the estimated export rate from a Lagrangian transport model. We set up the study on the well-known invasive Pacific oyster in Irish coastal waters. The findings should provide useful insights for the management of coastal ecosystems. For example, showing the places with risks of larval export can be useful for the spatial allocation of shellfish licenses and controlling the spread of this invasive species.

2. MATERIALS AND METHODS

To estimate and predict the export rates, we used a Lagrangian transport model coupled with outputs from hydrodynamic models of 2 study areas within the Irish coastal waters (Fig. 1), and a statistical model.

2.1. Study areas

The 2 study areas are located on the west coast of Ireland and are the only 2 Irish coastal regions with available hydrodynamic models having spatial resolution high enough to study coastal larval transport. In general, the coastlines of the 2 areas are exposed to Atlantic Ocean water masses and a shelf current, the Irish coastal current, which flows northward.

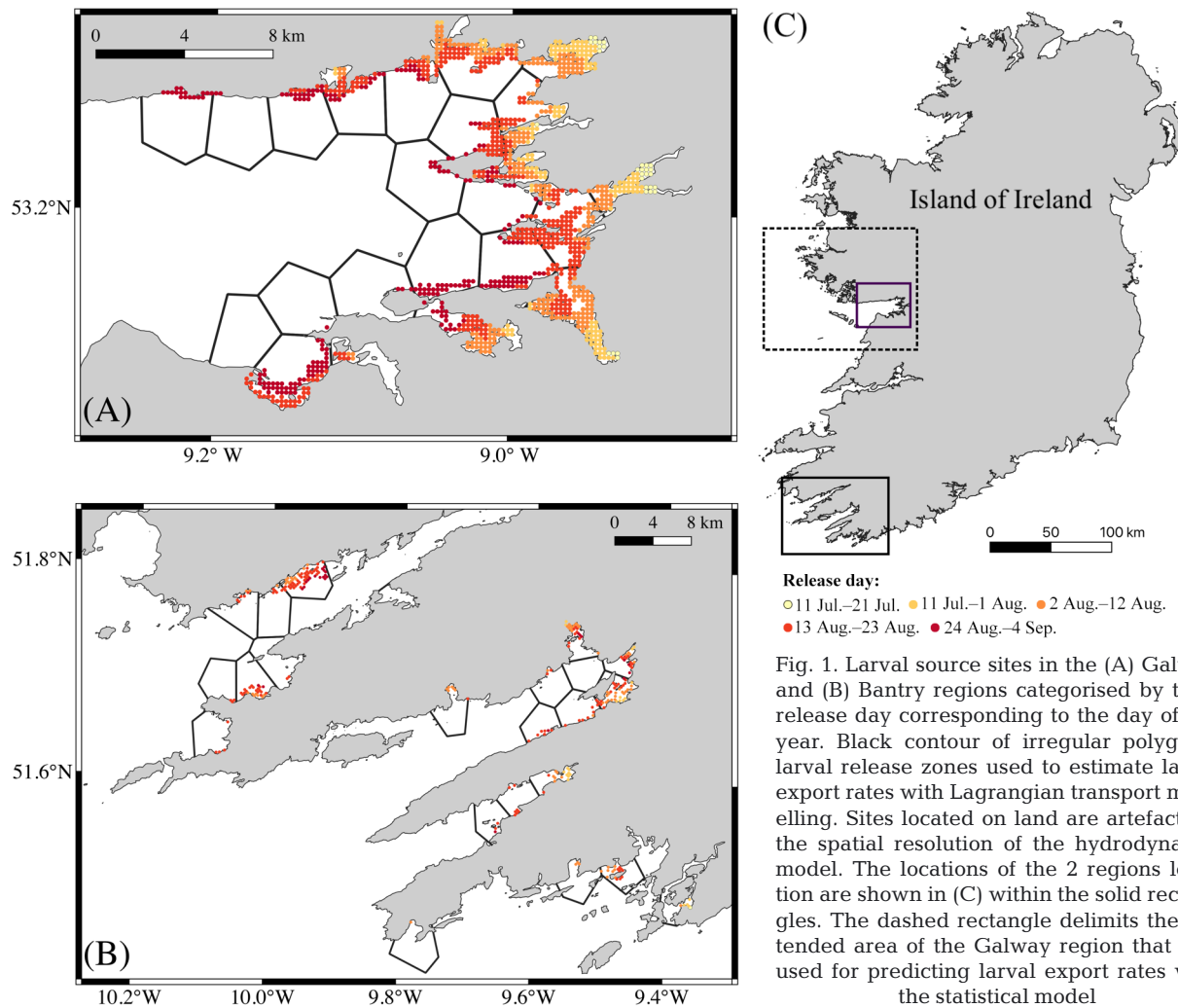


Fig. 1. Larval source sites in the (A) Galway and (B) Bantry regions categorised by their release day corresponding to the day of the year. Black contour of irregular polygons: larval release zones used to estimate larval export rates with Lagrangian transport modelling. Sites located on land are artefacts of the spatial resolution of the hydrodynamic model. The locations of the 2 regions location are shown in (C) within the solid rectangles. The dashed rectangle delimits the extended area of the Galway region that was used for predicting larval export rates with the statistical model

Both study areas in Ireland have many sub-bays and different coastal features which should be relevant to consider potential applicability to other ecosystems or retention-oriented species. The first study area is a large bay with several semi-enclosed sub-basins that will be referred to as the Galway region. The second study area has a coast deeply indented by long, parallel, and narrow bays, and will be referred to as the Bantry region. In both regions, the shoreline is mainly defined by rocky shores and cliffs, which have different exposures to wind-driven wave action (Cross & Southgate 1983, Atan et al. 2016, McCullagh et al. 2020). In the Galway region, the water is well-mixed and has an anti-clockwise general circulation induced by the wind and tide (Hartnett et al. 2011, Ren et al. 2015). The water circulation in the Bantry region is stratified during summer, has low tidal activity, and is mainly wind-driven due to the local topography (Edwards et al. 1996).

2.2. Hydrodynamic models

We used two 3D operational models, implemented by the Marine Institute based on the Regional Ocean Modelling System (ROMS), which is a free-surface, hydrostatic, primitive equation ocean model described in Shchepetkin & McWilliams (2005). The 2 model configurations are detailed in Nagy et al. (2020a) for the Galway region and in Dabrowski et al. (2016) for the Bantry region. Overall, their configurations were similar, aside from some parametrisation inputs (Table 1).

The ROMS used orthogonal curvilinear coordinates on an Arakawa-C grid in the horizontal while utilizing a terrain-following (i.e. sigma layers) coordinate in the vertical. The prognostic variables of the hydrodynamic model were surface elevation, potential temperature, salinity, and horizontal velocities. Surface forcing was obtained from the hourly

Table 1. General Regional Ocean Modelling System configuration for the Galway and Bantry regions

Region	Galway	Bantry
Domain	10.8°–8.9° W, 52.95°–53.73° N	11.0°–8.6° W, 50.54°–52.0° N
External time		1 h
Available years		2018, 2019, 2020
Horizontal resolution		200 m
Vertical discretisation		20 sigma layers
Open ocean boundaries	From the North East ATLantic model (NEATL); Nagy et al. (2020b)	
Atmospheric forcings	From the hourly 0.125° atmospheric model forecasts of the European Centre for Medium-Range Weather Forecasts (ECMWF)	
Freshwater discharges	Corrib, Dunkellin, and Clarin rivers	Five minor rivers in Bantry Bay, one river in Kenmare Harbour
Further details on the model configuration	Nagy et al. (2020a)	Dabrowski et al. (2016)

0.125-degree atmospheric model forecasts of the European Centre for Medium-Range Weather Forecasts (ECMWF). Heat fluxes were calculated from the bulk formulae, and surface freshwater fluxes were obtained from the prescribed rainfall rates and the evaporation rates computed by the model. At the open boundaries, clamped boundary conditions have been imposed for 3D momentum and tracers, whilst a combination of Flather (1976) and Chapman (1985) conditions have been applied for the free-surface and the barotropic velocity. In both local scale models, a third-order upstream bias advection of 3D momentum and a fourth-order, centred, finite difference scheme for the vertical advection of momentum were used. The Multidimensional Positive Definite Advection Transport Algorithm (MPDATA; Smolarkiewicz & Margolin 1998) was used for the advection of tracers, and for vertical mixing, a *K*-profile vertical parameterization (Large et al. 1994) was applied. Further details about the model validations of the Galway and Bantry region models are presented in Nagy et al. (2020a) and Dabrowski et al. (2016), respectively. These 2 studies also indicate that the 2 regional models reproduced the tidal patterns well.

2.3. Lagrangian transport model with biological realism

Pacific oyster larvae were considered as particles and tracked with a Lagrangian transport model coupled to the hydrodynamic fields (ROMS model output) of the study areas for 2018. The year 2018 was used from the 3 years of available data (2018–2020) because oyster spawning was most likely to occur in

2018 for both Galway and Bantry regions. This was based upon the daily average bottom water temperatures during summer at depths suitable for the Pacific oysters (i.e. at intertidal and subtidal seafloor up from 0 to 1 m deep based on the ROMS seafloor depth) being relatively warm in 2018 compared to 2019 and 2020. On average, from 21 June to 21 September 2018, the bottom water temperature was 16.9°C in the Galway region and 16.1°C in Bantry Bay, which was 0.25–1°C higher than in 2019 and 2020.

Larval tracking was initialised by releasing particles within the depth distribution of the adults and at places where the temperature complied with oyster spawning requirements. These spawning requirements were (1) a threshold of 592 degree-days has been reached (degree days are calculated as the cumulative sum, starting on 1 January 2018, of the excess daily water temperature above a baseline of 10.55°C) and (2) all 7 d following the 592 degree-days have a daily-averaged water temperature of at least 16°C (Mann 1979, Dankers et al. 2004, Kochmann 2012). The degree-days and the water temperature conditions for larval release were calculated from the near-bottom water temperature in each grid cell of the ROMS simulations. These depth and spawning requirements gave 1077 and 273 suitable release points, hereby named source sites, in the Galway and Bantry regions, respectively (Fig. 1). In the Galway region, the simulated spawning took place between 11 July and 4 September 2018, and in the Bantry region, between 21 July and 29 August 2018. These are timespans in accordance with the summer spawning timeframe observed in European waters (Enríquez-Díaz et al. 2009, Bernard et al. 2016). The differences in the starting day and period of release were due to the slower accumulation of degree-days in the Bantry

region (on average, $3.75^{\circ}\text{C d}^{-1}$ starting 1 January) than in the Galway region (on average, $4.63^{\circ}\text{C d}^{-1}$) and to the fewer number of days with water temperatures above 16°C in the Bantry region (on average, 60 d in 2018) than in the Galway region (on average, 83 d). The simulated spawning event occurred at midnight of degree-day 592. In total, 10770 and 27300 larval tracks were simulated, which, according to a preliminary analysis following the protocol of Simons et al. (2013), would be enough particles in the region to represent 95% of the dispersal variability (see Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m724p081_supp1.pdf). At each source site, we simulated the release of 10 larvae in the Galway region and 100 larvae in the Bantry region.

Larval transport simulations were carried out with the open source LTRANS algorithm (Schlag & North 2012) using a fourth-order Runge-Kutta scheme for advection of particle-like larvae. Random displacement schemes (Visser 1997) were accounted for in the transport simulation by using constant vertical and horizontal diffusivity coefficients of 0.0001 and $0.1\text{ m}^2\text{ s}^{-1}$, respectively. These values were selected after carrying out a preliminary analysis based on Okubo's relationship (see Table S1 in Supplement 1) and values given in studies targeting coastal and tidal systems (Okubo 1971). An advection time step of 60 s was used to update the tracking, and larval positions were recorded each hour. If a larva collided on the coastline or virtually crossed the oceanic boundaries of the model, the larva was put back to its previous location. Larval tracking lasted a maximum of 30 d, which corresponded to an estimate of the pelagic lifetime of the oyster larvae metamorphosing through the pelagic trochophore (first 2 d of the pelagic life), veliger (from days 2 to 21), pediveliger (from days 21 to 30), to the sessile spat stage in cold waters ($\sim 16^{\circ}\text{C}$) like in the summer Irish coastal waters (Kheder et al. 2010, Troost 2010). In our study, mortality was not accounted for because it was beyond our main scope and is poorly known for Pacific oyster larvae.

To quantify the effect of behaviour on larval export rate, we simulated 2 larval transport scenarios. In the first scenario, larvae were passively advected. In the second, larvae had an active tidal behaviour controlling their vertical position that corresponds to known Pacific oyster larval behaviour (Pauley et al. 1988, Arakawa 1990, Robins et al. 2017). The trochophore larvae were passive, and the veliger larvae avoided the ebbing currents by swimming towards the sea bottom at ebb tide and towards the surface at flood tide (Fig. S1 in Supplement 2 www.int-res.com/articles/suppl/m724p081_supp2.pdf). When turning

into pediveliger larvae, vertical swimming actively maintained the larvae near the bottom. The tidal behaviour of the veliger larvae is known to favour high retention rates (Hill 1991, Knights et al. 2006). At each time step, the vertical swimming velocities of larvae were randomly selected between 0 and a maximum speed. The value of the maximum speed linearly increased from 0.1 to 1 mm s^{-1} from the start of the veliger stage until the start of the pediveliger period (on the 21st day). These values approximated the ones found in Troost et al. (2008), Suquet et al. (2012), and Gamain et al. (2020).

2.4. Larval transport modelling analysis

2.4.1. Larval export calculation

Before calculating the larval export rate, larvae were assigned to release zones which overlapped with their respective source sites (Fig. 1). The release zones capture the main coastline irregularities of the 2 regions (e.g. semi-enclosed bays and estuaries whose breadth could measure a few hundred meters to 8–10 km). The release zones were obtained by objectively splitting the studied regions into polygons of roughly equal surface areas using QGIS software (version 3.20.3). The method was adapted to the irregular shape of the area and consisted of (1) randomly seeding enough points (i.e. 20 000) to cover the release region, (2) clustering the points with a k -means approach (40 and 100 clusters in the Galway and Bantry regions, respectively), (3) using a Voronoi tessellation to get polygon edges of each cluster, and (4) retaining the polygons which overlapped with source sites. After the fourth step, we obtained 22 release zones of $7.5 \pm 1.7\text{ km}^2$ in the Galway region and 25 release zones of $10.7 \pm 3.9\text{ km}^2$ in the Bantry region. The pediveliger stage corresponds to the phase when the larvae become competent to settle and reduce the transport in pelagic water until finding a suitable habitat for settlement. Therefore, a larva was considered exported if all larval positions during the pediveliger stage were outside the larva's zone of release (Fig. 1). When a back-and-forth movement in and out of the release zone was detected during the pediveliger stage, the larva was identified as exported if the time spent in the release zone was lower than half the duration of the pediveliger stage. This condition was set up to compensate for the absence of settlement conditions.

The rate of larval export (the ratio of the exported larvae to total released larvae) was computed for the

2 regions and the 2 behaviours. We calculated the least-cost distance between the source site of a larva i and its position f as a pediveliger larvae on the 21st day (Dist_{i-f}) using Dijkstra algorithm. The least-cost path is the shortest path in the coastal water that does not cross land. The computation of least-cost distance was carried out with the 'gDistance' R package (version 1.6). For exported larvae, we also computed the average time taken for the larvae to leave the release zone, in order to determine the specific larval stage when export had occurred.

We carried out 2 short analyses to better frame the impact of the release zone delimitation on the export rate. First, we tested if the position of the source site's proximity to the release zone edge would imply higher export rates. The test was carried out by calculating the Pearson correlations between the export rate and the least-cost distance from a source site i to the closest edge of its release zone ($\text{Dist}_{i\text{-edge}}$). An edge was a section of the release zone which was not part of the coastline. All these sections were straight lines. Second, we tested if the release zone surface area had an impact on the export rate. We computed the difference between $\text{Dist}_{i\text{-edge}}$ (e.g. the least-cost distance between the final position of the 21 d old larvae f to the closest edge of its release zone) and a value, d_x , ranging from -500 m to 500 m incremented by 50 m. The value d_x represented the distance of the edge to its initial position, and by expansion, the increase or decrease of the release zone surface area (Fig. S2 in Supplement 2). If the difference was negative, it meant that the final position of the larva passed on the other side of the edge, and therefore the retention or exportation status of the larva would have changed to the opposite condition. We recalculated the larval export rate for each incrementation of d_x .

2.4.2. Predicting the larval export from coastal features at source sites

We considered 6 coastal features at each source site: wave exposure, the shortest distance from the source site to the coastline ($\text{Dist}_{\text{coast}}$), with the coastline being defined by the sea–land border of the ROMS model, the seafloor slope, the bathymetry at the source sites, the log-transformed mean kinetic energy (MKE) of the water and the larval release's day of the year as a proxy for the warming of the water temperature. The seafloor slope and bathymetry at the source sites were extracted from the ROMS grid. Wave exposure was based on an algo-

rithm from Burrows et al. (2008). Briefly, this involves calculating the log (base 10) value of the average distance between a source site and the coastline along 15 equally spaced radii (i.e. 24° apart) centred on the source site (if a radius does not intersect the coastline within 25 km, the distance of 25 km is used). The MKE was based on the average kinetic energy over 30 d (15 d before and after the release date) from the ROMS simulations. The source sites were categorised into distinct types based on these coastal features. We subjected the results from a principal component analysis (PCA) on the centred and scaled coastal features to a hierarchical clustering analysis (R package 'FactoMineR', version 2.7; Lê et al. 2008).

We established the relationship between the export rate of larvae and the coastal features at the source sites across the Galway and Bantry regions using 3 common statistical models: a gradient boosted trees model (GBM; Friedman et al. 2000), a generalized additive model (GAM; Hastie & Tibshirani 1986), and a random forest model (RFM; Breiman 2001). The 3 models were implemented in R with the 'mgcv' package (version 1.8-35) for GAM, the 'gbm' package (version 2.1.8) for GBM, and the 'randomforest' package (version 4.6-14) for RFM. The export rate was arcsine square root transformed, which is one of the common transformations for proportion in ecology modelling analyses. GBM and GAM were fitted with a Gaussian distribution and an identity link. The coastal features, hereby called variables, were all centred and scaled before training the statistical models. In GAM, all variables were smoothed with a thin plate regression spline basis of the package 'mgcv'. In GBM and RFM, 300 and 500 trees were used, respectively.

We conducted a block cross-validation to evaluate the predictive performance of the 3 spatial distribution models (Valavi et al. 2019) using the 'BlockCV' package (version 2.1.5) in R. The data set was divided into 5 folds by assigning data to spatial blocks (Fig. S3 in Supplement 2). A spatial block was a square with a side length of 1 km and was randomly distributed over the studied area. We used the root mean square error (RMSE) as a measure of model predictive performance for the block cross-validation. As the GBM and RFM were machine-learning models, hence not having outcomes like the equations in the GAM, we focused on identifying and comparing the relative importance of the variables among the models as a useful takeaway to understand export rates. The relative importance was inspected using approaches assigned to the model type: a decrease in the least-square value if a given variable is discarded in the GAM, a mean increase in the predictor error when a

given variable is permuted in GBM (Friedman et al. 2000), and a mean decrease in node impurity if a given variable is used to split a node in RFM. Then, we predicted the export rate with GBM, GAM, and RFM in the Bantry region and an extended domain around the Galway region (Fig. 1), which fitted in the domain of the ROMS model (Table 1).

Last, we carried out a small-scale validation of the statistical modelling by calculating the RMSE between predictions and new independent estimations of export rate. These new estimations of the export rate were obtained from larval transport modelling initialised at 32 new source sites that were not used in the original larval transport modelling. Oyster populations (wild and farmed) have been observed at all these sites in the south-eastern Galway region along the coastline (Table S1 in Supplement 2). The release conditions, larval behaviour, and exportation computation followed the same protocol as described in Section 2.3. In total, 12 800 particles were released between 22 July and 6 September 2018, with 400 particles at each site.

3. RESULTS

3.1. Larval transport analyses

Tidal larval behaviour reduced the percentage of larvae that were exported from their source sites compared to passive larval behaviour (Table 2). The general export rate dropped by 20.9 and 27.6% if larvae had an active behaviour instead of being passively transported (Table 2) in the regions of Bantry and Galway, respectively. Larvae began to leave the release zones within a few days of the release time, at the beginning of the veliger stage. On average in the 2 regions, the export began for 3.3 ± 4.2 d old lar-

vae when they had an active behaviour and at 4.5 ± 5.3 d old (1.2 d later) when their behaviour was passive. In terms of transported least-cost distance between source sites and the final position of larvae (i.e. Dist_{i-f}), exported larvae with retention-oriented behaviour were transported 2.3 and 3.5 km closer to their source in Galway and Bantry regions, respectively, compared to passive larvae (Table 2).

A positive correlation existed between the distance of the source sites to the edge of the release zones ($\text{Dist}_{i-\text{edge}}$) and the export rate. This correlation was modest (Pearson correlation coefficient, $r = 0.54$ and 0.52 , in Galway and Bantry regions, respectively) for retention-oriented larvae. It was almost negligible (Pearson correlation coefficient, $r = 0.08$) in the Galway region and modest (Pearson correlation coefficient, $r = 0.65$) in the Bantry region for passive larvae. On average, exported retention-oriented larvae came from source sites that were closer to their release zone ($\text{Dist}_{i-\text{edge}} = 1.2 \pm 0.6$ km) compared to retained larvae ($\text{Dist}_{i-\text{edge}} = 2 \pm 1.1$ km). There was a negative relationship between the release zone size and the export rates regardless of the larval behaviour and the region (Fig. 2). The slope of this relationship was stronger for a passive behaviour than a retentive behaviour ($-7.4\% \text{ km}^{-1}$ for passive larvae against $-2.1\% \text{ km}^{-1}$ in the Bantry region and $-9.1\% \text{ km}^{-1}$ for passive larvae against $-5.3\% \text{ km}^{-1}$ in the Galway region). The release zone size also had a bigger impact in the Galway region (slope coefficient of $-5.3\% \text{ km}^{-1}$) compared to the Bantry Region (slope coefficient of $-2.1\% \text{ km}^{-1}$) for larvae with retention-oriented behaviour. Overall, the export rate was moderately impacted by the release zone size; however, with respect to the short-scale irregularities of the coastline in the 2 regions, the sizes of the release zone were adjusted and representative for our study objectives.

Table 2. Rates (%) of larvae exported from their source sites, age of larvae when leaving the release zone (d), and travelled least-cost distance between source and larvae's position on the 21st day of transport (Dist_{i-f} ; km) according to the regions and the larval behaviours. Values are mean \pm standard deviation

Region	Galway		Bantry	
	Passive	Active	Passive	Active
Behaviour	Passive	Active	Passive	Active
Export rate (%)	83.3	55.7	84.0	63.1
Age of exportation (d)	3.9 ± 5.0	2.6 ± 3.6	5.0 ± 5.5	4.1 ± 4.7
Dist_{i-f} (km)				
Exported	8.3 ± 6.9	6.0 ± 3.8	10.7 ± 11.5	7.2 ± 4.6
Retained	0.9 ± 1.0	1.3 ± 1.0	1.5 ± 1.3	1.4 ± 1.1

3.2. Coastal features at source sites and consequences for export of retention-oriented larvae

The export rate of retention-oriented larvae had similar variations depending on the spatial location of the release zone in the 2 regions (Fig. 3). The export rate of retention-oriented larvae increased in the release zones where coastline morphology was open and decreased in inlets and relatively closed bays. More specifically, in the

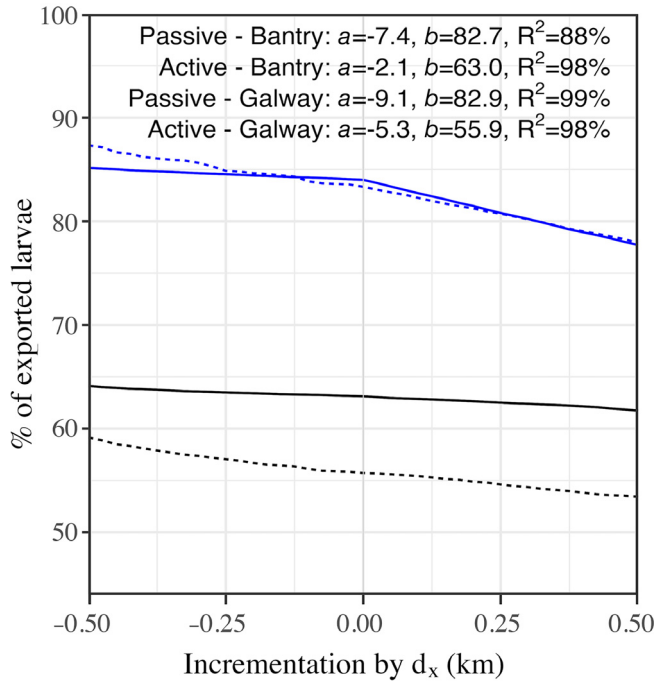


Fig. 2. Percentage of exported larvae according to the change of the release zone size for passive larvae (blue lines) and retention-oriented larvae (black lines) released in the Bantry region (full line) and the Galway region (dashed line). The change of the release zone size was approached by the incrementation of the $Dist_{f-edge}$ by d_x . a , b and R^2 are, respectively, the slope coefficients, intercepts, and R-squared estimated by linear regression models

Galway region, larvae were poorly (2.4–20%) to relatively moderately (40–60%) exported if their source sites were in release zones localized in semi-enclosed bays or along irregular coastlines. In the Bantry region, we noted low export rates (0–10.7%) along sheltered coastal waters. By contrast, the export rates of passive larvae were mostly high (>60%, Fig. 3) for release zones with any coastline morphologies (irregular or open).

The classification and clustering of the source sites based on their assigned coastal feature revealed 3 types of source sites (Fig. 4). The clustering was pro-

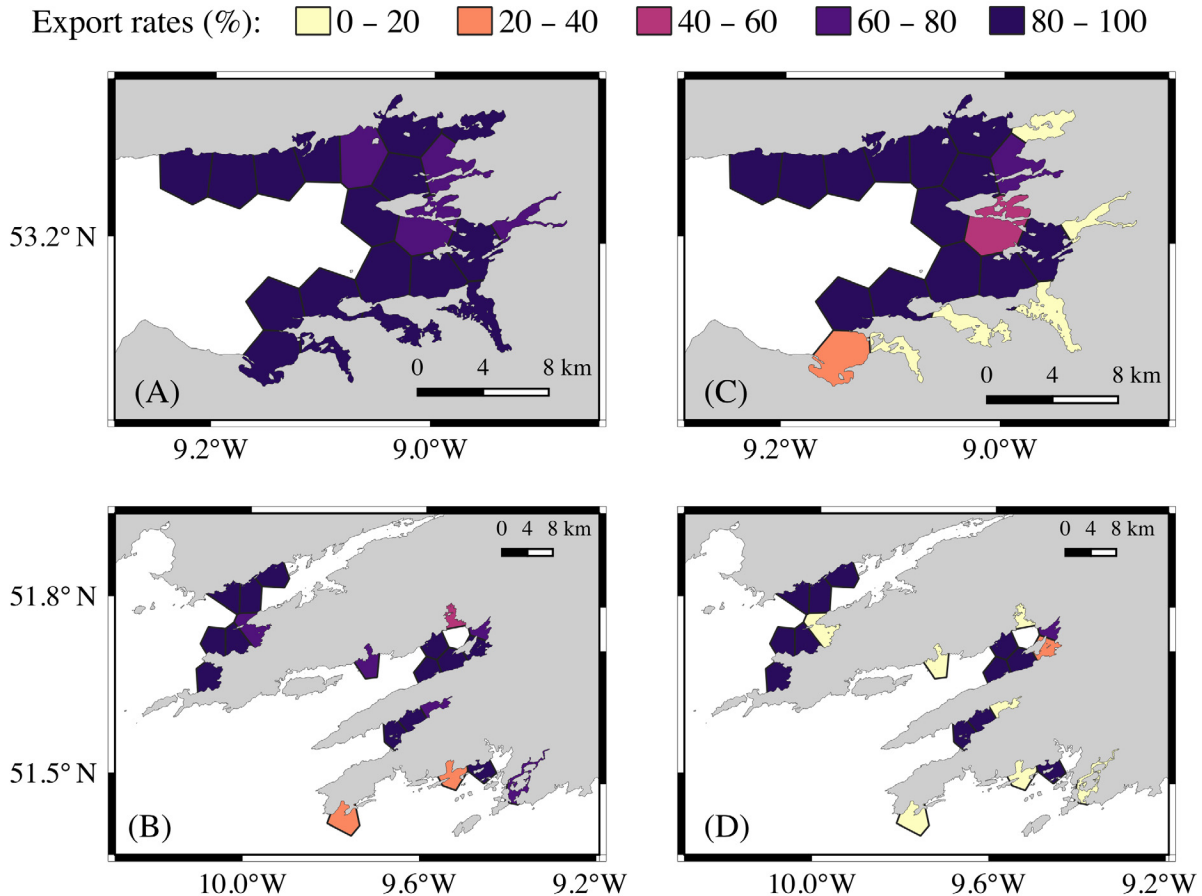


Fig. 3. Export rates (%) for larvae with (A,B) passive behaviour and (C,D) retention-oriented behaviour by release zones of the (A,C) Galway and (B,D) Bantry regions

cessed over a PCA whose 2 first dimensions represent 55.3% of the data set variance. The number of clusters was set up to 3 types based on the elbow points over the inertia gain variation. Type 1 corresponded to source sites that were in a protected environment close to the coast and shallow with substantial movements of the water body (i.e. low wave exposure, short distance between the source and the coast, high MKE; Table S2 in Supplement 2). This corresponded to source sites in the inner part of semi-enclosed areas and inlets mostly exposed to the tidal cycle (Fig. 4). Type 2 was largely the opposite of Type 1, except for the sea bottom depth which was relatively close to the surface (i.e. high wave exposure, low MKE, shallow bathymetry). Type 3 corresponded to source sites in a turbulent open environment over a deep and irregular sea bottom (i.e. high wave exposure, high MKE, deep bathymetry; Table S2). Most

source sites in the Galway region were Type 1 (55.1%), while for the Bantry region, most source sites were Type 2 (74.4%). In the Bantry region, the dominance of Type 2 was explained by the important differences in the MKE and slope features between regions (Fig. S4 in Supplement 2). The MKE was 100 times higher in the Galway region ($1.1 \times 10^{-3} \text{ m}^2 \text{ s}^{-2}$) than in the Bantry region ($1.9 \times 10^{-5} \text{ m}^2 \text{ s}^{-2}$) and the slope values (i.e. 3rd quartile) were more extensive in the Galway region (0.010°) than in the Bantry region (0.006°).

The characterisation of the source types by coastal features partly explained the spatial distribution of the export rates. Export rates of retention-oriented larvae were relatively high (67.8–82.6%; Table 3) when larvae came from source sites of open coast areas (i.e. Types 2 and 3; Fig. 4). The lowest export rates were estimated at source sites of Type 1 (36.5 and 43.8% in Galway and Bantry regions, respectively), which were in inlets (Fig. 3). For passive larvae, the export rates in the different source types were high (ranges are between 66.2 and 88.6%) in both regions and the coastal features of source sites of type 1 were less impactful in the exportation of larvae.

3.3. Prediction of export rate for retention-oriented larvae based on coastal features

Estimated export rates were related to 5 coastal variables in the 3 statistical models GAM, GBM, and RFM. The following model structure to estimate larval export rates based on 5 coastal features was retained: Arcsine-transformed Export Rate \sim Wave Exposure + Slope + $\log_{10}(\text{MKE})$ + $\text{Dist}_{\text{Coast}}$ + Day of the Year + ϵ , where ϵ represents the residuals. Bottom depth at the source sites was discarded from the model. The models explained over 50% of the export rate variation in the data sets (i.e. 52.4% in GAM, 56.5% in GBM, and 53.4% in RFM). The 3 statistical

Table 3. Rates (%) of passive and active retention-oriented larvae classified as exported in 3 source types in the Galway and Bantry regions. Type 1: source sites occur in a protected environment; Type 2: source sites occur in an exposed shallow environment; and Type 3: source sites occur in a turbulent open environment

Source site types	Galway		Bantry	
	Passive	Active	Passive	Active
Type 1	81.3	36.5	66.2	43.8
Type 2	88.2	68.0	88.5	71.8
Type 3	84.9	82.6	88.6	67.8

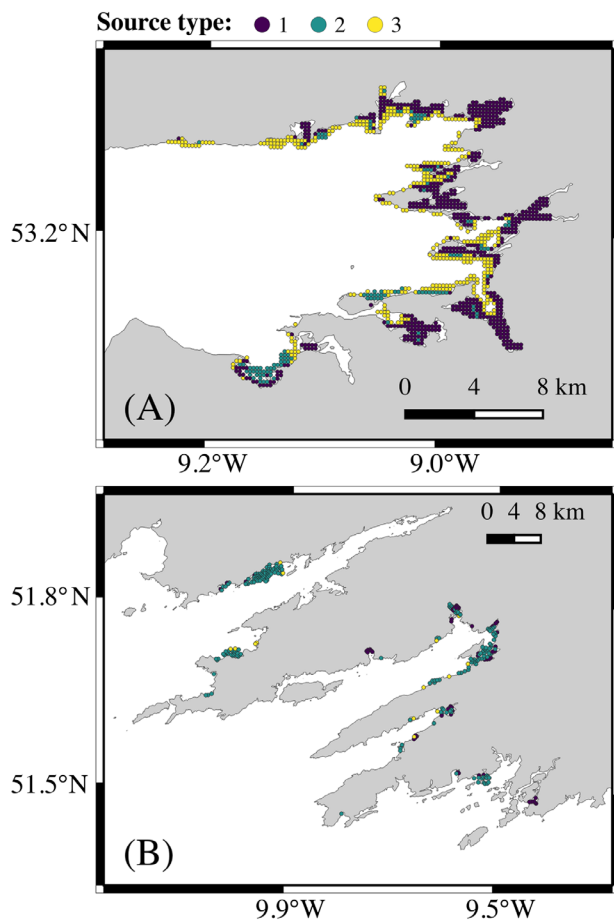


Fig. 4. Source sites in the (A) Galway and (B) Bantry regions clustered by the similarities of their coastal features. Type 1 (purple dots): source sites in a protected environment; Type 2 (green dots): source sites in an exposed shallow environment; Type 3 (yellow dots): source sites in a turbulent open environment

models had similar modelling performances with an RMSE from the block cross-validation at around 0.323 ± 0.003 , and the assumption of Gaussian distributions of the residuals was relatively respected (see Fig. S5 in Supplement 2). In the 3 models, the relative importance of the coastal features in the statistical models (Fig. 5) had the same order: wave exposure and $\text{Dist}_{\text{Coast}}$ were the most and least important model variables, respectively. With GBM and RFM, contrary to GAM, $\text{Dist}_{\text{Coast}}$, the log-transformed MKE, and the slope had similar low influence. The marginal plots of the export rate in relation to the variables presented similar variations among models (Fig. 6). For the most important variables (i.e. day of the year and wave exposure), there was a relatively linear increase of the export rate with day of the year and variation of the export rate without specific patterns with increasing values of the wave exposure. We noted a positive relationship of the export rate with the 3 other variables. The performances of the 3 models were similar and could not encourage the selection of one model. Thus, our analysis of the export rate predictions was carried out on the averaged predictions made by the GBM, RFM, and GAM (Fig. 7) instead of on each model's prediction (see Figs. S6 & S7 in Supplement 2).

The models performed well in predicting the variation of the export rate with the coastal morphology. Low export rates were predicted in inlets and sheltered sites of the 2 regions (Fig. 7). High export rates were predicted along straight coastlines, as seen with values between 90 and 99% at a latitude around 53.2°N in the extended Galway region and in the indented sub-bays of the Bantry region. The export rate for independent dispersal simulations at the 32 source sites was 30% on average. Only 8 source sites had an export rate above 75%. The statistical models predicted an export rate of 41%, on average. The RMSE between these new estimates

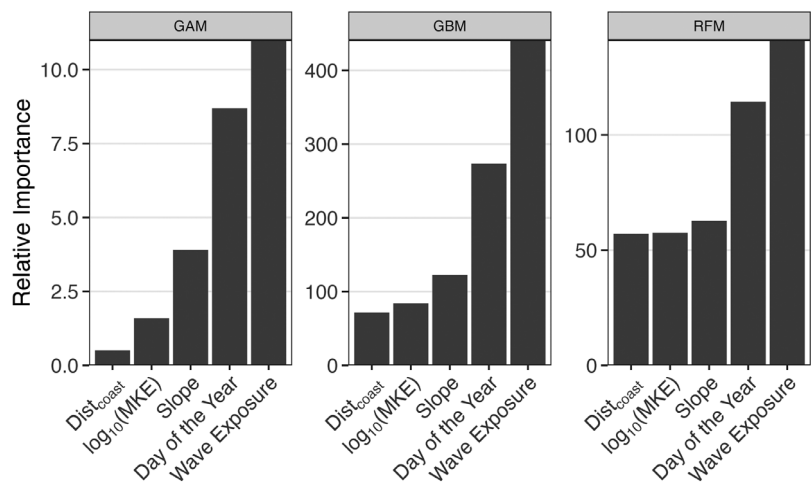


Fig. 5. Relative importance of the variables in the generalized additive model (GAM), gradient boosted trees model (GBM), and random forest model (RFM) from least to most important. Scale of importance of the variables (y-axis) is not comparable across models because the computation is different for each model. $\text{Dist}_{\text{coast}}$ is the least-cost distance from the source site to the coastline, $\log_{10}(\text{MKE})$ is the log-transformed mean kinetic energy (MKE) of the water, and slope is the seafloor slope

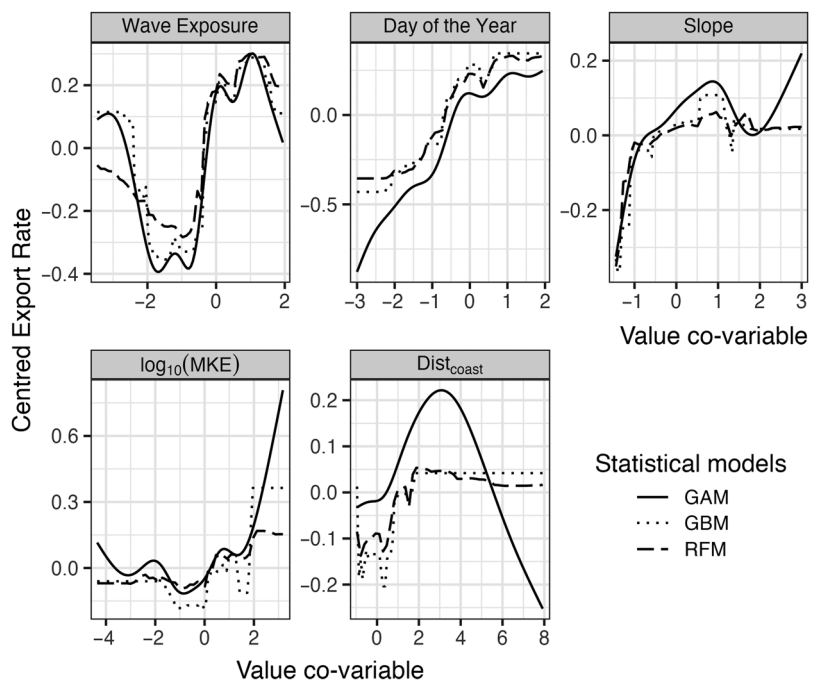


Fig. 6. Marginal relationships of the centred export rates with the 5 variables in the generalized additive model (GAM), gradient boosted trees model (GBM), and random forest model (RFM). Variables are scaled and centred. $\text{Dist}_{\text{coast}}$ is the least-cost distance from the source site to the coastline, $\log_{10}(\text{MKE})$ is the log-transformed mean kinetic energy (MKE) of the water, and slope is the seafloor slope

and predictions of the export rates was 0.31, which was close to the RMSE computed with the block cross-validation.

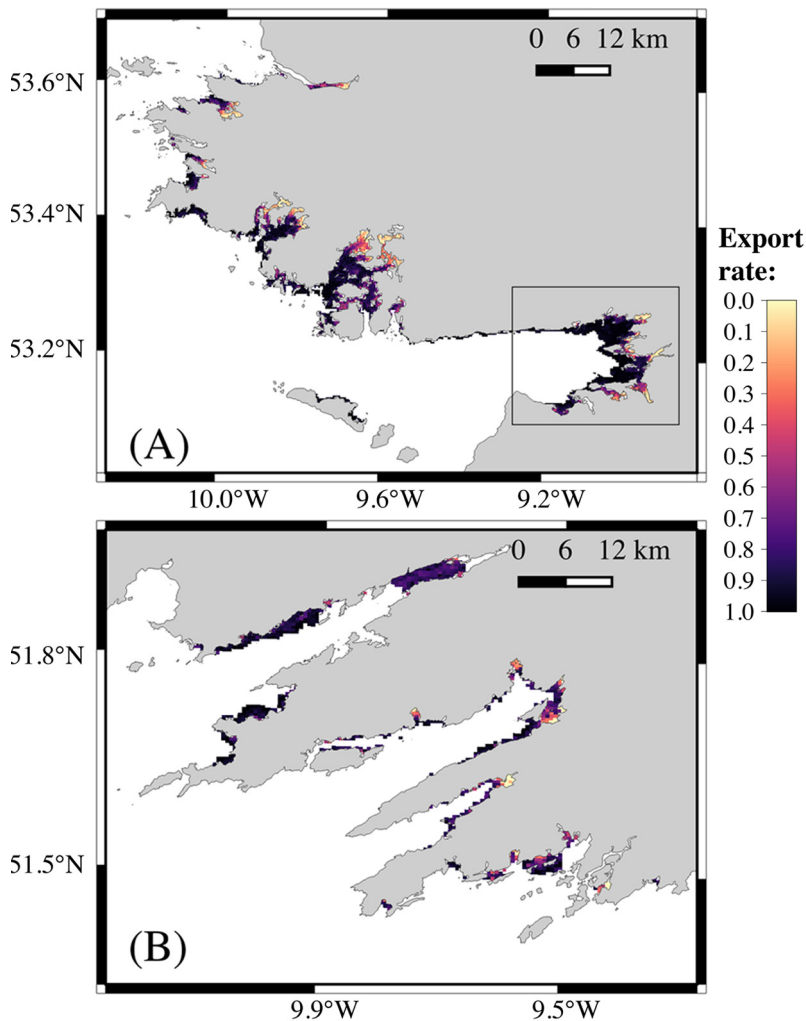


Fig. 7. Mean predicted export rates of larvae with active behaviour from an ensemble of the generalized additive model (GAM), gradient boosted trees model (GBM), and random forest model (RFM) models in the (A) extended Galway and (B) Bantry regions. The rectangular polygon in (A) shows the area in which the source sites of larvae were located for initialising the Lagrangian transport model

4. DISCUSSION

The present study highlights a relatively moderate export of larvae beyond their source sites even though retention-oriented larval behaviour was simulated. While our results also suggest a better retention of the larvae like many studies (e.g. Paris & Cowen 2004) compared to when larvae are passive, a portion of larvae get carried away. Since retention-oriented larvae limit their offshore dispersal, the coastal morphology and habitat topology were partly responsible for the dynamics of export and retention of these larvae. The coastal morphology can protect against wave exposure, influence mesoscale circulations and

water residence times, and limit the mixing of larvae into strong currents (Archambault & Bourget 1999, Jessopp & McAllen 2007, Jessopp et al. 2007, Burrows et al. 2008). In particular, the semi-enclosed areas trap, retain, and pool larvae (Jessopp et al. 2007). In this sense, our modelling analysis corresponds with the results from field sampling-based studies that highlighted this coastal impact on larval spread (e.g. Jessopp et al. 2007, Teschke et al. 2020). Furthermore, our results highlight the importance of the wave exposure variable, agreeing with earlier published works showing that shielded sites with low dynamics were ones with high success of oyster settlement (Teschke et al. 2020). Indented coastal areas can indeed reduce the physical impact of tides that energize the water movements. It is found that the highest residence times in indented areas occur over intertidal areas (Wheat et al. 2019). However, tidal systems in coastal areas can also be amplified because of the shallow topography. Where the water is funnelled in narrow passes, channels, or basin entrances, the water flows are strong in every layer of the water column, and larvae are exported regardless of their depth in the water column (Brown et al. 2000, Roegner 2000). These 2 opposing consequences of an indented coastal morphology may explain why we found 2 nearby source sites classified as 2 different types of sources. To investigate this finding further, it would be interesting to include additional coastal features, such as the width of the inlet entrance, the water flushing time, and the tidal power in the different inlets of the regions, because these features are known to have an impact on larval assemblages and rocky marine communities (Jessopp et al. 2007, Burrows 2012). We did not include these features in our study because it would have meant reducing our data sets to just source sites within the inlets. In contrast to indented sites, sites along the open coastline are exposed to strong hydrodynamic environments, which can transport larvae away from the coast and potentially prevent larval retention. The consequences of source sites along exposed coastline on oyster larval dispersal have al-

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ready been highlighted by other transport model results (Aiken et al. 2007, Hubbard & Reidenbach 2015). With our study, we showed that this consequence is applicable for larvae with simulated retention-oriented behaviour. Nonetheless, even when exported, larvae can be transported to coastal areas with suitable habitats and successfully settle. Whether the retention-oriented larval behaviour is a driver facilitating the ability to settle after transport is something that needs to be examined in future studies.

Spatially modelling the relationship between coastal features and export rates, themselves estimated from larval transport modelling, was an unusual but convenient approach to lessen the use of hydrodynamic and larval dispersal model runs. To date, the common approach of spatial modelling is to obtain outputs from species distribution modelling for use in the larval dispersal model (Palmas et al. 2017, Puckett et al. 2018, Ross et al. 2019, Castro et al. 2020, Clavel-Henry et al. 2021) instead of the opposite. Nonetheless, it is worth remembering that the uncertainties in our export rates from transport modelling are also not reflected in the statistical models (i.e. GAM, GBM, and RFM) and could be a source of misinterpretation in the predictions. These uncertainties are partly due to choices in the transport modelling and analysis. Specifically, uncertainties from 2 parameters that were simplified in the present study (the vertical swimming velocities of the larvae and the mortality rates) should be targeted in further investigations. Vertical swimming velocity changes with the age of the larvae and the water properties, which would boost the vertical migration during the flood and ebb tide (Dekshenieks et al. 1996). In this study, we assumed an oyster vertical swimming speed which was independent of the water properties. Considering the wide range of depths travelled by the larvae at each tidal cycle, we expect the variation of vertical swimming speed value to have a low impact on our conclusions. As for the mortality rate, this parameter encompasses several mechanisms (i.e. water property tolerances, predation, and larval condition) and can decrease the success of export. In the case of the Pacific oyster, for which knowledge is lacking, an approach would be to gather information from similar taxa as a proxy for the oyster, as previously done by Kakehi et al. (2020). Beyond the uncertainties, validation of the models makes the results believable and helps to select transport models with a given larval behaviour (Bode et al. 2019). It is highly recommended to test the model results with empirical data (Swearer et al. 2019) that can come from interdisciplinary collaborations (i.e. genetics,

oceanographic observatories, larval sampling). In our case study, a validation analysis using the aquaculture sites as source sites of larvae can be carried out and used to compare whether the present configuration of the transport model allows connections to sub-bays in Galway where the wild population has been observed. This step of validation shall be taken once a settlement criterion for the Pacific oyster larval pediveliger has been defined.

Estimates of exportation and retention rates are often outcomes of analyses dealing with marine population dynamics, sampling surveys, and modelled larval dispersal simulations (Cetina-Heredia & Connolly 2011, Wolanski & Kingsford 2014). Larval dispersal models help to inform management decisions and the protection of marine species and areas (Criales et al. 2019, Manel et al. 2019). Our study has transformed the results of the larval transport model into a tool that can predict export rates using only data on the coastal features at a site. This methodology should be convenient because it will permit the estimation of export rates from relatively available data (e.g. *in situ* measurements from mooring devices) and will not require larval transport model simulations or the availability of gridded hydrodynamic fields. Being able to predict the larval export rate has potential repercussions for spatial management strategies. In the case of marine invasive species, like *Magallana gigas*, sites with wild populations can be prioritised according to their export rates. High export rates would imply a quick capacity to spread and colonise the regional ecosystem (Dunstan & Bax 2007), provided that the system is suitable and that larval mortality during transport is relatively low. Conversely, low export rates would imply the possibility of the establishment and growth of a population (Dunstan & Bax 2007), hence stressing the local endemic ecosystem. Predicting export rates can also be useful when modifying the structural connectivity by setting up facilities such as aquaculture equipment from which an introduced species can escape. In the Republic of Ireland, the decision to grant a shellfish license is partly taken after carrying out an environmental impact assessment (Irish Statute Book 2012). One suggested criterion for this assessment is the spatial risk of escape for the species as predicted by our statistical model.

5. CONCLUSIONS

In this study, we focused on the coastal features that enhance the export of retention-oriented larvae away from their natal population. The simulated lar-

val dispersal of the Pacific oyster *Magallana gigas* in 2 Irish coastal regions showed that despite their behaviour, the larvae were exported away at relatively moderate rates (55 and 63%) and at a young age of their pelagic life. A spatial prediction of export rates using only coastal features has been established by fitting spatial models to the outputs of the larval transport model. The statistical modelling indicated that coastal morphology and habitat topology have an important influence in facilitating the export of retention-oriented larvae. Overall, this study gives a first insight into the use of coastal features to estimate the export rate of retention-oriented larvae with computational models. These models can provide large volumes of data and enable further analysis of statistical relationships, making them an interesting complement to empirical data. These results, in the case of *M. gigas*, can be of interest when assessing the risks of oyster escape from potential licensed oyster farms through the measurement of some environmental values at these sites (i.e. currents and water temperature). More generally, the analysis can be of help for other areas in the world or for other species with retention-oriented larval behaviour once the international and interspecies robustness of the relationship between export rates and coastal features has been established.

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