ORIGINAL ARTICLE

Long-term interannual variability in larval dispersal and connectivity of the Norway lobster (Nephrops norvegicus) around Ireland: When supply-side matters

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Abstract
Dispersal of meroplankton larvae in the ocean is a key process which determines larval supply to areas of suitable habitat and enables connectivity between populations, particularly for nonmigratory species. Our objective was to use a biophysical larval transport model to create a time series (2000–2019) of larval retention, dispersal distance and connectivity estimates for the commercially important Norway lobster (Nephrops norvegicus) on mud grounds off Ireland. Where time series of population estimates were sufficiently long to conduct analysis, we also investigated if larval dispersal indices could be used to predict variations in adult density, after a lag period, hypothesising that this would only apply to grounds with consistently low larval supply. Grounds off Ireland had varying characteristics related to their ability to retain and exchange larvae which was influenced by the local hydrodynamic regime and spatial isolation from other grounds. Larval supply was consistently low on the Aran grounds to the west of Ireland, which have experienced abundance declines in the past. The time series of modelled larval dispersal indices at the Aran grounds was linked to empirical adult burrow densities with a 3-year lag. Whereas the western Irish Sea, which has consistently high larval supply, showed no such relationship. Models can provide important larval recruitment information early in the life cycle for species of commercial or conservation importance.

KEYWORDS
connectivity, dispersal, larvae, Nephrops norvegicus, Norway lobster, recruitment, supply-side ecology

1 | INTRODUCTION

For species with nonmigratory adult stages, dispersal of meroplankton larvae, that is, spread from spawning site to settlement location in the ocean, enables connectivity, (i.e. exchange between separated populations) and colonisation of new habitat areas (Cown & Sponaugle, 2009; Pineda et al., 2007). Physical and biological factors interact to determine larval dispersal. For example, the dispersal of planktonic larvae is heavily influenced by ocean currents (Gilg & Hilbish, 2003; White et al., 2010). However, larvae may influence horizontal transport by regulating their vertical distribution in the presence of depth-varying currents (McGeady et al., 2019; Queiroga & Blanton, 2005). Moreover, for ectothermic species, whose development is strongly influenced by ambient temperature, warmer
conditions lead to faster larval growth rates and reduced planktonic larval dispersal durations (O’Connor et al., 2007). Temperature during embryo incubation can also influence the time of larval hatching (McGeady et al., 2021) which in turn determines the initial thermal, hydrodynamic and trophic conditions encountered by larvae (Cushing, 1990; Fernand et al., 2006; Gilbert et al., 2010).

Meroplankton larvae rely on finding suitable habitat for successful settlement; hence, oceanography can act as an important constraint on larval recruitment (Pearce & Phillips, 1988; Sánchez & Gil, 2000). Significant interannual variability in oceanography could result in larval supply and settlement (arising from local retention and imports from nearby subpopulations) fluctuating widely from 1 year to the next, with consequences for recruitment and abundance (Ospina-Alvarez et al., 2015; Siegel et al., 2008). By contrast, consistently high rates of larval settlement may result in adult densities being limited by environmental carrying capacity and significant postsettlement mortality once that capacity is exceeded (Hill & White, 1990; Minchinton & Scheibling, 1991). For example, Steele (1997) reported such significant density-dependent postsettlement mortality in gobies that it almost removed the link between densities of adults and recruits. Recognising scenarios leading to low larval settlement is important, particularly for commercially harvested species. For example, age-1 Atlantic cod recruitment success in the Gulf of Maine was linked to northward wind velocity during May due to its influence on larval retention (Churchill et al., 2011). Moreover, Wilderbuer et al. (2002) reported that years in which modelled flatfish larvae were dispersed to nursery areas coincided with higher recruitment in the Bering Sea.

The Norway lobster (Nephrops norvegicus) is an important commercial species throughout its range in the Northeast Atlantic Ocean and Mediterranean Sea with European landings worth €360 million in 2016 (EUROSTAT, ec.europa.eu/eurostat/web/fisheries/data/database). The benthic juvenile and adult stages have a patchy distribution due to a requirement for mud habitat to construct burrows (Bell et al., 2006). The species is relatively sedentary and spends most of its time in burrows, only leaving to search for food or to mate (Sardà, 1995). Due to its sedentary nature, N. norvegicus do not migrate between mud grounds separated by uninhabitable substrate. Instead, connectivity between mud grounds is enabled by the planktonic larval phase where transport is driven by ocean currents.

Prior to larval hatching, eggs are carried on the female abdomen during the temperature-dependent embryo incubation period (Farmer, 1974). Planktonic larvae predominantly inhabit the upper 40 m of the water column (McGeady et al., 2019) and progress through three larval stages (I–III). Larval development is temperature-dependent, and pelagic larval durations (PLDs) can last 1–2 months at temperatures averaging 8.5–14°C for Stages I–III (Dickey-Collas, McQuaid, et al., 2000; Smith, 1987; Thompson & Ayers, 1989). Larvae also perform a diel vertical migration that involves two ascents and two descents per day (McGeady et al., 2019). At the end of the pelagic phase, the postlarvae begin to descend to the benthos while searching for suitable mud habitat which is crucial to their survival.

Calculating recruitment estimates for N. norvegicus is problematic as hard structures are lost during moulting, preventing the use of persistent anatomical features to determine age (Hartnoll, 2001; Sheridan et al., 2016). Juveniles are rarely observed due to a tendency to remain in burrows (Cobb & Wahle, 1994), and efforts to estimate recruitment via burrow counts are complicated by adults and juveniles sharing burrows (Tuck et al., 1994). Finally, length-frequency distributions from fisheries surveys tend to lack multimodal structure and are difficult to separate into year classes (Farmer, 1973), again hampering recruitment estimation. In the absence of more direct methods, a proxy for larval recruitment may be provided by measuring larval dispersal using biophysical larval transport models. These could be used to estimate larval supply for N. norvegicus mud grounds. For example, Ospina-Alvarez et al. (2015) reported a link between the proportion of modelled anchovy larvae reaching a nursery area and the proportion of age-0 anchovies from an acoustic survey. Similarly, modelled larval retention indices were linked to annual anchovy biomass in the central Mediterranean (Patti et al., 2020).

Several N. norvegicus grounds are situated off the coast of Ireland and are assessed as discrete functional units (FUs) using underwater TV (UWTV; Figure 1). The longest time series of UWTV burrow density estimates are for the Aran grounds (FU17, 2002–2020) and western Irish Sea (WIS) ground (FU15; 2003–2020; ICES, 2020). To the west of Ireland, densities on the Aran grounds have declined from a historical high of 1.08 burrow m⁻² in 2004 to 0.29 burrow m⁻² in 2020 (Figure S1). Periodically low larval retention levels on the grounds suggest potential issues with larval supply (McGeady et al., 2019) coupled with its relative spatial isolation which limits larval imports from other grounds (O’Sullivan et al., 2015). In stark contrast, the WIS ground has remained stable over time with adult densities remaining above 0.73 burrow m⁻² (Figure S1). The WIS ground is characterised by high densities of small sized adults which is linked to postsettlement factors, namely, density-dependent suppression of size and growth (Johnson et al., 2013; Merder et al., 2020). The population exhibits significant interannual variability in larval dispersal although retention consistently remains above 14% (McGeady et al., 2021).

The contrasting Aran and WIS N. norvegicus grounds offer an opportunity to examine how larval ‘supply’ and recruitment affect adult density fluctuations in two contrasting scenarios: an apparent recruitment-limited population (Aran) and a stable population (WIS) that is more likely to be influenced by postsettlement processes, such as competition, due to high population densities. ‘Supply-side’ ecology was first defined in rocky shore populations and recognises the role that recruitment plays in the structure of open populations (Gaines & Roughgarden, 1985). When larval supply is low, adult stock size is more supply-driven. Whereas when larval supply is high, post-settlement mortality is more important in governing population dynamics (including spatial abundance). Could the same principle apply in N. norvegicus grounds with contrasting larval supplies? If so, we might expect to see a relationship between an index of supply and adult density on grounds with supply-side issues, after a lag period to allow recruits to be counted in UWTV surveys. In grounds with no larval supply issues, no such relationship would be expected since these stocks are more prone to postsettlement processes.
Other significant areas with *N. norvegicus* populations are situated to the west and south of Ireland. The Porcupine Bank (FU16) ground, off the west coast, is characterised by low densities of large adults (Johnson et al., 2013). This population is relatively isolated and receives few larvae from other grounds (O’Sullivan et al., 2015), and past stock declines have led to seasonal fishery closures since 2010 (Aristegui et al., 2019). By contrast, in the Celtic Sea to the south, a network of closely-situated grounds act as a metapopulation with high levels of larval exchange (O’Sullivan et al., 2015).

Several studies have used biophysical larval transport models to estimate *N. norvegicus* larval dispersal (Marta-Almeida et al., 2008; McGeady et al., 2021; Melaku Canu et al., 2020; O’Sullivan et al., 2015; Phelps et al., 2015). However, none have simulated larval transport on multiple mud grounds over a long time series (>10 years) to determine the extent of interannual variability in larval dispersal and population connectivity. The *N. norvegicus* grounds around Ireland provide good examples of populations with varying characteristics in terms of adult density and spatial isolation. Therefore, creating a time series of larval dispersal estimates could provide valuable insights into the extent of between-year fluctuations in larval supply, which are often important to recruitment success (Underwood & Fairweather, 1989). The time series could also be used to increase knowledge and characterise *N. norvegicus* populations in terms of their robustness or vulnerability to periods of low larval retention and how these characteristics relate to population density and long-term stability. Such information would be highly beneficial to sustainable fishery management, particularly for a species with high commercial value and problematic recruitment estimation, such as *N. norvegicus*.

The aims of the present study were (1) to parameterise and run a biophysical larval transport model for *N. norvegicus* mud grounds off Ireland; (2) simulate larval retention, dispersal distance and connectivity between mud grounds over a 20-year (2000–2019) time series; (3) to examine the effect of release timing on larval dispersal; and (4) to test the hypothesis that larval supply (i.e. modelled larval dispersal indices) is linked to adult burrow density fluctuations in scenarios where supply is limited for grounds with sufficiently long time series of UWTV burrow density estimates (i.e. Aran and WIS grounds).

## 2 | METHODS

### 2.1 | Timing of larval season

Due to the lack of *N. norvegicus* larval phenology information off the west coast of Ireland, the timing of the larval season on the Aran grounds (Figure 2) was assessed using light traps which were used to collect larvae on several sampling dates during the larval period. Light traps have previously been used to sample *N. norvegicus* larvae in Swedish waters and have the advantage of maintaining larvae in good condition which is important for the correct identification of larval stage (Øresland, 2007). Light traps were deployed between 14:00 and 19:00 and collected the following day between 09:00 and 12:00 on...
seven sampling dates between March and June 2018 (March 10, April 1, April 12, April 27, May 17, May 29 and June 12). Sampling dates were subject to weather conditions and boat availability. Light traps consisted of 500-μm mesh with a LED light and several funnel shaped openings for larvae to enter. On each sampling date, five to six light traps were deployed individually at 20-m depth on an anchored line. Pairs of light traps were placed separately, approximately 500 m apart, at three distinct stations on the Aran grounds (Figure 2). At least one light trap sample was successfully retrieved from each of the three stations on each sampling date. Due to malfunction or loss of equipment, only five light trap samples were recovered on April 1, April 12 and May 29 and four samples were recovered on May 17. Therefore, 37 light trap samples were successfully collected in total. Upon recovery, the contents of light traps were carefully washed down and preserved in buffered 4% formaldehyde solution. Samples were then transported to the laboratory where _N. norvegicus_ larvae in each sample were counted and sorted according to developmental Stages I–III.

2.2 Underwater television

The UWTV survey has been conducted since 2002 in Ireland to provide a fishery-independent estimate of stock size for _N. norvegicus_ grounds. Data from UWTV surveys were obtained from the Marine Institute for all available years. Survey data were available between 2002–2020 for Aran, 2003–2020 for WIS, 2006–2020 for Smalls, 2011–2020 for South Coast, 2012–2014 and 2016–2020 for Porcupine Bank and 2013–2020 for Labadie and Banana (Figure 1, S1). The UWTV-based assessment methodology is described in detail in Leocádio et al. (2018) but can be summarised as follows: a camera-mounted sledge is deployed to the seabed and once stable, a 7- or 10-min tow is recorded with vessel and sledge position recorded every 2 s. _N. norvegicus_ burrows are identified by their characteristic crescent-shaped opening which leads to a shallow tunnel, excavated material at the entrance, and linear tracks left by individuals entering or leaving the burrow (Leocádio et al., 2018). Two trained observers independently count burrows from UWTV footage, and if agreement (within a certain threshold) is not reached, a third counter is used. Mean burrow density (burrow m⁻²) was calculated as the total number of burrow systems divided by the observed survey area. UWTV data were used to determine the spatial point pattern of released particles in larval transport model and to examine the association between modelled larval dispersal indices and empirical adult burrow densities.

2.3 Biophysical larval transport model

To represent the oceanographic conditions during the _N. norvegicus_ larval period, output (current velocity and temperature) from the Hybrid Coordinate Ocean Model 3.1 was used (HYCOM; Chassignet et al., 2007). HYCOM is a 3D hybrid isopycnal coordinate circulation model (i.e. isopycnal in the open stratified ocean, terrain-following in shallow coastal regions and has fixed depths in the mixed layer and/or stratified areas) and accurately resolves mesoscale processes such as fronts, meandering currents and eddies (Chassignet et al., 2007). The model is data-assimilative and receives information from satellite observations and in situ data from the ARGO observation programme, expendable bathythermographs, moored buoys and other sources.
HYCOM output was coupled with a Lagrangian particle-tracking tool (Ichthyop v3.3; Lett et al., 2008) to simulate advection and dispersal of *N. norvegicus* larvae. Simulations were conducted using HYCOM output for the years 2000–2019. For each simulated year, batches of particles were released separately from six mud grounds or FUs (Figure 1), namely WIS (FU15), Porcupine Bank (FU16), Aran (FU17), South Coast (FU19), Labadie and Banana (FU2021) and Smalls (FU22). For each FU, 10,000 particles were released into the ocean domain every 5 days over a 50-day period encompassing the larval season, resulting in a total of 11 release events. A sensitivity test for 2019 on the Aran grounds was used to compare the 5-day release interval with a 1-day interval to ensure that the former was not overly coarse. Release timing of virtual larvae for all mud grounds, except WIS, was between 70 and 120 Day of Year (DOY; March 11 to April 30) which was based on the temporal distribution of Stage I *N. norvegicus* larvae in light trap samples (see Section 3). On the WIS ground, release timing was between 90 and 140 DOY (March 31 to May 20) to reflect a later larval hatching phenology (Dickey-Collas, Briggs, et al., 2000; McGeady et al., 2019). Particles were released at midnight on each of the release dates based on empirical observations (Farmer, 1974). In total, 110,000 particles were released from each of the six mud grounds each year, resulting in 13.2 million tracked particles over the 20-year study period. A total of 1320 release events were simulated (11 release dates × 20 years × 6 grounds).

The spatial distribution of adults on *N. norvegicus* grounds is not uniform and often varies from year to year. As a result, the initial spatial distribution of hatching larvae also varies and initial hatching location can influence dispersal of larvae (McGeady et al., 2021). Female *N. norvegicus* remain in their burrows throughout the incubation period with limited movement, and there is no evidence of spatial segregation between male and females (Farmer, 1974; Maynou et al., 1998). Therefore, the spatial distribution of adult burrows offers a good proxy for larval hatching distribution. The initial point pattern of modelled particles for each mud ground was based on the spatial distribution of adult burrows from UWTV surveys in the same year. This ensured that more particles were released from areas of a ground that had higher burrow densities and thus higher adult abundance. Ordinary kriging was used to spatially interpolate burrow densities from UWTV stations across the spatial extent of the mud ground (Figures S2–S7). A point grid, distanced 0.02° apart, was overlain on the burrow density raster, and densities were extracted at each grid point. The burrow density at each grid point determined the number of particles released from that location, that is, more particles were released from areas of a ground with higher burrow densities. For each release event, the total number of particles remained constant at 10,000 (i.e. burrow densities were not used to determine number of particles released—only their spatial starting position across each ground). The number of particles released at each grid point (*P*) was calculated using the following:

\[
P = \frac{x_i}{\sum x_i} \times 10,000,
\]

where *x_i* is the density of *N. norvegicus* burrows for the year at the *i*th location of the mud ground. For occasional years with no UWTV survey, the average spatial distribution of all available years was used (Figures S2–S7).

To compute trajectories of particles, Ichthyop used a Runge–Kutta fourth-order numerical scheme and a turbulent dissipation rate of \(1 \times 10^{-9}\) (following Peliz et al., 2007). An integration interval of 5 min was used, and information (latitude, longitude and temperature) was recorded every 3 h. For each simulation, particles were released at 20-m depth at 12:00 a.m. and programmed to perform a vertical migration to mimic larval vertical movements in the water column. Particles migrated between 10- and 20-m depth, following the observations of McGeady et al. (2019) where larvae made a descent to 20 m at dawn, an ascent to 10 m at dusk and a ‘midnight sink’ to 20 m followed by a subsequent ascent to 10 m.

In postprocessing of larval transport simulations, each annual larval season was adjusted to reflect higher abundances of larvae released at the time of peak larval hatching. This involved using empirical light trap observations to identify dates in the middle of the larval hatching season with highest densities of Stage I larvae. This information was then used to apply a larval release schedule that gave a greater weighting to these dates (i.e. release dates during peak larval hatching had a greater weighting when calculating larval dispersal indices than those very early or late). As such, release schedules for the Porcupine Bank, Aran, South Coast, Labadie and Banana and Smalls grounds were centred on 95 DOY (see Section 3) and the WIS ground was centred on 115 DOY.

A temperature-dependent PLD for each particle was estimated using parameters from previous experimental studies describing the inverse relationship between temperature and PLD of

<table>
<thead>
<tr>
<th>Stage</th>
<th>Slope</th>
<th>Intercept</th>
<th>Source</th>
<th>Duration at 8°C (days)</th>
<th>Duration at 10°C (days)</th>
<th>Duration at 12°C (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>−0.161</td>
<td>4.265</td>
<td>Dickey-Collas, McQuaid, et al. (2000)</td>
<td>19.6</td>
<td>14.2</td>
<td>10.3</td>
</tr>
<tr>
<td>II</td>
<td>−0.175</td>
<td>4.646</td>
<td>Dickey-Collas, McQuaid, et al. (2000)</td>
<td>25.7</td>
<td>18.1</td>
<td>12.8</td>
</tr>
<tr>
<td>III</td>
<td>−0.133</td>
<td>4.188</td>
<td>Smith (1987)</td>
<td>22.7</td>
<td>17.4</td>
<td>13.4</td>
</tr>
</tbody>
</table>

Note: Also included is the duration of each stage at 8°C, 10°C and 12°C temperature.
N. norvegicus larval Stages I–III (Dickey-Collas, McQuaid, et al., 2000; Smith, 1987; Thompson & Ayers, 1989) following Dickey-Collas, McQuaid, et al. (2000) (Table 1). Temperatures experienced by simulated particles were recorded every 3 h and used to determine PLD. When particles came to the end of their PLD, their position was used to determine ‘settlement’ location. The final position of all particles at ‘settlement’ was used to calculate larval retention (%) for each ground, that is, the proportion of larvae settling within the boundary of their natal ground—Figure 1. Settlement position was also used to define connectivity (%) larval imports and exports) between all combinations of mud grounds. Particles settling outside the boundaries of any of the N. norvegicus mud grounds (Figure 1) were considered as larval wastage. The straight-line distance from initial release location to final settlement location was also calculated as dispersal distance (km).

Larval mortality was also applied in postprocessing, whereby an instantaneous daily mortality rate was applied to annual larval retention estimates. Viable retention, that is, retention after mortality is taken into account, was estimated as follows:

\[
\text{Viable retention} = \text{Larval retention} \times \exp(-Z \times \text{PLD}),
\]

where \(Z\) is the instantaneous daily mortality rate (0.027) according to Briggs et al. (2002) and PLD is the temperature-dependent dispersal duration. The mortality component accounts for higher mortality risk in larvae that had longer PLDs.

2.4 | Statistical analysis

An analysis of variance (ANOVA) was used to examine the effect of release timing on modelled larval retention (%), dispersal distance (km) and PLD (days) for each mud ground using individual release events as data points (20 years \(\times\) 11 release dates = 220). In instances where residual normality was not attained, variables were log or square-root transformed. When transformations did not work, the nonparametric Kruskal–Wallis test was used.

To examine the association between annual larval dispersal indices (i.e. viable retention [%] or dispersal distance [km]) and adult burrow densities from empirical UWTV observations, distributed lag models were used (Demirhan, 2020). Distributed lag models are a type of regression analysis for time series data, which enable the use of lagged values of the predictor variable when a delayed effect on the response variable is expected (in this case due to the lagged effect of larval settlement on adult burrow density). The Aran and WIS grounds were tested in these analyses as they were the only grounds with sufficiently long time series of UWTV burrow density estimates, 2002–2020 and 2003–2020, respectively, noting that the time lag in this analysis further shortens each time series. The Aran grounds have experienced stock declines in the past, suggesting limited larval recruitment. In contrast, the WIS ground has remained stable with high adult densities, suggesting high larval recruitment. Therefore, the contrasting nature of the grounds provides a good comparison of how larval supply influences burrow density.

Annual UWTV adult burrow density was used as the response variable and modelled larval dispersal indices, that is, viable retention (%) and dispersal distance (km), were used as predictor variables, each in a separate model. Despite UWTV burrow data being used as a response variable and also to spatially weight particle release position—ing which predictor variables were derived from, its inclusion did not bias the analysis as burrow data were not used to vary particle abundance and the same number of particles were released in all simulations (Figures S2–S7). The model with viable retention as a predictor variable did not include larval imports from other mud grounds; instead, the proportion of locally produced larvae retained on the mud ground was used. Larval imports were excluded because larval supply from each mud ground could not be accurately weighted according to stock abundance for each year due to the short UWTV time series at most N. norvegicus mud grounds (Figure S1). However, simulations indicated that both the Aran and WIS grounds predominantly relied on retention of native larvae for larval settlement (see Section 3).

To account for the delayed (and unknown) relationship between larval settlement and adult burrow densities, lag periods of 1, 2, 3 and 4 years were used as predictor variables. An assumption of the distributed lag model is stationarity, that is, mean and variance remain constant over time. Therefore, first-order differencing (i.e. difference between consecutive years in the time series) was used and all variables were subsequently checked for stationarity using the Dickey–Fuller test. Thus, response and predictor variables represented annual changes in relevant values, that is, \(\Delta\) Burrow density (burrow \(m^{-2}\)) represents the change in density from the previous year and \(\Delta\) Viable retention (%) is the change in retained larvae from the previous year.

Prior to running analyses, correlations between lagged predictor variables were examined by obtaining variance inflation factors (VIFs). When VIFs were <10, it was concluded that variables were not strongly correlated (Montgomery et al., 2012; Zuur et al., 2010). The model simplification process followed a stepwise backward selection of variables (i.e. lags of different lengths). Akaike’s information criterion (AIC) was used to find the optimal model and when the removal of further variables did not bring a reduction in AIC, the model was considered optimal. The AIC method allows users to fit the optimal model by balancing complexity and goodness-of-fit (Akaike, 1974). Model residuals were inspected to check for nonnormality, heteroscedasticity and autocorrelation. To account for multiple testing, \(p\)-values were adjusted using the Bonferroni correction in order to minimise the likelihood of type-I errors. Distributed lag models were implemented using the R package dLagM (Demirhan, 2020), and all analyses were conducted using R version 4.0.1 (R Core Team, 2020).

3 | RESULTS

3.1 | Timing of larval season

Figure 3a,b describes larval seasonality on the Aran grounds. Stage I N. norvegicus larvae were first observed in light traps in low densities
of 0.5 ± 0.2 ind. per trap (mean ± SE) on the first sampling date 69 DOY (March 10), and densities increased to 7.0 ± 1.5 ind. per trap on 91 DOY (April 1). By 102 DOY (April 12), there were 6.7 ± 3.5 ind. per trap. Densities then decreased to 0.2 ± 0.1 ind. per trap on 117 DOY (April 27) and were absent thereafter (Figure 3a). Stage II larvae first appeared at a density of 0.5 ± 0.2 ind. per trap on 91 DOY (April 1) and reached a peak of 2.5 ± 1.2 ind. per trap on 102 DOY (April 12). Stage III larvae were generally low in abundance, appearing at a density of 0.2 ± 0.1 ind. per trap on 117 DOY (27 April) and reaching a peak of 0.7 ± 0.1 ind. per trap on 137 DOY (17 May). No larvae of any stage were observed on 149 DOY (May 29) and 163 DOY (June 12; Figure 3b).

### 3.2 Larval dispersal

Release timing had a significant effect on modelled larval retention on the Aran (Kruskal-Wallis test, $\chi^2 = 26.5$, df = 10, $p < 0.01$) and Porcupine Bank grounds (Kruskal-Wallis test, $\chi^2 = 21.9$, df = 10, $p < 0.05$), where larval retention was lowest for releases early in the season and highest for late releases (Figure 4a). Similarly, release timing had a significant effect on dispersal distance on the Aran (ANOVA, $F_{10, 209} = 5.09$, $p < 0.001$) and Porcupine Bank grounds (ANOVA, $F_{10, 209} = 3.86$, $p < 0.001$). On both grounds, late season releases were associated with a decrease in dispersal distance (Figure 4b). PLD of virtual larvae was significantly affected by release timing on all six mud grounds (ANOVA, $p < 0.001$), being reduced with a later release in each case (Figure 4c). The reduction in PLD from the first to last release date was greatest on the WIS (19.1 days), Aran (18.5 days) and Smalls (18.2 days) grounds and was lowest on Porcupine Bank (8.1 days).

Using a larval release schedule whereby release dates at the peak of the larval hatching season had a greater weighting (see Section 2; dashed line Figure 3a), the WIS had the highest average retention across the study period (Larval retention: 23.9%, Viable retention: 5.7%; Figure 5), followed by Labadie and Banana (21.6%, 6.1%), Porcupine Bank (7.3%, 2.1%) and the Smalls (6.9%, 1.8%). Retention was low on the Aran (2.6%, 0.6%) and South Coast (3%, 0.8%) grounds. Annual larval retention was highest overall in 2007 on the WIS (42.2%) and lowest overall in 2018 on the Aran grounds (<0.1%). Annual larval retention was <2% for 12 of the years included in simulations on the Aran grounds (Figure 5c), 8 years on the South Coast grounds (Figure 5d) and 3 years on the Smalls ground (Figure 5f; please note y-axis change). On the Aran and South Coast grounds, a decreasing trend in retention was evident over the time series (Figure 5c,d). Average larval retention in the first half of the study period, 2000–2009 (Aran: 3.4%, South Coast: 3.9%), was approximately twice that of the second half, 2010–2019 (Aran: 1.7%, South Coast: 2.1%).

Dispersal distances mostly mirrored retention; that is, when distance increased, a corresponding decrease occurred in retention (Figure 6). Lowest average dispersal distances were recorded on the Labadie and Banana (93.6 km; Figure 6e) and WIS (108.8 km; Figure 6a) grounds. In contrast, highest average distances were...
observed on Porcupine Bank (134.1 km) and South Coast (133.0 km) grounds. On the Smalls, a high degree of interannual variability was apparent with distances >180 km in 2008, 2012 and 2017 and <70 km in 2001, 2004 and 2009 (Figure 6f). On the Aran grounds, dispersal distances were also higher in the second half of the study period (2010–2019; 128.1 km) compared with the first (2000–2009; 105.8 km) (Figure 6c). This trend was also apparent on the South Coast grounds with lower average dispersal distance from 2000 to 2009 (110.4 km) than 2010–2019 (155.7 km) (Figure 6d). By contrast, larval dispersal distance on the Porcupine Bank was rather stable over time (Figure 6b).

The WIS received few imports from the Smalls (0.1%) and also exported few larvae to other Irish grounds (Figure 7a). Porcupine Bank had minor infrequent imports from South Coast (0.4%), Aran (0.1%) and Smalls (<0.1%) and predominantly relied on retention of locally produced larvae (Figure 7b; please note y-axis change). The Aran grounds received relatively minor imports mostly from the South Coast (1.2%; Figure 7c), although considerable interannual variation existed. In general, the Aran, Porcupine Bank and WIS grounds were reliant on retention of native larvae because imports were low.

The Celtic Sea mud grounds (South Coast, Labadie and Banana and Smalls) were the most interconnected in terms of larval exchange (Figure 7). South Coast mostly received imports from Smalls (1.4%) and Labadie and Banana (0.9%) and also had small irregular imports from Porcupine Bank and the WIS in the middle of the time series (Figure 7d). Overall, South Coast was the most important source of larval exports to other grounds as it exported 8.0% of its larvae and was the only area that exported more larvae than it retained (3.0%). The South Coast exported larvae to all mud grounds, apart from the WIS. Labadie and Banana had imports from the South Coast (4.7%) and Smalls (2.2%). However, larval imports from these grounds were at a low level since 2015 (Figure 7e). The Smalls received 1.7% of larvae originating from the South Coast grounds, on average. It also received imports from Labadie and Banana (0.4%) and small infrequent imports from the WIS ground (Figure 7f). In 2002, the Smalls relied almost exclusively on the South Coast grounds for larvae (10.8%), as larval retention was very low (0.2%).

Optimal distributed lag models explaining variations in *N. norvegicus* adult burrow densities with modelled larval dispersal indices were found using AIC (Table 2). On the Aran grounds, Δ Viable retention (%; i.e. annual changes in viable retention from 1 year to the next) had a significant positive effect (Figure 8a) on Δ Burrow density with a 3-year lag. A 1% increase in Δ Viable retention corresponded to an increase of 0.1 burrow m⁻² Δ Burrow density 3 years later ($R^2 = 0.48$, Bonferroni-adjusted $p = 0.009$). With a 3-year lag, fluctuations in modelled viable retention and burrow density appeared to
match quite closely, particularly in the first half of the time series when burrow densities exhibited a steep decline (Figure 8b). A significant negative effect of $\Delta$ Dispersal distance on $\Delta$ Burrow density with a 3-year lag was also observed at the Aran grounds (Figure 8c). A 10-km increase in $\Delta$ Dispersal distance corresponded to a 0.03 burrow m$^{-2}$ decrease in $\Delta$ Burrow density ($R^2 = 0.52$, Bonferroni-adjusted $p = 0.005$). Particularly for the first half of the time series, an opposite response was observed between dispersal distance and burrow density, whereby an increase in dispersal distance corresponded to a decrease in burrow density with a 3-year lag (Figure 8d).

By contrast, on the WIS ground, no significant associations were observed between $\Delta$ Burrow density and $\Delta$ Viable retention or $\Delta$ Dispersal distance. No other grounds were tested due to a lack of adequate temporal coverage in burrow density time series, compounded by several lag lengths of >1 year.

Sensitivity testing that compared 5-day and 1-day release intervals for the Aran grounds in 2019 indicated minor differences in larval retention (5-day release: 0.77%, 1-day release: 0.72%), dispersal distance (5-day release: 150.8 km, 1-day release: 150.6 km) and PLD (5-day release: 48.9 days, 1-day release: 48.9 days) using a larval release schedule.

4 | DISCUSSION

The present study is the first to create a long time series of *N. norvegicus* larval dispersal estimates for multiple mud grounds and to demonstrate the link between modelled larval dispersal indices and empirical adult burrow densities (with a 3-year lag) when larval supply is limiting, as it was on the Aran grounds. The findings demonstrate
the potential of biophysical larval transport models to provide a proxy for larval recruitment in species like *N. norvegicus*, which lack more direct methods to measure recruitment. Such models can be used to identify instances (i.e. particular years or functional management units) when recruitment is constrained by low larval supply and to identify grounds (e.g. South Coast) which are important sources of larvae to other grounds.

Light trap sampling was used to establish the start of the larval season and to document larval temporal distribution on the Aran grounds, off the west coast of Ireland. Previously, little was known of *N. norvegicus* larval timing to the west of Ireland, but a high-intensity plankton sampling campaign in 2018 showed Stages I and II larvae in early April, with densities of Stage I being much higher (McGeady et al., 2019). Similarly, high densities of Stage I larvae were recorded in early to mid-April 2018 in the present study, indicating peak hatching. It should be acknowledged, however, that release timing is likely to vary interannually due to differences in average incubation temperatures. For later larval stages, densities were very low and absent after May 17 (Figure 3). Due to high larval mortality (Figure 5), only a fraction of Stage I larvae survive to Stage III (Nichols et al., 1987), which may explain low Stage III densities observed in light trap samples. Added to this, extremely low levels of modelled larval retention in 2018 (Figure 5d) indicated that most larvae were transported northwards, away from the Aran grounds that year, further depleting densities of late-stage larvae in samples.

Underlining the importance of correctly defining larval timing in model parameterisation, release timing had a significant effect on larval dispersal patterns for the Aran and Porcupine Bank grounds. Earlier releases were associated with lower larval retention and higher dispersal distances (Figure 4). On the Aran grounds, earlier released larvae had a higher likelihood of being transported north along the Irish coast due to longer PLDs and strong northward currents.

**Figure 6**  Time series of simulated annual larval dispersal distance (km) using release schedule (see Figure 3a) for mud grounds/functional units (FUs) (a)–(f) around the Irish coast
Similarly, on the Porcupine Bank ground, early releases were transported away from mud habitat due to strong early-season currents (although PLD variation between early and late releases was relatively low). Temperature is an important determinant of PLD in *N. norvegicus*, as it is with many ectotherms (Dickey-Collas, McQuaid, et al., 2000; O'Connor et al., 2007). For this reason, on all mud grounds, PLDs were reduced with a later release as water temperature increased over the larval season (Figure 4).

In terms of larval connectivity, model estimates indicated that Celtic Sea grounds (South Coast, Labadie and Banana and Smalls) had the highest levels of larval exchange. In contrast, the Aran grounds and WIS ground were relatively isolated and received low levels of imports. In a study of the 2011/2012 larval seasons, O'Sullivan et al. (2015) similarly documented high interground metapopulation connectivity in Celtic Sea grounds. Overall, the South Coast grounds had the highest propensity for larval exports to other grounds and were the only grounds to export more than they retained. However, spawning stock biomass determines the quantity of larvae produced on a mud patch and therefore how much can be exported. Abundance (320 million) on the South Coast grounds is relatively low and has been decreasing in recent years (Aristegui, Doyle, et al., 2020). Low abundance grounds would produce less larvae compared with high-abundance populations on larger grounds, such as the nearby Labadie and Banana (~1 billion; Aristegui, Tully, et al., 2020). Perhaps better protection from exploitation on the South Coast could enhance the potential for larval supply from these grounds to mitigate poor retention elsewhere, for example, on the Aran grounds.

Interannual variability was an important feature in larval exchange between grounds, and variation in the Irish coastal current had a large influence on the northward dispersal from coastal grounds (Figures 7 and S8). For most of the time series, the Labadie and Banana grounds had high imports from other Celtic Sea grounds. However, the increasingly northward transport of South Coast larvae in recent years contributed to decreasing exports to the Labadie and Banana grounds. The Smalls and South Coast grounds were the most interconnected in terms of larval exchange, and in 2002, very low larval retention on the

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**Figure 7** Simulated proportion of settled larvae on Irish *Nephrops norvegicus* mud grounds/functional units (FUs) through larval retention and imports from other FUs (see legend indicating ‘origin FU’) from larval transport models from 2000 to 2019. Please note that the y-axis varies on plots (a) and (e).
TABLE 2  Distributed lag model selection process based on backwards selection of variables that minimised Akaike’s information criterion (AIC) for the Aran grounds

<table>
<thead>
<tr>
<th>Structure</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Predictor: Δ Viable retention</strong></td>
<td></td>
</tr>
<tr>
<td>1  ( \Delta ) Burrow density ( \sim ) Δ Viable Retention Lag 1 + Δ Viable Retention Lag 2 + Δ Viable Retention Lag 3 + Δ Viable Retention Lag 4</td>
<td>-11.9</td>
</tr>
<tr>
<td>2  ( \Delta ) Burrow density ( \sim ) Δ Viable Retention Lag 1 + Δ Viable Retention Lag 3 + Δ Viable Retention Lag 4</td>
<td>-13.9</td>
</tr>
<tr>
<td>3  ( \Delta ) Burrow density ( \sim ) Δ Viable Retention Lag 3 + Δ Viable Retention Lag 4</td>
<td>-15.4</td>
</tr>
<tr>
<td>4  ( \Delta ) Burrow density ( \sim ) Δ Viable Retention Lag 3</td>
<td>-18.5</td>
</tr>
</tbody>
</table>

\( R^2 = 0.48 \)

**Predictor: Δ Dispersal distance**

<table>
<thead>
<tr>
<th>Structure</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1  ( \Delta ) Burrow density ( \sim ) Δ Distance Lag 1 + Δ Distance Lag 2 + Δ Distance Lag 3 + Δ Distance Lag 4</td>
<td>-15.0</td>
</tr>
<tr>
<td>2  ( \Delta ) Burrow density ( \sim ) Δ Distance Lag 1 + Δ Distance Lag 2 + Δ Distance Lag 3</td>
<td>-17.9</td>
</tr>
<tr>
<td>3  ( \Delta ) Burrow density ( \sim ) Δ Distance Lag 2 + Δ Distance Lag 3</td>
<td>-18.7</td>
</tr>
<tr>
<td>4  ( \Delta ) Burrow density ( \sim ) Δ Distance Lag 3</td>
<td>-19.9</td>
</tr>
</tbody>
</table>

\( R^2 = 0.52 \)

Note: Model 4 (bold) was selected as the optimal model based on AIC. Lags refer to 1, 2, 3 and 4 years.

**FIGURE 8**  Association on the Aran grounds between \( \Delta \) Burrow density (annual changes to adult density) and (a) \( \Delta \) Viable retention (annual changes to % viable retention of larvae after mortality) and (c) \( \Delta \) Dispersal distance (annual changes to larval dispersal distance) with a 3-year lag.  Comparison of modelled (b) viable retention (%) and (d) dispersal distance (km) with 3-year (backwards) lagged burrow densities on the Aran grounds.  Trend lines indicate significant relationships from distributed lag models (see Section 3), shading represents 95% confidence intervals and p-values have been adjusted for multiple testing using the Bonferroni correction.
Smalls (0.2%) was mitigated by receiving 10.8% of larvae from the South Coast to compensate. This is a stark example of the interreliance of mud grounds for larval exchange, which is significant for sustainable fishery management (Kough et al., 2013). It is also ecologically significant, as a marine example where persistence of local populations (via larval supply) is facilitated by larval connectivity within the larger metapopulation (Cowen & Sponaugle, 2009).

By contrast, the Porcupine Bank ground was the furthest offshore and spatially isolated. High interannual variability and few larval imports meant that Porcupine Bank had low larval supply in several years, particularly from 2006 to 2011. The ground is characterised by large N. norvegicus individuals occurring at low densities, and this area has undergone stock declines in the past, although recently, better recruitment levels have improved the outlook for the stock (Aristegui et al., 2019; Johnson et al., 2013). Low and variable larval retention levels (relative to other large grounds, like the WIS) and spatial isolation are further compounded by relatively low larval production due to low adult densities. These factors likely render the Porcupine Bank vulnerable to periods of low recruitment which have contributed to past stock declines (Aristegui, 2019).

The WIS ground had the highest average larval retention (23.9%). The enclosed nature of the Irish Sea, along with relatively weak currents near the coast, proved conducive to larval retention (Figure 5f). Larvae transported out of the Irish Sea mostly did so via the North Channel and were often dispersed along the west coast of Scotland or to the Eastern Irish Sea (EIS), where other N. norvegicus mud patches are situated. Therefore, despite low levels of exports to Irish mud grounds in the current study, the WIS is an important source of larvae to Scottish and EIS grounds (McGeady et al., 2021).

Adult burrow density estimates indicate that the WIS population has been in a stable healthy state since 2003 (Figure S1) and has always well-exceeded the Maximum Sustainable Yield (MSY) trigger of 3 billion burrows (the abundance at which management advice should be implemented to prevent further decline; Lundy et al., 2019). N. norvegicus occur at high densities in the WIS, and adults grow to small sizes relative to other grounds (Johnson et al., 2013). Density-dependent suppression of growth in size has been shown in high-density areas (Merder et al., 2020). Therefore, high larval retention on the WIS ground (see also O’Sullivan et al., 2015; Phelps et al., 2015) likely contributes to high adult densities and strong competition for space and resources (Johnson et al., 2013). As argued by Hill and White (1990), high densities in the WIS mean that more larvae would settle than can be accommodated, and as a result, settlement exceeds carrying capacity. This implies that N. norvegicus recruitment rates are heavily influenced by postsettlement mortality such as starvation, predation and cannibalism which would be more intense in such high-density scenarios (Bell et al., 2006). Therefore, larval dispersal is a poor indicator of adult density fluctuations for the WIS ground, which explains why no association was detected between larval dispersal indices and adult burrow densities for this ground. Instead, adult density fluctuations in the WIS are most likely determined by factors that occur postsettlement, such as predation, starvation and/or fishing pressure (Bell et al., 2006; Hill & White, 1990).

The Aran grounds, by contrast, had the lowest retention overall in the study (Figure 5d). Larvae were consistently transported north by the Irish coastal current (Fernand et al., 2006). Northward currents along the west coast of Ireland tended to be strongest in March and April. However, in the final 5 years of the time series (2015–2019), they were consistently strong across all months of the larval season, resulting in low retention (Figures 5 and S8). Larval retention estimates were lower than reported previously for individual years, 15.8% in 2011 and 14.4% in 2012 (O’Sullivan et al., 2015). Our larval retention estimate for March 16, 2018 (0%) was, however, similar to results in McGeady et al. (2019) for March 15, 2018 (0.2%) although the latter used a different ocean model, the Northeast Atlantic Regional Ocean Modelling System model (Nagy et al., 2020). A vertical migration was implemented in both cases.

UWTV surveys have been conducted on the Aran grounds since 2002, providing the longest time series of N. norvegicus adult burrow estimates in Irish waters (Figure S1). At the beginning of the time series (2002–2005), burrow densities were considered high (0.8–1.1 burrow m$^{-2}$). From 2004 to 2012, densities fluctuated widely with a general decline before stabilising at a lower level (0.3–0.4 burrows m$^{-2}$) from 2012 until 2020 (Figure S1). Since 2012, abundance estimates for the Aran grounds have been below the MSY abundance trigger of 540 million burrows in all but 2 years, which results in catch advice below the MSY harvest rate to rebuild the stock.

We have discussed the persistently low larval retention on the Aran grounds, which indicates supply-side issues. In agreement with our hypothesis, evidence of recruitment limitation was seen at these grounds—modelled larval dispersal indices were linked to empirical changes in adult burrow density with a 3-year lag (Figure 8). Hence, the findings of the present study suggest that persistent low levels of viable retention on the Aran grounds have led to poor recruitment and contributed to a reduction in adult densities. Sardà (1995) provided age–length relationships for N. norvegicus compiled from nine studies where 3-year-old males had an average size of 25.20 ± 2.95-mm carapace length (CL; mean ± SD) and 3-year-old females were 24.50 ± 1.82-mm CL. By applying these age–length relationships to length-frequency distributions from beam trawl surveys for the Aran grounds (2006–2018), 3-year-old individuals comprise approximately 40% of the male and 30% of the female population (see Doyle et al., 2018). This indicates that any large fluctuation in 3-year-old year class strength would have an observable effect on adult burrow densities 3 years later. Furthermore, the increase in viable retention in 2013 on the Aran grounds may correspond to the large increase in 14- to 16-mm CL individuals observed in 2014 which would have been the 1-year-old age cohort (male: 13.90 ± 3.18 mm, female: 14.3 ± 1.60 mm) using the same length–age relationship (Doyle et al., 2018; Sardà, 1995). We suggest that larval transport models may help to identify if poor larval supply contributed to low recruitment in other areas with historic fluctuations or reductions in N. norvegicus abundance (Fariña & González Herraiz, 2003; ICES, 2020).
Despite the demonstrated link between larval dispersal and subsequent adult burrow density, several alternative processes influence population density such as exploitation levels, predation, disease and/or parasites (Farmer, 1975; Johnson et al., 2013). Settlement on habitat is a key starting point, however, and without this, larval dispersal predictions can supplement existing monitoring and management procedures and may assist in reducing overexploitation during periods of low recruitment or in enhancing conservation measures, particularly timely in the face of climate change-induced effects on oceanography (Harley et al., 2006).

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CONFLICT OF INTEREST
The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTION
RMG conducted larval sampling, sorting and identification, larval transport modelling, data analysis and drafted the manuscript; CL and AMP conceived the study, designed the study, coordinated the study and helped draft the manuscript. All authors revised and gave final approval for publication, and all authors agree to be held accountable for the work performed therein.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding author upon reasonable request.

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