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James, M

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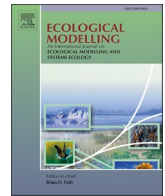
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# Assessing the influence of behavioural parameterisation on the dispersal of larvae in marine systems

M.K. James<sup>a,1,\*</sup>, J.A. Polton<sup>b</sup>, C.G. Mayorga-Adame<sup>b</sup>, K.L. Howell<sup>a</sup>, A.M. Knights<sup>a</sup>

<sup>a</sup> School of Biological and Marine Sciences, University of Plymouth, Drake Circus, Plymouth, PL4 8AA, UK.

<sup>b</sup> National Oceanography Centre, Liverpool, L3 5DA, UK

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## ABSTRACT

Predicting dispersal and quantifying ecological connectivity are increasingly referenced as fundamental to understanding how biodiversity is structured across space and time. Dispersal models can provide insight, but their predictions are influenced by our capacity to simulate the biology and physics known to influence dispersal. In a marine context, vertical swimming behaviour is considered important in influencing the spatial organisation of species across seascapes, but the mechanisms underpinning these movements remain unresolved, making it unclear how best to incorporate behaviour within models. Here, using a 3-D hydrodynamic model coupled with a Lagrangian particle tracker, we show how different modelled larval behaviours, alongside spatial and temporal hydrodynamic changes, influence larval dispersal predictions. Additionally, we compare the application of a novel approach of reverse-engineered larval swimming behaviour against two commonly modelled behaviours: passive dispersal and tidal vertical migration (TVM). We used statistical models (LME and GAM) to test the effects of change in tidal state conditions, season, and planktonic larval duration in conjunction with behavioural parameters on dispersal. For shorter PLDs (i.e., 1 day), we find that passive models match 'behaving' model outputs, but for longer PLDs, excluding behaviour leads to overestimates of dispersal; an effect that increases with time. Our results highlight the sensitivity of biophysical models to behavioural inputs, specifically how vertical migration behaviour can significantly reduce dispersal distance - especially for species with longer planktonic durations. This study demonstrates the disproportionate effects that even a single behaviour - vertical swimming - can have on model predictions, our understanding of ecosystem functioning, and ultimately, the ecological coherence of marine systems.

## 1. Introduction

In marine systems, the production and dispersal of planktonic life-history stages creates connections fundamental to the spatial organisation of species across local and seascape scales (Baguette et al. 2013) for a range of taxa (Blanco et al. 2019; Zeng et al. 2019). Increasingly, ensuring ecological connectivity is promoted as one solution to biodiversity loss and considered a key feature of sustainable ecological networks (Gonzalez et al. 2017), but assessment is often challenging - especially when considering small planktonic organisms that are difficult to track. Predicting dispersal of planktonic organisms requires the use of genetics (Gill and Hilbish, 2003), geochemical markers (Thorrold et al., 2007) or increasingly, biophysical models, which combine hydrodynamics and biological processes (see Swearer et al., 2019 for

review) to simulate movement. These models are used for a range of theoretical and applied questions, but their accuracy is reliant on our understanding of and ability to reproduce abiotic and biotic mechanisms that drive directed movement in nature.

Biophysical models of larval dispersal can be implemented by adopting relatively simple advection-diffusion models (Hill, 1990; Cowen et al, 2000) or by combining a general ocean circulation model describing local hydrodynamics with an individual particle tracker to incorporate biological traits (e.g., Schlag and North, 2012; Paris et al., 2013). In recent years, advances in computational power and efficiency have allowed for circulation models to include greater spatial and/or temporal resolution, allowing complex velocity flow fields over intricate topography to be resolved. Due to this, dispersal modelling using ocean circulation models has become the dominant method of larval dispersal

\* Corresponding author.

E-mail address: [moja@pml.ac.uk](mailto:moja@pml.ac.uk) (M.K. James).

<sup>1</sup> Present Address: Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth, PL1 3DH, UK

research in order to capture realistic hydrodynamics as experienced by the larvae (Sweaver et al., 2019). However, increasingly it is the parameterisation of biological traits or ‘behaviours’ assigned to individual particles within the particle-tracking component of the model that continues to attract research attention - given the potential of those traits to influence model predictions (Hill 1990; Cowen et al., 2000; Phelps et al., 2015; Daigle et al., 2016; Gary et al., 2020), and decouple model predictions from patterns in nature (Marshall et al. 2010, James et al. 2019).

Biological parameterisation has previously relied heavily on the results of laboratory studies and current literature to infer traits and larval behaviours. Typically, larval behaviours and behavioural triggers are parameterised using directly observed values from the laboratory (e.g. Robins et al., 2013; Phelps et al., 2015; Daigle et al., 2016; Bode et al., 2019; Gary et al., 2020), for instance to quantify swimming speeds (Fisher and Wilson, 2004; Chang et al. 2018). It is argued, however, that laboratory-derived swim speeds and behaviours are unlikely to represent realistic behaviours in nature due to an absence of one or more exogenous cues in those contrived contexts, but which likely influence the expression of behaviour in natural settings (e.g. Bonar et al. 1990; Kingsford et al. 2002; Queiroga & Blanton 2005; Morello and Yund, 2016). Recent research has endeavoured to bridge the gap between individual larval ability and behavioural manifestation in nature by considering how realistic *in-situ* swimming speeds can best be incorporated within dispersal models (James et al., 2019; Leis, 2020). These studies have shown that laboratory-derived behaviours fail to accurately capture how larvae behave in the field, and critically, affect the vertical position of larvae, which has repeatedly been shown to be an important mechanism for transport in a number of taxa (e.g. Garrison et al. 1999; Knights et al. 2006; Ospina-Alvarez et al. 2018). Indeed, Sweaver et al. (2019) suggest that behaviour should not be considered as an individual metric, but instead as a product of its environment in any given space and at any given time. Given that biophysical models are increasingly being applied to fisheries management and marine conservation efforts, effective decision-making and confidence in those interventions requires accurate models (Botsford et al., 2009; Knights et al. 2014), and a mismatch between modelled dispersal and realised ecological connectivity (Marshall et al., 2010; James et al. 2019) may undermine management and conservation efforts. Given behaviour may well be critical to this mismatch, some suggest the omission of behaviour in its entirety may well be preferential to the inclusion of one or more inaccurate behaviours (Bode et al., 2019).

Recreating the complexity of the natural environment: identification of the cues used to govern when and where behaviour is expressed, and assessment of the relative importance of each cue to the organism when multiple cues are present, realistically cannot be captured in a laboratory setting. Studying larvae in their natural environment instead can provide insight. For instance, observed *in-situ* change in vertical distribution profiles (e.g. Knights et al. 2006) can be used in conjunction with a fine-scale one-dimensional ocean turbulence model (e.g. Brereton et al., 2018) to ‘reverse-engineer’ larval behaviours and generate estimates of larval swimming speeds under variable environmental contexts that allow replication of observed vertical distribution patterns (see James et al. 2019). This study found that if models are to match *in-situ* observations of vertical distribution profiles, larvae must actively modify swimming behaviour in response to changes in tidal forcing conditions. Importantly, this research showed that this swimming response would not be captured using a ‘simple’ behavioural rule often implemented in models, such as a tidal vertical migration (TVM) signature (i.e. upward swimming during flood and downwards swimming during ebb – or vice versa, *sensu* Forward et al., 2003; Kunze et al., 2013). Further, James et al. (2019) revealed a 2.5-fold differential in upward and downward swimming speeds, suggesting differential response/capacity to utilise vertically stratified horizontal advection for transport.

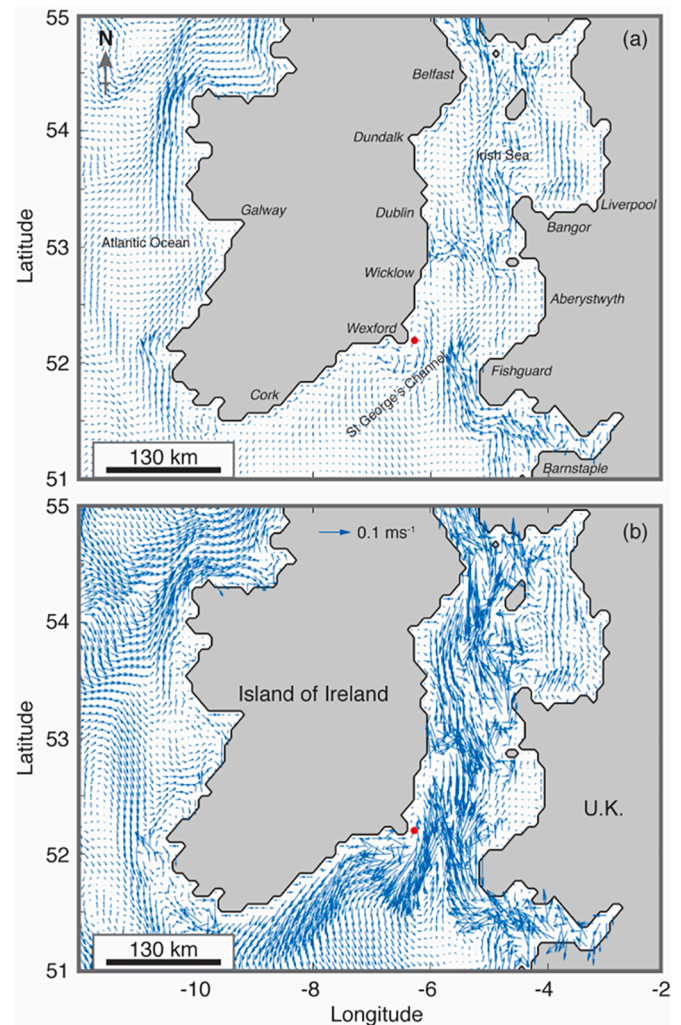
While James et al. (2019) revealed previously undescribed

idiosyncrasies in larval swimming over temporal scales ordinarily not considered, the effect(s) of these nuanced ‘behaviours’ on dispersal predictions have yet to be evaluated i.e. do they actually make a difference to dispersal predictions? Here, we explore how this reverse-engineered swimming behaviour affects larval dispersal estimates within a biophysical model framework, and compare the output with those produced by a passive model (i.e. without ‘behaviour’) and a model implementing TVM behavioural rules.

## 2. Methods

### 2.1. The Study Area

*In-situ* vertical distribution data of *Mytilus* spp. collected in the southern Irish Sea (described in Knights et al. 2006) were used to reverse-engineer temporal changes in larval swimming behaviour over a tidal cycle (described in James et al. 2019). Here, we assess the effect of differential behavioural parameterisation on dispersal using an ocean circulation model coupled to a particle tracking module for the same Irish Sea region (Fig. 1). Water depths in this region are typically less



**Fig. 1.** Mean surface flows in (a) Spring 2005 (April 1<sup>st</sup> – June 30<sup>th</sup>) and (b) Summer 2005 (July 1<sup>st</sup> – September 30<sup>th</sup>) derived from v3.4 of the Nucleus of European Modelling of the Ocean (NEMO AMM7 (Met Office, UK)). Location of the *in-situ* sampling regime undertaken by Knights et al. (2006) on which reverse engineered behaviours were calculated (James et al., 2019) is indicated by the red dot and was the location for particle release within the model framework.

than 100 m, although depths can reach up to ~150 m in the central channel and tidal flows typically oscillate in the North-South direction. The Irish Sea represents a typical semi-enclosed tidally influenced coastal basin with dynamical length scales of 10-1000 km.

## 2.2. The Hydrodynamic Model

Hydrodynamics in the study domain were simulated using the Coastal Ocean version 5 (CO5, O'Dea et al. 2017) of the 7km Atlantic Margin Model (AMM7), which uses the NEMO (Madec et al., 2016) ocean circulation model. The NEMO AMM7 model was developed by the Met Office in collaboration with the National Oceanography Centre and has been extensively refined and validated against observations for the UK shelf seas region to be a good representation of the coastal ocean for the study region. This model resolves prognostic variables (velocity, turbulence, salinity, temperature) on a curvilinear orthogonal horizontal grid with a horizontal resolution of approximately 7 km, and a vertical grid derived from 51 stretched- $\sigma$  levels with realistic GEBCO bathymetry (Madec et al., 2016; O'Dea et al., 2017). It includes atmospheric (ERA-interim), tidal (TPX07.2), and open boundary (ORCA0083) forcing, providing realistic 3D current velocities. The AMM7 model domain encompasses the entire northwest European shelf region, but here we focus on the Irish Sea subregion for which a suitable subdomain was selected. The model was re-run for a 6-month period from 1<sup>st</sup> April 2005 to 31<sup>st</sup> September 2005 to coincide with the time-frame of an *in-situ* sampling programme undertaken by Knights et al. (2006) and hourly velocity fields were stored for the subdomain in order to capture the strong tidal flows present in the Irish Sea (Brown et al., 2003).

## 2.3. The Particle Tracking Model

Particles were tracked using a version of the Lagrangian TRANSport model (LTRANS v.2: Schlag and North, 2012), in which larval behaviours can be governed by the tidal state (see detailed explanation in the Swimming Behaviours subsection), modified to work with NEMO model output (Mayorga-Adame et al., 2022). LTRANS is an offline individual-based particle tracking model that runs with the stored predictions of a 3D hydrodynamic model, tracking the trajectories of particles in three dimensions based on advection, diffusion and individual particle behaviours. The model includes a 4<sup>th</sup> order Runge-Kutta scheme for the advection of particles and a random walk, scaled by the spatially and temporally variable vertical viscosity coefficient of the underlying hydrodynamic model to simulate vertical movement due to turbulence at sub-grid scales (Visser et al., 1997; Ross and Sharples, 2004). This scheme solves for the *u*, *v*, and *w* current velocities (representing the *x*, *y*, and *z* directions) at the location of each particle using an iterative process that incorporates velocities at previous and future times to provide the most robust estimate of the trajectory of particle motion in water bodies with complex fronts and eddy fields, such as the Southern Irish Sea (Dippner 2004).

Preliminary convergence testing was undertaken to determine the appropriate number of particles to be released within the model. This test, following Robins et al. (2013), indicated that simulations with 10,000 particles were sufficient to capture variation within the population whilst maintaining computational efficiency.

## 2.4. Swimming Behaviours

Larval behaviours can be specified within LTRANS via the behaviour sub-routine. Modifications were made to the behavioural sub-routine to test two active swimming behaviours: (1) Applying a tidal vertical migration (TVM), whereby individuals are parameterised to swim-up during the flood tide and down during the ebb tide at a fixed rate of 1  $\text{mm s}^{-1}$  in alignment with values in the literature (e.g. Chia et al. 1984; Sprung, 1984; Young, 1995) and values used by other biophysical

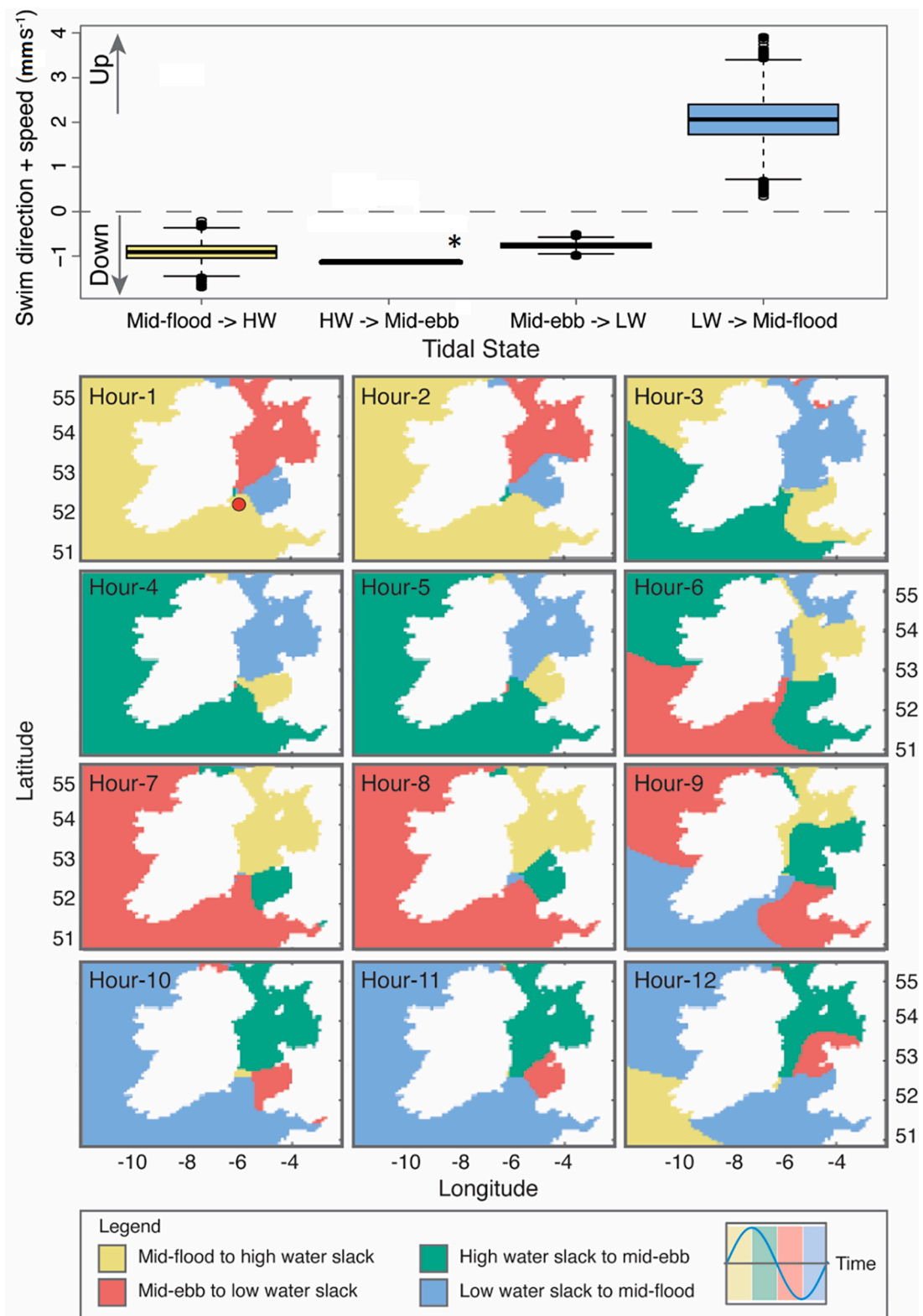
modelling studies focussing on bivalves (e.g. Robins et al., 2013; Daigle et al., 2016), and (2) Reverse-engineered swimming behaviour (REV), in which virtual larvae were configured to swim at a random speed taken from a normal distribution profile fitted over the Modelled Predictive Capability (MPC) for a range of swimming speeds for each tidal state (James et al., 2019). The MPC approach for calculating swimming speed is described in full in James et al. (2019). Approximations of best-fit swimming speeds were identified for three of the four tidal states (Fig. 2 top). Estimated swim speeds ( $\text{mm s}^{-1}$ ) were:  $-0.91 \pm 0.2$  (mid-flood  $\rightarrow$  HW);  $-0.74 \pm 0.07$  (mid-ebb  $\rightarrow$  low water); and  $2.06 \pm 0.5$  (low water  $\rightarrow$  mid-flood). For the 3-h tidal period ranging from high-water to mid-ebb, predictive capability of the MPC model was low. During this stage of the tide, particles were configured to swim downward at a fixed rate of  $1.1 \text{ mm s}^{-1}$ , which was the speed that achieved the closest match based on lowest total sum of squares error (James et al. 2019). Both TVM and REV behavioural models were also compared against a passive model with no larval behaviour applied.

The NEMO output was augmented with two additional gridded variables, as functions of time (hourly), latitude and longitude. These variables were: 1) 'stateid', which stored the current tidal state ((a) mid flood to high water slack, (b) high water slack to mid ebb; (c) mid-ebb to low water slack; or (d) low-water slack to mid-flood. (See Fig. 2)); and 2) 'tchange', which stored the time (in seconds) of the state change if it occurs during the gridded hour period. These variables were computed using the modelled sea surface height data. Every modelled hour, LTRANS was configured to read the variables 'stateid' and 'tchange' from the underlying hydrodynamic model. The 'tchange' variable was used so that if a change in the state occurred during the modelled hour, larval behaviour changed at this point, rather than at the next timestep. To achieve this, larval behaviour within the model was reconfigured at each internal timestep (30s). In the case of the REV simulation, the exact swimming speed of each individual particle was chosen randomly from a normal distribution around the best fit approximation, allowing representation of behavioural stochasticity within the larval population. This approach of quantifying the tidal state in space and time was chosen over simpler methods of determining the tidal state (i.e., using tidal charts and a time counter within the model: *sensu* Daigle et al., 2016), as at a single time-point (e.g., 'Hour 1'), the tidal state could be fundamentally different depending on its position within the study domain relative to an amphidromic point (Fig. 2 bottom) resulting in an incorrect behavioural response in both space and time.

## 2.5. Particle Release and Tracking

The particle release location within the model was chosen to match the location of *in-situ* sampling (52.2N, 6.15W; Knights et al., 2006). Particles were released following observed proportional distribution patterns for each tidal state, binned according to the vertical grid of the hydrodynamic model (following the methodology of Daigle et al., 2016), and individual runs were undertaken for each starting profile correlating to the 4 identified tidal states. Runs simulating each of the three behavioural parameterisation approaches (namely: Passive, Tidal Vertical Migration (TVM), and Reverse-Engineered Vertical Migration (REV)) were undertaken for spring (April) and summer (July) to account for potential differences in dispersal due to seasonal stratification and the frontal system that develops in the Southern Irish Sea (Neill et al., 2012). No difference in vertical distribution patterns of larvae with respect to tidal phase (i.e. neap vs. spring) were identified in the field (Knights et al., 2006), so phase was not considered here. Particles were released on the first spring tide following April 1<sup>st</sup> (spring) or July 1<sup>st</sup> (summer). Particles were tracked for a duration of 28 days, which is within the typical range for ciliated larvae (Siegel et al. 2003; Hartnett et al. 2007; Tian et al. 2009). LTRANS was configured to output the location (lat/lon) and depth of each updated particle every 30 minutes. Output files were then processed in MATLAB (v. 2020a) to calculate: (i) radial distance travelled by the particle from its source to its end point,





**Fig. 2.** *Top.* Bootstrap distributions of predicted larval swimming speed ( $\text{mm s}^{-1}$ ) and direction (upward (+)/downward (-)) based on mean  $\pm$  standard deviation estimates based on 'best match' observed vertical distribution profiles (after James et al. 2019) during each tidal state condition. \*indicates no match determined based on Model Predictive Capacity testing and the best estimate shown. *Bottom.* Variation in spatio-temporal tidal propagation and state condition around an amphidromic point over a 12-h (Hour-1 to Hour-12) period, relative to the observation site (red dot on Hour-1 plot). Four state conditions are shown: mid -flood to high water slack (yellow); high water slack to mid -ebb (green); mid-ebb to low water slack (red); and low- water slack to mid-flood (blue).

and (ii) the cumulative distance travelled by the particle (i.e. the total path length), at 30 minute intervals.

## 2.6. Statistical Analysis

All analyses were undertaken in R (R Core Team, 2020). A Linear Mixed Effects (LME) model in the R package, 'nlme' (Pinheiro et al. 2020), was used to test the effects of four fixed variables on mean distance travelled by a particle. Model factors were: (1) **Behaviour** (levels: Passive; Tidal Vertical Migration; Reverse-engineered); (2) **Season** (levels: Spring; Summer); (3) **Tidal State at Release** (levels: flood; low water slack; ebb; high water slack); and (4) **Prediction** (levels: radial distance; cumulative distance). **Time** (days) was included as a random variable, and an autocorrelation structure (AR(1)) applied following identification of temporal/spatial autocorrelation using the auto-correlation function (ACF, package 'nlme'; Pinheiro et al. 2020). The maximal model (AIC = 1289.2) was therefore as follows:

$$\begin{aligned} \text{Maximal Model} &\leftarrow \text{LME}(\sqrt{\text{mean distance}} \\ &\sim \text{Behaviour} * \text{Season} * \text{Tidal State at Release} * \text{Prediction}, \text{random} = \\ &\sim 1 | \text{Time}, \text{correlation} = \text{corAR1}()) \end{aligned} \quad (1)$$

A stepwise model reduction approach based on Akaike Information Criterion (AIC; Sakamoto et al. 1986) and likelihood ratio (performed using the function anova() in R) was used to test the effect of model simplification on estimates (Appendix 1). The following reduced model was identified without loss of predictive power (AIC = 1225.7):

$$\begin{aligned} \text{Reduced Model} &\leftarrow \text{LME}(\sqrt{\text{mean distance}} \\ &\sim \text{Behaviour} * \text{Prediction} + \text{Season} + \text{Tidal State at Release}, \text{random} \\ &= \sim 1 | \text{Time}, \text{correlation} = \text{corAR1}()) \end{aligned} \quad (2)$$

Generalised Additive Models (GAMs) were used to assess relationships between behaviour, tidal state, and season and their effect on radial distance and cumulative distance over a 28-day planktonic larval duration. The GAM modelling incorporated fitting a smooth function (a thin plate regression spline) to the timestep covariate (days since release) and followed a gamma distribution for each of the response variables. GAM models were fitted using the R package 'mgcv' (Wood, 2011). By default, this package uses the log link function for gamma distributions which is a good fit as the log link can represent well underlying multiplicate process common in ecology (Anderson, 2014).

Pettitt's test (Pettitt, 1979) was used to estimate the mean time point for a shift in central tendency in radial distance over the time series, using the R package 'trend' (Pohlert, 2020). Pettitt estimates from model simulations were then compared using one-factor ANOVA on a randomised normally distributed sample (n=100 using the rnorm() function in R) of values based on the mean and standard deviations of the Pettitt's test outcome. ANOVA and Tukey post-hoc pairwise comparison tests were used to compare the mean radial distances travelled for each explored timepoint and Mood's Pairwise median tests (Mood, 1954) used to formally compare kernel medians of model outputs.

The 'meanm' function in MATLAB (v.2020a) was used to calculate the central tendency of the dispersal cloud as a lat/long coordinate for each season (spring/summer), behaviour (passive/REV/TVM) and day (1, 7, 14, 21, 28 days) combination, and the Euclidean distance between central tendencies calculated using the 'sp' package in R (Pebesma and Bivand, 2005). The 'meanm' function calculates the geographic mean position of input latitude and longitude coordinates while correcting for the sphericity of the Earth (modelled as an ellipsoid) thereby calculating the geographic mean rather than an arithmetic mean. Full details of this correction can be found here (<https://uk.mathworks.com/help/map>

/geographic-statistics-for-point-locations-on-a-sphere.html). The 'cor' function in R was used to calculate the correlation between the central tendencies and correlation plots were formally tested using Spearman's rank correlation coefficient (Spearman, 1904).

## 3. Results

### 3.1. LME modelling

There was a significant interaction between behaviour and prediction method (LME (Behaviour × Prediction):  $F_{2,226} 8.16$ ,  $p < 0.001$ ) on mean dispersal distance. Season and tidal state of release had no significant effect on mean dispersal distance (Table 1). Mean radial and cumulative distances after 28 days were greatest in passive simulations, travelling on average 79 km from source and 1359 km along their path, respectively. REV particles travelled significantly shorter distances, travelling a mean radial distance of 33.7 km ( $2.3 \times$  shorter), and a mean cumulative distance of 359 km ( $3.8 \times$  shorter). Notably, mean radial distance of REV particles increased by only 1.6 km between 14 and 28 days, with no significant difference in the radial distances between 14 and 21 days (Tukey's HSD:  $p = 0.329$ ). In contrast, TVM particles travelled 52 km ( $+1.5 \times$  REV;  $-1.5 \times$  Passive) after 28 days, and a mean cumulative distance of 1024 km ( $+2.9 \times$  REV;  $-1.3 \times$  Passive) (Fig. 3).

### 3.2. GAM fitting and identifying points of change

In general, GAM models were a good fit, with behaviour, season, and tidal state explaining 75.7% of the deviance in radial distance travelled by particles from their source, and 97% of the deviance in cumulative distance travelled by particles along their dispersal path (Tables 2 and 3). All incorporated covariates could significantly predict radial distance travelled from source (Table 2). Results demonstrated that both radial distance and cumulative distance path length differed with respect to behavioural modelling approach and season, although seasonal effects were only observed in passive model simulations, and not in behavioural models (Fig. 4). Differences between dispersal depending on tidal state release point occurred only in the passive model, with particles traveling greatest radial distances from source and shortest cumulative (path) distances when released on the ebb tide (Fig. 4b, h).

Estimates of mean time point for a shift in central tendency of the time series indicated significant differences in the point of change for each behaviour × season interaction combination (Fig. 5). Passive particles released in the spring were the latest to shift, occurring at  $15.59 \pm 0.57$  days, and 1.7 days later than in the summer ( $13.91 \pm 0.73$  days). Shifts in the TVM model occurred at 14.92 days ( $\pm 0.15$  days) and 14.42 days ( $\pm 0.25$  days) in Spring and Summer, respectively. REV particles exhibited a shift in central tendency after just 9.68 days ( $\pm 0.17$  days) in Spring, but unlike the passive and TVM models, showed an increase to 10.27 days ( $\pm 0.29$  days) in Summer.

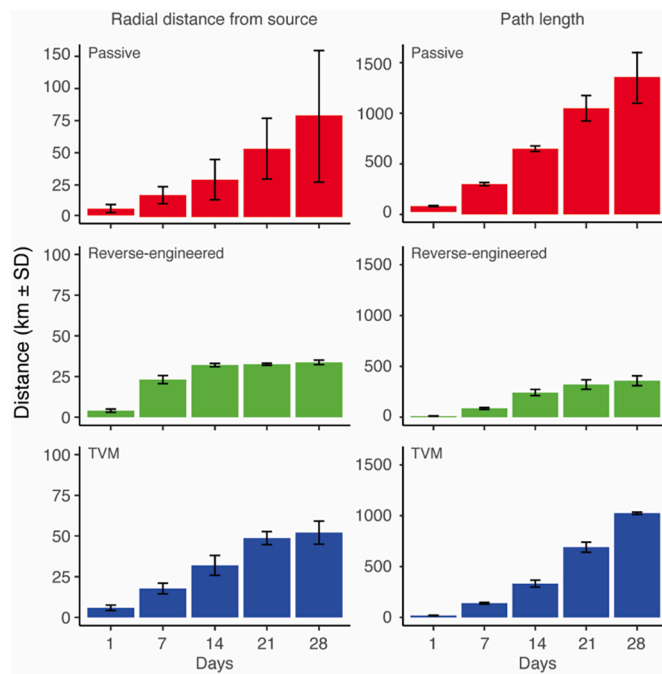
### 3.3. Density Kernels (Probability Density Functions)

Comparison of dispersal kernels revealed differences between the modelling approaches that increased in magnitude over time. Differences in dispersal distance between behaviors were small when larval

**Table 1**

Effects of fixed factors in the reduced LME model [Eqn. 2] on mean distance travelled by a particle.

Source of Variation	numDF	denDF	F-value	P-value
Behaviour	2	226	232.62	< 0.0001
Season	1	226	1.49	0.223
Tidal State	3	226	0.02	0.995
Prediction	1	226	112.16	< 0.0001
Behaviour × Prediction	2	226	8.16	< 0.001



**Fig. 3.** Left column. Radial distance (km  $\pm$  SD) travelled ‘as the crow flies’ from a single point source location. Right column. Mean path length (km  $\pm$  SD) travelled by particles after 1, 7, 14, 21 and 28 day planktonic larval durations for each model scenario (passive (red); reverse-engineered (green); TVM (blue)) aggregating over both release seasons and all states of the tide.

**Table 2**

Summary of the GAM  $\log(\text{RadialDistance} + 1) \sim s(\text{Days}) + \text{Behaviour} + \text{Season} + \text{TidalState}$ .

Parametric Coefficients	Estimate	Std. Error	T value	Pr ( $> t $ )
(Intercept)	3.318387	0.005069	654.54	$<2e-16$ ***
Behaviour REV	-0.053756	0.004693	-11.45	$<2e-16$ ***
Behaviour TVM	0.062178	0.004693	13.25	$<2e-16$ ***
Season Summer	0.085295	0.003832	22.26	$<2e-16$ ***
TidalState Flood	0.120265	0.005419	-22.19	$<2e-16$ ***
TidalState HW	-0.085168	0.005419	-15.72	$<2e-16$ ***
TidalState LW	-0.071867	0.005419	-13.26	$<2e-16$ ***
Smooth Terms	Edf	Ref.df	F	p-value
S(Days)	8.95	8.999	11815	$<2e-16$ ***

Significance codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05

**Table 3**

summary of the GAM  $\log(\text{PathTravelled} + 1) \sim s(\text{Days}) + \text{Behaviour} + \text{Season} + \text{TidalState}$ .

Parametric Coefficients	Estimate	Std. Error	T value	Pr ( $> t $ )
(Intercept)	6.2108180	0.0029394	2112.935	$<2e-16$ ***
Behaviour REV	-1.2002112	0.0027214	-441.03	$<2e-16$ ***
Behavior TVM	-0.5749442	0.0027214	-221.269	$<2e-16$ ***
Season Summer	0.0585558	0.0022220	26.353	$<2e-16$ ***
TidalState Flood	0.187068	0.0031424	5.953	2.66e-09 ***
TidalState HW	0.0040826	0.0031424	1.229	0.194
TidalState LW	0.0005868	0.0031424	0.187	0.852
Smooth Terms	Edf	Ref.df	F	p-value
S(Days)	8.997	9	102768	$<2e-16$ ***

Significance codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05

duration was  $<1$  day: TVM particles travelled 1.8 km farther from source than REV particles, and 1.7 km farther from source than passive particles, and the median distance travelled by TVM particles (5.3 km) was 1.4 km and 1.5 km greater than REV and passive particles, respectively. After 7 days, median dispersal distance of REV particles (23 km) was

significantly greater than that of passive or TVM models (both 18.2 km). After 14 days, there was a small, but significant difference (pairwise Moods median test,  $p < 0.001$ ) in the median dispersal distance between REV (31.9 km) and TVM particles (32.4 km). Interestingly, REV particles showed markedly lower propagule dispersion (SD = 5.5 km) in comparison to passive (SD = 16.9 km) and TVM (SD = 9.6 km) simulations (Fig. 6) with 50% of the population within 4.3 km of the median, in contrast to passive (13.1 km) and TVM (12.9 km) simulations. REV particles became increasingly clustered over time, unlike in passive and TVM experiments, in which, particles continued to undergo dispersion over time (Fig. 6). After 28 days, there were significant differences in median radial dispersal distance for all models. REV particles travelled shortest distances (median distance: 32.9 km) and 50% off the population were aggregated between 30.5 km and 35.3 km from source. In contrast, median dispersal distance was 46.4 km (41% further) and 54.9 km (67% further), and propagule dispersion 16.7 $\times$  and 9.6 $\times$  greater in passive and TVM simulations, respectively.

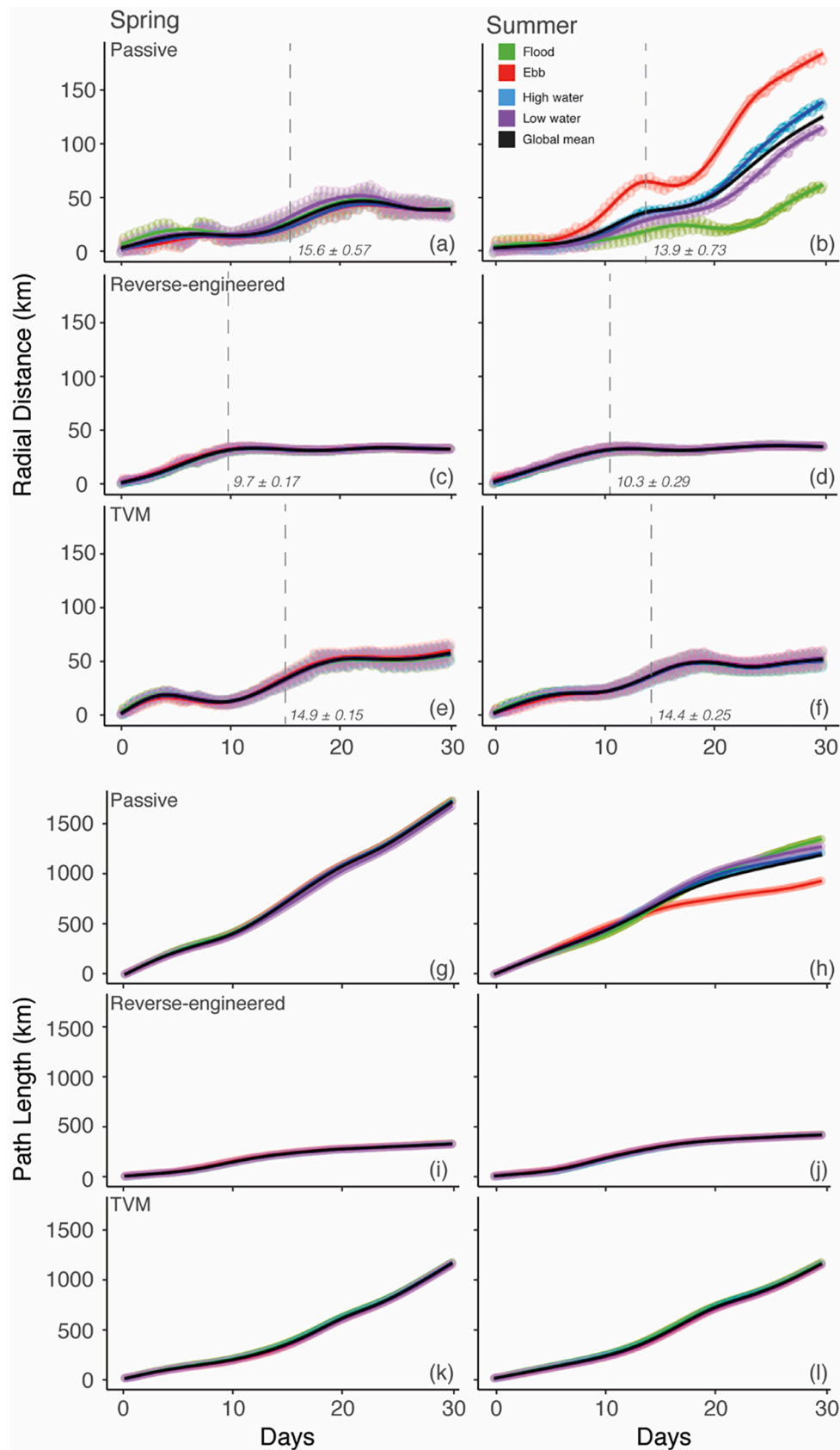
### 3.4. Biogeography

The modelling approach implemented led to markedly different biogeographic distributions of larvae, both in terms of biogeographic spread and direction of travel (Fig. 6). REV simulations suggested a net south-westerly movement, whereas the TVM model predicted a net northward movement over time. Passive simulations indicated a considerable effect of season on dispersal, with particles travelling offshore in spring, and both north and southwest in summer, and with a change in central tendency of up to 217 km (Fig. 8). There were strong positive correlations between behavioural models and seasons for short planktonic durations, lasting up to 14-d in summer, and just 7-d in spring (Fig. 7).

## 4. Discussion

The capacity of biophysical models to predict dispersal and allow spatial and temporal assessment of connectivity are currently at the forefront of larval dispersal research and central to on-going management and conservation efforts. Yet understanding if, when, and how to parameterise the ‘biological’ component of these models and the potential effects of inaccurate representation of biological traits on model predictions has remained a key challenge (Metaxas and Saunders, 2009). It is largely accepted that larval behaviour plays a key role in larval transport and wider ecological functioning but despite this recognised importance, many dispersal models still assume passive dispersal (see Swearer et al., 2019 for review). There is clear recognition of the need to include behaviour in biophysical models (e.g. Garland et al., 2002; Phelps et al., 2015; Daigle et al., 2016; Mayorga-Adame et al., 2017; Bode et al., 2019; James et al. 2019) but how behaviour should be incorporated remains debatable. Here, we highlight the sensitivity of model predictions to modification of just a single behaviour, larval swimming, that results in markedly different dispersal predictions.

It has long been recognised that small changes in the vertical position of a larva could greatly influence dispersal trajectory due to depth-related differences in the magnitude and direction of the current (Pringle, 2007; Correll et al., 2012; Torres et al., 2018), and that some organisms actively migrate in the vertical in order to take advantage of favourable currents (i.e. Selective Tidal Stream Transport: Forward et al., 2003; Knights et al., 2006; Kunze et al., 2013; Peterio and Shanks, 2015), avoid predation (i.e. Diel Vertical Migration – Lampert, 1993; Scheuerell and Schindler, 2003; Gibson et al., 2016; Pinti and Visser, 2019), and access available food sources (Gibson et al., 2016). However, what remains uncertain is the extent to which a larva can manipulate its position *in-situ*. Here, we incorporated a state-of-art assessment of larval swimming behaviour (REV) based on statistical models of likelihood of match between model simulations and field-derived observations of vertical distribution profiles after James et al. (2019); an approach



**Fig. 4.** Fitted Generalised Additive Model (GAM) of (a-f) radial distance from source over time (days), and (g-l) path length (km) grouped by modelled behaviour (passive, reverse engineered, tidal vertical migration) and season (Spring; Summer). Vertical dashed lines on plots (a-f) and accompanying text indicate the estimated mean time point for a shift in distributional central tendency of the time series based on Pettitt's test outcomes.



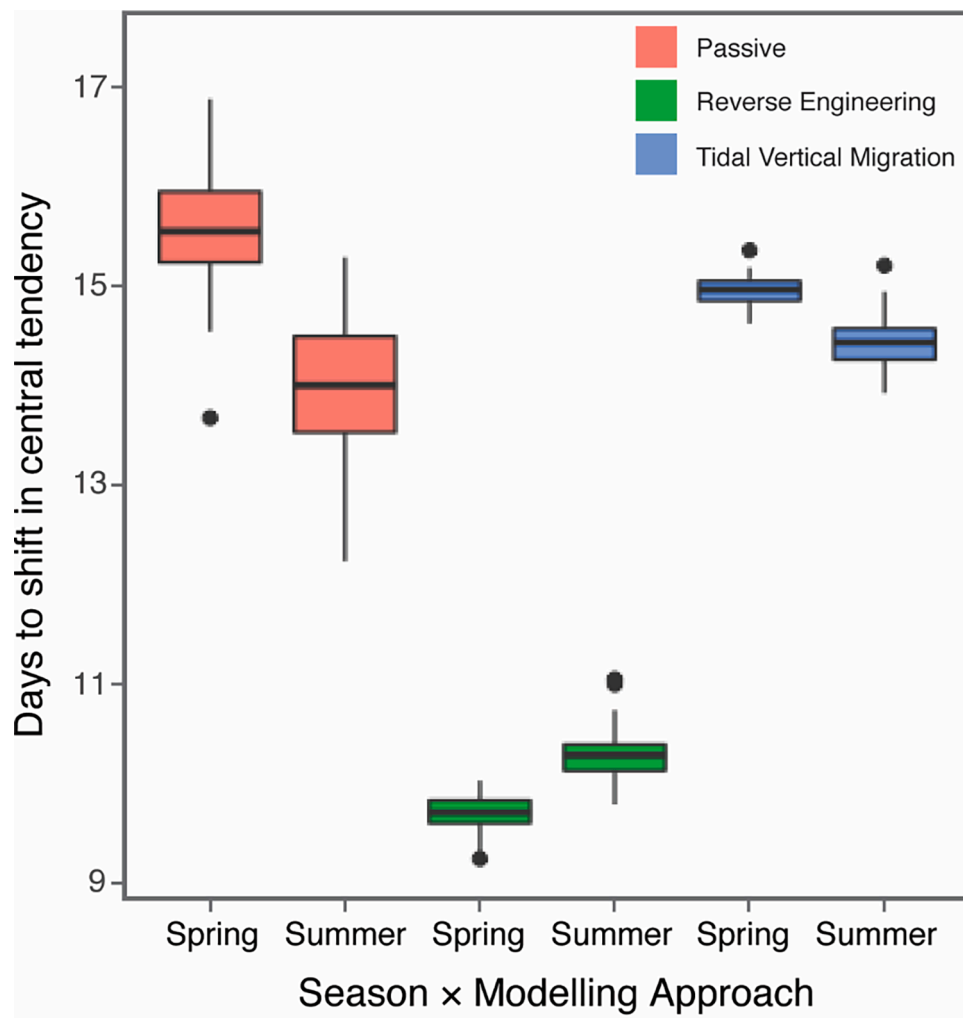


Fig. 5. Estimated time to shift in central tendency (days) following Pettitt's test for each of model approach  $\times$  season combination. Dots indicate outliers in the data. All pairwise comparisons are significantly different from each other ( $p < 0.001$ ).

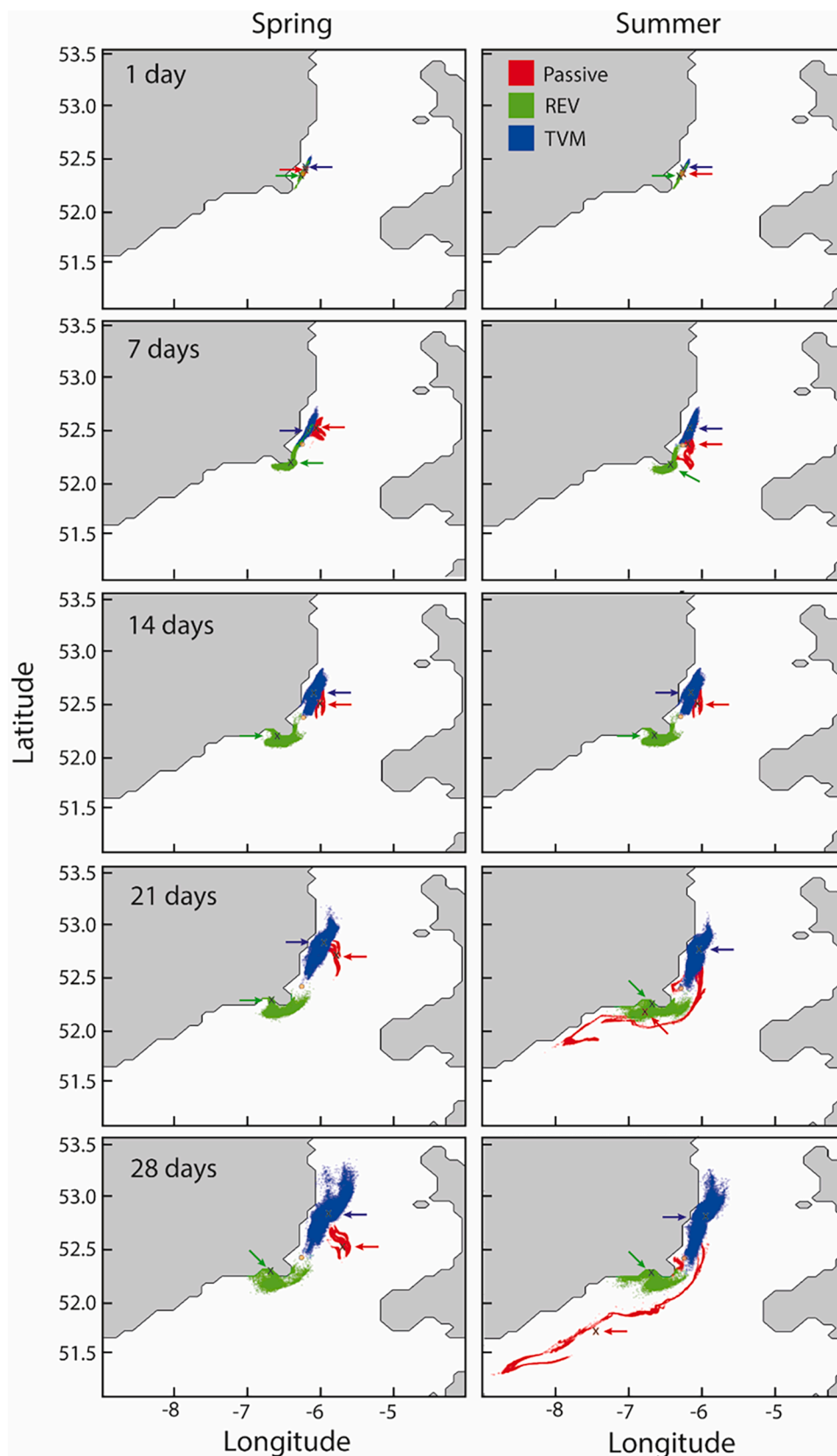
developed to address some of the limitations of laboratory observations of behaviour, specifically their failure to capture 'real-life' interactions between larvae and their environment (Bowler and Benton, 2005) and subsequent expression of a behaviour as movement. There is also mounting evidence that not all larvae are equal (see Toonen and Pawlik, 2001; Marshall et al., 2010 and Nanninga and Berumen, 2014 for reviews) with a high degree of intra-specific variability. The REV method of behavioural parameterisation developed in James et al. (2019) inherently captures this intra-population variation by stochastically assigning behaviours within the larval cohort based on a range of likely swimming speeds inferred from the field; an approach previously advocated by Fisker et al. (2007). Interestingly, we demonstrate that even with inclusion of intra-population variability in capacity to 'behave', the dispersal of REV particles displayed the lowest variance and dispersal distances of all three model scenarios, with particles travelling considerably shorter distances than passive or TVM equivalents (on average 1000 km less than passive particles and 665 km less than TVM particles). These results further reinforce the potential for active behaviours such as vertical migration (Knights et al. 2006) to be an effective transport mechanism for even small, relatively slow-swimming organisms despite exposure to flow-fields that are often orders of magnitude faster.

Our results suggest that for organisms with short planktonic durations (i.e., 1 day), dispersal predictions are largely the same irrespective of the exclusion/inclusion of behaviour, suggesting that a passive

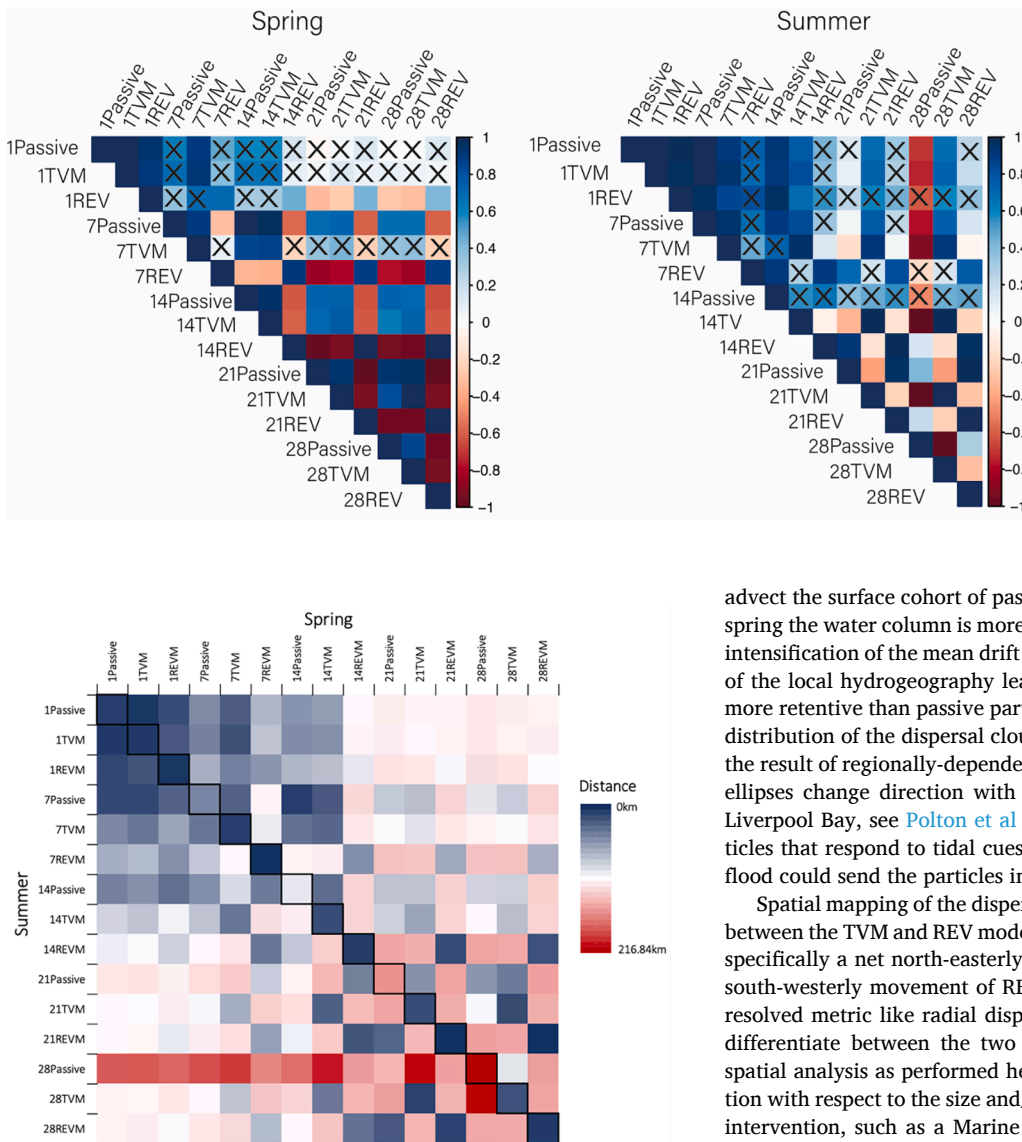
dispersal model will provide comparable dispersal predictions to behaviourally complex models. Over time, however, we show that the incorporation of (a) behaviour, and (b) differences in behaviour parameterisation, become increasingly important. James et al. (2019) suggested that inaccurate parameterisation of behaviours would lead to additive errors in model predictions as a function of time. Here, all model comparisons, but especially that of REV vs. TVM simulations reinforce this concern, where after 14 days, the REV modelling approach results in biogeographic 'stability' and promotes localised retention irrespective of time, whereas the TVM and passive models indicate continued dispersal away from source over time (Fig. 3).

#### 4.1. Cohort clustering

Implementation of the REV approach led to rapid early dispersal followed by high levels of clustering and short median dispersal distances from their source. Clustering of the larval cohort has ecological pros and cons; it can provide advantages, such as allowing organisms to evade predation and offer protection through a 'safety in numbers' approach but may lead to increased mortality due to intraspecific competition for resources (Hixon and Jones, 2005). Mortality was not considered here as its inclusion was beyond the scope of our objectives but it is a key factor to consider in estimating population dynamics from dispersal models (Trembl et al., 2015), and hence the design of connectivity-informed conservation agendas should endeavour to



**Fig. 6.** Biogeographic predictions of larval dispersal over time (1-28d) modelled in LTRANS v2.0 using three behavioural classifications (red - passive; green - reverse-engineered; blue - TVM) in spring (left) and summer (right). Larvae are dispersed from the same single-point source (orange dot). The centre of gravity (CoG) for each of the dispersal clouds are shown by an 'X' and indicated with a coloured arrow.



**Fig. 8.** Heatmap of Euclidean distance (km) between central tendencies of paired dispersal kernels generated over time (1, 7, 14, 21 and 28 days) from model predictions using passive, reverse-engineered (REV) and tidal vertical migration (TVM) behaviour in spring and summer. Boxes with thick borders are comparisons between seasons for the same model class (behaviour). The colour ramp indicates minimum (0 km) and maximum (217 km) distances between centre of gravity pairs.

include temporal and spatial species-specific mortality rates (Carr et al., 2017).

#### 4.2. Biogeography – the need for a 3D approach

Inspection of the tidal hydrogeography (Fig 2) illustrates spatial gradients in the timing of the tides, and errors in particle placement manifested as differences in behavioural cue timing. Clearly then, it is unsurprising that passive particles will have a different dispersive kernel when compared to TVM or REV that respond to the tides and which are not significantly different from one another. There is also a notable difference between the seasons for the passive particles. These particles, which are not being vertically mixed, remain at their initial depths. On the other hand, TVM and REV particles experience a degree of vertical homogenisation because of the particle behaviours. In summer, the stratification results in enhanced surface currents which persistently

**Fig. 7.** Correlation matrix of the distance of centre of gravity of the dispersal clouds for each day  $\times$  season  $\times$  behaviour combination. Labels denote the day and the behavioural mode. Pairwise comparisons range from strong positive correlation (close proximity of centre of gravity of dispersal clouds) to strong negative correlation (large distances between centre of gravity of dispersal clouds). Pairs with no significant correlation (Spearman's rank correlation coefficient:  $p > 0.05$ ) denoted by 'X'.

advect the surface cohort of passive particles southwards (Fig 1). In the spring the water column is more evenly mixed and so there is no surface intensification of the mean drift currents. It is likely that specific details of the local hydrogeography lead to the TVM and REV particles being more retentive than passive particles, and that differences in the spatial distribution of the dispersal clouds of REV and TVM particles were also the result of regionally-dependent phenomena. For example, when tidal ellipses change direction with depth (Soulsby 1983; for examples in Liverpool Bay, see Polton et al 2011: Fig 3), we might expect the particles that respond to tidal cues to be more dispersive as both ebb and flood could send the particles in the same direction.

Spatial mapping of the dispersal clouds revealed a marked difference between the TVM and REV models not identified by the dispersal kernel, specifically a net north-easterly movement by TVM particles and a net south-westerly movement of REV particles. Using a single, non-spatial resolved metric like radial dispersal distance in this instance failed to differentiate between the two behavioural models, which without a spatial analysis as performed here, would provide misleading information with respect to the size and/or positioning of a spatial management intervention, such as a Marine Protected Area. Furthermore, distance travelled from source was also an order of magnitude shorter than cumulative distance travelled (path length), irrespective of behaviour and timing of release. We therefore strongly advocate for the use of a Lagrangian approach for predicting dispersal that couples local circulation models with individual based models (Cowen et al., 2006; Rochette et al., 2012) over other 'simplified' approaches that apply mean estimates of dispersal distance (Lockwood et al., 2002; Sala et al., 2002; White et al., 2010) or  $distance = speed \times time$  calculations (Shanks et al 2003; Shanks, 2009).

#### 4.3. Implications

Despite the importance of dispersal to the ecological and evolutionary success of marine organisms, our results highlight our limited understanding of the role of behaviour in dispersal predictions and the need to integrate *in-situ* and modelled data more effectively. Dispersal is a key consideration in estimates of population connectivity and models continue to play a critical theoretical and applied role in science today, whether being used to design Marine Protected Areas (MPAs: Gaines et al, 2003; 2010; Almany et al, 2009; Kaplan et al., 2009; Costello et al., 2010; Krueck et al., 2017; Ross et al. 2017), identify pathways of invasion (Viard et al., 2006; Kitchens et al., 2017), or understand meta-population dynamics and biogeography (Sanvicente-Añorve et al., 2018). We consider models to be an invaluable tool in these endeavours, but the results here highlight the disproportionate effects that even a

single behaviour - larval swimming - can have on model predictions, our understanding of ecosystem functioning, and ultimately, the ecological coherence of marine systems (Jonsson et al., 2020). Although the question of which behavioural modelling approach is best still remains, the results of our REV model are in broad alignment with the findings of other studies (Woodson and McManus, 2007; Shanks 2009; Sundelöf & Jonsson, 2011) and reinforces our thinking that: (1) active larval behaviour does serve as a mechanism to reduce larval dispersal; (2) coastal marine systems, and even physically dynamic systems like the Irish Sea can be relatively 'closed' (*sensu* Cowen et al., 2000), and (3) MPAs and other coherent networks may need to be closer together to ensure coherence. Our results suggest that management decisions made on incorrect behavioural assumptions in dispersal models may overestimate the connectivity between local populations, in contention with the suggestions of Costello and Connor (2019) and Manel et al., (2019) who argue that the spatial scale of marine connectivity is underestimated, leading to a false sense of security in the ecological coherence of protected networks. Although further work is needed, we suggest that - in the meantime - best estimates of dispersal, and specifically biogeography, requires (i) use of a Lagrangian particle-tracking approach coupled with localised circulation models, and ii) empirical data of vertical distribution profiles that allow estimation of larval swimming speeds likely to occur *in-situ* to be resolved and their subsequent application in model simulations.

## 5. Conclusion

Dispersal models play a critical role in theoretical and applied science and remain invaluable tools, contributing to our understanding and management of sustainable ecological networks. The work undertaken in this study provides a novel framework that describes i) implementation of field-derived descriptors of larval behaviours in a dispersal model and ii) comparative analysis of such behaviours against other methods of behavioural parameterisation in these models. To the best of our knowledge, our study is the first to use field data both to inform larval behaviour in a dispersal model, and to seed the 'behaving' particles at the same location as the field study - bridging the gap between models and nature, and providing a unique insight into how the manifestation of larval behaviour *in-situ* may influence dispersal.

## Appendix

Appendix 1. ANOVA of the best fit linear mixed-effects model ( $\text{sqrt}(\text{meandist}) \sim \text{ReleaseState} * \text{Season} * \text{Behaviour} * \text{method}$ ,  $\text{random}=\sim 1|\text{days}$ ,  $\text{correlation}=\text{corAR1}()$ ).

Intercept	1	188	19.849	<0.0001
Behaviour	2	188	206.705	<0.001
Distance metric	1	188	94.079	<0.001
State : Behaviour	6	188	0.157	0.988
Season : Behaviour	2	188	2.038	0.133
State : Distance metric	3	188	0.19	0.903
Season : Distance metric	1	188	1.712	0.192
Behaviour : Distance metric	2	188	6.162	0.003
State : Season : Behaviour	6	188	0.107	0.996
State : Season : Distance metric	3	188	0.182	0.909
State : Behaviour : Distance metric	6	188	0.109	0.995
Season : Behaviour : Distance metric	2	188	0.219	0.803
State : Season : Behaviour : Distance metric	6	188	0.192	0.978

The methodologies and analytical techniques designed in this study can be applied to any species with a planktonic dispersal phase in any location, and provide an important step towards improving the biological 'realism' of behavioural parameterisation in dispersal models.

## CRediT authorship contribution statement

**MKJ:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – Original draft preparation; **GMA:** Software, Data Curation, Writing – Review and editing; **JAP:** Software, IT Resources, Data Curation, Writing – Review and editing; **KLH:** Writing – Review and editing; **AMK:** Conceptualization, Formal analysis, Writing – Review and editing, Supervision, Funding acquisition.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data Availability

Data will be made available on request.

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