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around Ireland

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Irish Fisheries Investigation No. 26

Sediment characteristics and local hydrodynamics and their influence on the population of *Nephrops* around Ireland

September 2014

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ISSN: 1649-5055

Keywords: *Nephrops norvegicus*, fishing grounds, larval drift modelling, hydrodynamics



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Abstract

The Norway lobster, *Nephrops norvegicus*, is the second most valuable commercial species landed from Irish waters. The species is dependent on muddy seabed sediment in which burrows are constructed. Larvae are hatched from the seabed into the water column. The distribution of *Nephrops* depends in part to the presence of suitable sediment and also from larval supply modulated by existing local hydrodynamic regimes. The pelagic stage of the life-cycle is governed by both physical and biological factors including temperature, water speed and larval maturation rate. This study encompasses three aims, 1: to synthesise available sediment data and examine the spatial extent of potential *Nephrops* habitat in waters around Ireland, 2: investigate local hydrodynamic conditions on *Nephrops* fishing grounds which are likely to be encountered by planktonic larvae following hatching and 3: to employ a particle tracking model to study the potential dispersal fields of *Nephrops* larvae from individual fishing grounds and assess stock connectivity. The study finds that larval distribution between fishing grounds is dependent on variable seasonal conditions, the geographical size of an area and its proximity to other grounds. Fishing grounds in the Irish Sea and Porcupine Bank are isolated from other areas, whereas grounds in the Celtic Sea exhibit a high degree of connectivity and should be considered as a meta-population. Successful annual recruitment to the adult population of this species is largely dependent on favourable environmental conditions which enable the re-seeding of the same or adjacent grounds.

Keywords: *Nephrops norvegicus*, fishing grounds, larval drift modelling, hydrodynamics

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I. Introduction

The Norway lobster, or Dublin Bay prawn, *Nephrops norvegicus*, is the second most valuable commercial species landed from Irish waters worth €80 m at first sale in 2012 (Lordan *et al.* 2013). *Nephrops* are widely distributed around the east, west and south coasts of Ireland and on the continental shelves of the North East Atlantic but its overall distribution is discontinuous because the species is dependent on muddy seabed sediment which exist as disparate variable sized patches. In wider European waters there are at least 30 different populations which are physically isolated from each other (Bell *et al.* 2006) producing annual landings of around 60,000 t/annum. The *Nephrops* fisheries around Ireland are mainly exploited using trawls and account for around 30% of European landings.

The spatial extent of mud-patches suitable for *Nephrops* fisheries in Irish waters has been mapped in high resolution using a combination of fishery dependent data such as Vehicle Monitoring Systems (VMS) (Gerritsen and Lordan 2011) and also fishery independent data including multibeam backscatter available from the Irish National Seabed Survey and INFOMAR project (<http://www.infomar.ie/>), sediment samples, *Nephrops* density estimates (burrows / m²) from UWTV surveys and trawl catch data from Irish Groundfish surveys. The stocks are assessed and scientific advice on the state of the stock, and catch options are provided by ICES at a Functional Unit (FU) level (ICES 2013).

The distribution of *Nephrops* depends on the presence of suitable sediment but also on larval supply modulated by existing local hydrodynamic regimes (Johnson *et al.* 2013). Planktonic larvae are subject to certain controls in a pelagic environment particularly horizontal advection which is more noticeable at the surface i.e. tidal flow, and random turbulent diffusion within the 3d water column (Hill 1990). This pelagic part of the life-cycle is governed by both physical and biological processes. Larvae are initially carried passively, subject to both advection and diffusion, before a limited, independent swimming behaviour commences and metamorphosis through a series of developmental stages (Stages I-III) (Cobb and Wahle 1994). Temperature is an important driver de-

termining the larval stage durations of planktonic Crustacea with considerable variation in the developmental rate observed at various temperature regimes (Smith 1987, Dickey-Collas *et al.* 2000a). Following metamorphosis, settlement upon soft muddy sediment and the construction of burrows is crucial as post-larvae juveniles dispersed to unsuitable substrate are unlikely to survive (Bell *et al.* 2006). *Nephrops norvegicus* exhibit relatively low fecundity with females producing 500 – 3 000 eggs and so a reproductive strategy that reduces larval losses in the planktonic stage would favour survival (Brown *et al.* 1995).

It is important to consider the degree of connectivity between individual fishing grounds. Because adult *Nephrops* do not migrate, the only opportunity for transfer between populations is during the pelagic larval phase. A network of mud-patches facilitating larval transfer between them will promote genetic variability and increase the overall resilience of the wider population to stochastic events. For example, predicted climate change over the next 100 years may have a considerable impact on the physical conditions in Irish waters, especially the Irish Sea (Olbert *et al.* 2012).

The aim of this study is to improve our understanding of the metapopulation structure and assess the degree of connectivity between *Nephrops* populations around Ireland. This will have important implications for stock assessments and effective fisheries management. This study has three specific objectives:

- 1) To synthesise available sediment data and examine the spatial extent of potential *Nephrops* habitat in waters around Ireland.
- 2) To investigate prevailing hydrodynamic conditions over the main *Nephrops* grounds.
- 3) To use a realistically parameterised particle tracking model to explore larval drift and potential dispersal field of planktonic *Nephrops*.

2. Materials and Methods

2.1 Biology and Ecology

There are about 20 main *Nephrops* fishing grounds in Irish waters. These are managed within 8 Functional Units (FU) which helps to prevent uneven exploitation (ICES 2013). FU's can entirely encompass one large fishing ground i.e. Porcupine Ground and the Smalls, or can consist of multiple small grounds in close proximity to each other i.e. Cork channels or Aran Grounds (see Figure 1). Catch composition analysis indicates there is high variability in population structure between these fishing grounds due to population density effects and different seasonal emergence patterns (Marine Institute 2013). *Nephrops* construct and occupy burrows within the muddy sediment at depths from 800m up to the 15m contour (Bell *et al.* 2006). Adult *Nephrops* do not migrate once they occupy a burrow and only emerge to forage and to mate. Following spawning, eggs are incubated by females sheltering within the burrows for about 9 months over-winter before the larvae hatch into the water column. The pre-zoea then migrate vertically to the warmer, well-mixed surface layer and pass through three temperature-dependent stages of development (Dickey-Collas *et al.* 2000a). Post-larvae (Stage IV), which resemble adult *Nephrops* after metamorphosis, descend to resume a benthic existence and either construct new burrows or opportunistically occupy vacant ones. The timing of hatching depends primarily on temperature (Hill *et al.* 1996) and is variable across fishing grounds. Peak hatching in the North East Atlantic (Porcupine Bank, Southwest Slope and the Aran Grounds) is thought to take place in April/May, whereas hatching in the Celtic Sea and Irish Sea probably occurs later during May/June and June/July respectively (Bell *et al.* 2006).

2.2 Mapping of sediment characteristics

Core sediment samples were used to determine the spatial extent of sediments with characteristics suitable for *Nephrops* burrow construction. Sediment cores were sam-

pled during annual Underwater TV (UWTV) surveys conducted by the Marine Institute. Particle Size Analysis (PSA) of sediments cores was carried out using a Low Angle Laser Light Scattering method. The percentage composition of sand, silt, clay and gravel was generated using Gradistat software for each sample. The percentage of 'mud' was calculated by combining the percentages of silt plus clay present in each sample as this ratio has previously been shown to have a positive effect on *Nephrops* burrow density (Campbell *et al.* 2009a, Johnson *et al.* 2013). Once these steps had been completed it was possible to calculate the spatial extent of mud patches in each FU. These multiple point data were interpolated within a GIS to produce a profile of sediment characteristics at each of these important fishing grounds. The available data that was used to interpolate the sediment characteristics of the Aran, Smalls and west Irish Sea Grounds are shown in Table 1. Further sediment data is available from the INFOMAR (Integrated Mapping for the Sustainable Development of Ireland's Marine Resources), a successor to the Irish National Seabed Survey (INSS). Data from selected fishing areas Porcupine Bank, Bantry Bay and Donegal Bay were too few to interpolate across the respective areas and sediment characteristics were examined for each individual grab sample per location. The resultant sediment profiles and individual grab samples are presented in Figure 2.

2.3 Hydrodynamic Model

In order to replicate the physical environment a hydrodynamic model, here the Regional Ocean Modelling System (ROMS), was used to describe the spatial and temporal changes in oceanographic conditions. ROMS is a member of a general class of three-dimensional, free-surface, terrain-following numerical models involving certain hydrostatic and Boussinesq assumptions (Haidvogel *et al.* 2007). The model is an implementation of ROMS which is an open source model with a large international user community. The Marine Institute of Ireland has used ROMS to build a hydrographic model for an area that encompasses all of Ireland's territorial waters with prognostic variables for surface elevation, potential temperature, salinity and velocity. The model simulates these parameters for a user-defined model domain which encompasses a significant

portion of the northeast Atlantic. The extent of the domain is shown in Figure 1. The model is forced with operational atmospheric and oceanographic data at the perimeter-boundary of the domain and at the air-sea boundary. Model validation of tides, sea-surface temperature (SST), vertical structure of temperature and salinity is continuous and the modelled fields agree well with observed data and can be found on the Marine Institute website (<http://www.marine.ie/home/services/operational/oceanography/ModelValidation.htm>).

The ability of the model to recreate significant hydrodynamic features is also effective and although not rigorously tested there is confidence in its predictions. For example, validation of the model currents against measured current data off the west coast of Ireland indicates that the model predicts local hydrodynamics for that part of the domain very well. Stored environmental data from 2011 were extracted from the ROMS model to study the hydrodynamic conditions over the whole domain. Differential tidal volumes and water flows at the local scale have the potential to bias accurate valuations of water speed and direction, especially in the short-term. Mean monthly velocity values per domain cell over the entire domain were used to overcome this bias and negate the effect of tidal cycles and provide a reasonable estimation of monthly net water speed (m/s^{-1}) and direction of movement about the study domain. The resolution of the model grid cells being approximately 1.5 km x 1.5 km. Temperature data was similarly extracted to produce monthly maps describing changing regimes which were interpolated using geo-statistical methods (Inverse Distance Weighting - IDW). The current study presents surface and bottom velocity vector maps to describe water speed and movement around the entire model domain in conjunction with interpolated temperature regimes (Figure 3). An average monthly velocity measure was extracted to investigate water speed.

2.4 Particle-tracking model

Water temperature and velocity have an important influence on the recruitment, growth and dispersal of *Nephrops*. In order to determine the influence of hydrodynamic conditions on the dispersal fields of *Nephrops* larvae, ROMS was coupled with a

larval transport model, LTRANS, to predict larval trajectories from the various fishing grounds. The model was initially developed by the University of Maryland to track the dispersal of oyster larvae through Chesapeake Bay, USA (North *et al.* 2008). In the present study hydrodynamic flowfields are used to advect the larvae throughout the model domain and track them in three dimensional space in real time as they are forced by stored environmental data from 2011. Boundary conditions were imposed such that if a particle passed through a vertical (i.e. seabed or sea-surface) or horizontal boundary (at the grid cells specifying the land-sea interface), it was reflected at an angle equal to the angle of approach and at an equal distance to that which it originally passed the boundary. The model produces 40 depth layers (i.e. sigma-levels) which are thinner at the sea surface and bottom than at mid-depths. The depth of these layers varied in accordance with bathymetry. The model assumes open water turbulence in both planes and further assigns a constant value for random horizontal diffusion at $1\text{m}^2\text{s}^{-1}$. A complete description of model functionality and LTRANS (v.2) design parameters are given by Schlag and North (2012).

Within the model specifications, larvae can be released from any location within the domain and at any time of year allowing for differential temperature regimes to be compared. Some Functional Units contain multiple small fishing grounds in close proximity and in these cases a subset of representative grounds were selected for study. For example three separate fishing grounds (Slyne Head, Galway Bay and the Aran grounds) make up FU17 on the west coast and larval dispersal was modelled from all three. Similarly four separate grounds (Bantry Bay, Helvick Head, Cork Channels and the Galley grounds) were studied within FU19 along the south coast. Multiple release sites were selected within the larger self-contained FU's to better capture local hydrodynamic variation. These were the Porcupine Bank (FU16), the western Irish Sea (FU15) and the Smalls (FU22). A single central location was chosen on the eastern Irish Sea (FU14) and the Labadie and Banana grounds (both within FU20-21) from which to release larvae. Larvae were also tracked from the Southwest Slope, south of the Porcupine Bank, although this ground has not been assigned as a Functional Unit. In total larval dispersal was examined from 14 release sites within *Nephrops* fishing grounds in Irish waters. The number of larvae released is user-defined but due to computational restraints was set in this study at 500 individuals per simulation. Particles were artifi-

cially released at a depth of 10 m (as opposed to the seabed) to allow for a more realistic simulation. Larvae are expected to ascend rapidly upon hatching to just above the thermocline (Bell *et al.* 2006). Basic biology was ascribed to the ‘larvae’ to determine the effect of growth and larval swimming behaviour on dispersal distance. Larvae were assumed to have no swimming ability for the first 10 days after hatching and were passively dispersed during this time. Swimming speed was specified to increase as a function of time from ten days after hatching/release, from 0.0001 to 0.0015 m/s⁻¹, until the larvae metamorphosed. Particles were tracked in 3D as per the relevant larval duration. On completion of the simulation the end position was recorded. The analysis grouped all simulations undertaken per ground to determine the average number of simulated hatchlings that were retained, donated to adjacent grounds or lost from the system and these results are presented in Figure 4.

2.5 Temperature

Previous experimental studies on the relationship between temperature and developmental rate of reared *Nephrops* larvae were used to determine larval duration. Dickey-Collas *et al.* (2000a) proposed an exponential regression equation that described stage I and stage II larvae quite well. Difficulties in continual successful rearing of larvae through to stage III resulted in those authors adopting an alternative stage III regression equation based on Smith (1987). The current study employs the regression equations used in both former studies to calculate larval duration and these are presented in Table 2. Dickey-Collas *et al.* (2000b) found that *Nephrops* larvae generally remained in surface waters throughout their three planktonic stages. Consequently, only average monthly sea-surface temperatures (SST's) extracted from the ROMS model were used in conjunction with the regression equations. Stage I and Stage II larvae are deemed to occur in the same month are thus subject to the same monthly temperature. The results of all three stages were summed to give total larval duration (see Table 3).

3. Results

3.1 Sediment Profiles

Sediment characteristics are more evident in those areas for which multiple data exists. A clear pattern emerges in the western Irish Sea where the extent of optimal habitat, characterised by dark brown zonation in Figure 2, is large and clearly defined. The sediment in the centre of the fishing ground consists of > 90 % mud with a clear transition to coarser sediment towards the north and also towards Dundalk Bay. This enclosed area is surrounded by a ring of sediment comprised of 50 % mud. Outside of this transition zone the benthos is characterised by sand with a low percentage of mud except for small mud patches which reach to the east and the south. Fewer sediment samples were collected over the Aran (n = 193) and Smalls (n = 117) grounds but the spatial extent of mud and thus potential habitat remains obvious. The centre, and towards the south, of the Aran ground is ~ 70 % mud which changes to ~ 50 % moving west. The transition to the east is more abrupt and suitable sediment is replaced by gravel. Galway Bay (~50 % mud) and Slyne Head (~ 30 % mud) contain smaller areas of suitable substrate. In the Smalls, a central patch contains sediment with about 70 % mud. This is surrounded by a broader band of sediment (~ 50 % mud) around the ground, gradually transitioning into less suitable habitat (~ 30 % mud). Sediment datasets from three areas of interest; Bantry Bay, Porcupine Bank and Donegal Bay, were too limited to interpolate effectively and individual grab sample data are presented where these exist. In the Porcupine Bank data only exist for the northern half of the fishing ground. Ten samples exist within the north-eastern tip, seven of which are comprised of 70 – 80 % mud, with the others containing between 40 - 70 %. In the centre of the fishing ground four samples contain a mud percentage of 60 – 90 % but this high value begins to fall towards the northern side of the patch. Data from Bantry Bay suggest the presence of suitable *Nephrops* substrate with most samples containing 60 – 90 % mud although data is limited in this area. In Donegal Bay, the only small patch of suitable substrate (60 – 80 % mud) is evident around Killybegs to the north of the bay.

3.2 Hydrodynamic conditions

The maps in Figure 3 show the change in water movement and temperature between April and August which are peak hatching times for *Nephrops* in Irish waters. The influence of slow-moving nutrient-rich deep water up-wellings forced by the bathymetry of the continental slope was clearly evident around the Rockall Trough and the Porcupine Seabight. Deeper areas of the model domain experienced faster more powerful water movement than shallower regions. In the Celtic Sea fast moving water was apparent around the southwest coast of Ireland in June and July. In August, water velocity increased moving south around the west coast of Galway and Mayo and clockwise along the south coast. Surface water consistently moved quickly through the northern channel of the Irish Sea and into the Clyde and through Georges Channel in the south. This is forced by strong tides in both areas. There is evidence of an anti-clockwise circular gyre in the western Irish Sea during June and July. Sea surface temperature regimes over the domain indicated a uniform increase between April and August. The temperature rose from $\sim 11 - 12^\circ$ in April and May to between $16 - 19^\circ$ in the warmer summer months with slightly higher temperatures in the southern Celtic Sea. Deeper waters off the continental slope were consistently about $2 - 3^\circ \text{C}$ from April through August. On the continental shelf including the Celtic Sea, Porcupine Bank and off the northwest coast of Ireland sea-bottom temperatures were uniformly $10 - 11^\circ$. Shallower bottom water temperatures in the Irish Sea increased in July and August, but colder water was still evident in the deeper northern channels during this time.

3.3 Temperature

The average monthly temperature predicted by ROMS between April and August 2011 for different sea areas and the resultant pelagic larval phase durations as described by regression equations are shown in Table 3. *Nephrops* hatched on the Porcupine Bank on the 1st April remained in the water column for 44 days decreasing to 35.1 days if

hatched on the 1st June. The difference in temperature regimes experienced by the larvae between April and June in this area was 1.6°C. Temperatures along the west coast of Ireland and encompassing the Aran Grounds were slightly warmer than those on the Porcupine Bank. These grounds experienced temperatures from 11.4° to 13° C, resulting in larval durations of between 44 and 35 days from April to June. Larval durations in the Celtic Sea between April, May and June lasted 52, 46 and 34 days. Warmer SST's in the Irish Sea during June, July and August (12.7°, 14.3° & 15.6° respectively) reduced larval duration considerably from 36.6 days in June to 24.4 days in August.

3.4 Larval drift modelling

Larvae were recorded as being retained over the same ground from which they hatched or donated to adjacent fishing grounds. Larvae that remain above a fishing ground have the potential to colonise and construct burrows as the sediment here is most suitable. We hereby refer to 'viable' larvae as those which metamorphose over fishing grounds with suitable sediment following pelagic dispersal and the remainder as being lost from the system entirely. Retention was highest in the western Irish Sea where 33.7 % of all larvae hatched, regardless of seasonality, remain above that fishing ground following metamorphosis. This ground did not donate any larvae to proximal grounds in 2011. Only two other grounds, the Labadie (33.4 %) and the eastern Irish Sea (32 %) retain > 30 % of larvae produced. The eastern Irish Sea did not contribute larvae to any other grounds while the Labadie donated 0.9 % of its larvae to the nearby Galley ground. Overall, the percentage of retained viable larvae is quite low with < 10 % at six fishing grounds studied. This indicates a significant loss of larvae from these systems. For example, 99 % of larvae produced in Bantry Bay in these simulations, are lost, as are 98.9 % from the Southwest Slope. Four fishing grounds produce between 10-20 % viable larvae. These are the Porcupine Bank, the Banana, the Aran grounds and the Smalls. 22.9 % of larvae hatched from the Galley ground remained over sediment suitable for burrow construction but just 1.6 % were actually retained over the ground. A stylised representation of dispersal from four *Nephrops* areas; the Porcupine Bank, Aran Grounds, Celtic Sea and Irish Sea (Figure 5), highlight the effect of seasonal

variation in the dispersal fields. Coloured-coded arrows indicate the approximate distance and direction travelled by larvae as predicted by LTRANS. Again, it is noted that dispersal patterns here are based on 2011 environmental data only, which may not be a typical representation of annual water movement.

Potential connectivity between proximal, or even distant *Nephrops* fishing grounds, was explored to differentiate between larval retention and dispersal as there are important consequences for stock connectivity and/or genetic isolation. The eastern Irish Sea, the western Irish Sea and the Southwest Slope do not donate larvae to any other ground, meaning they retain 100 % of viable larvae. The Porcupine Bank ground retained 99 % of all viable larvae hatched from it. The Aran ground donates 0.4 % of its larvae to both the Slyne and Galway Bay grounds and these adjacent grounds contribute to the larger Aran Ground (0.9 % and 1.5 % respectively). In total 89.2 % of larvae hatched from the Aran grounds (FU 17) are lost from the system but there is evidence that some larvae hatched in FU17 are dispersed north towards Clew Bay, Co. Mayo and Donegal Bay where smaller scale fisheries for *Nephrops* exist. The Smalls retains 17.2 % of its larvae while donating 2 % to the Labadie and 0.3 % to the Banana ground. Five fishing grounds of the 14 modelled were net donators i.e. they donated more larvae to other grounds than they retained themselves. The grounds and the percentage of larvae donated were the Galley grounds, 21.4 %; Banana, 13.1 %; Helvick, 7%; Cork, 6.9 % and Bantry Bay, 1 %. All are found in the Celtic Sea along the south coast of Ireland. The Cork Channel and Helvick grounds both contribute larvae to four other adjacent grounds. The Galley Head ground contributes larvae to six other grounds and receives larvae from five. Table 4 shows the degree of connectivity between each ground and the degree of retention versus donation. Finally, to better understand larval movement over time within a pelagic marine environment a 4D data visualisation tool (Eonfusion v 2.3) was used. The software allows clear visualisation and a better understanding of potential dispersal from each of the grounds. A short movie clip visualising this aspect of the work is available on the Marine Institutes' Vimeo site and can be viewed through the following link (<https://vimeo.com/107145708>).

4. Discussion

There is increasing evidence across a number of well studied *Nephrops* stocks that environmental factors impact on recruitment, density and ultimately growth (Johnson *et al.* 2013). The present study investigates the key environmental factors affecting two different aspects of the lifecycle of *Nephrops* populations around Ireland. Firstly, sediment characteristics were mapped to assess the spatial extent nature of *Nephrops* fishing grounds because this is an important factor governing the distribution, density and size of the adult benthic phase. Secondly, local hydrodynamic conditions, including net water movement patterns and temperature regimes, were explored to study their influence on the dispersal of *Nephrops* larvae during the pelagic phase.

Nephrops preferentially occupy muddy sediment which enables optimal construction of elaborate burrow systems. It is rare to find *Nephrops* in sediments with a mud fraction < 10 % (Tully and Hillis 1995). Most recent studies have found a domed shaped relationship between density and percentage mud with highest densities observed above 40 % mud (Campbell *et al.* 2009, Johnson *et al.* 2013). The various models developed in previous studies typically explain around 40 % of the variation in density. Slightly different relationships have been observed between areas and years. It is also well known that there is inverse relationship between *Nephrops* size and percentage mud (Tully and Hillis 1995, Maynou and Sarda 1997). It was immediately apparent that the sediment patch in the western Irish Sea has the highest mud percentages, of those FU's studied, over a relatively large and homogeneous area. This ground is the single most commercially important ground around Ireland yielding ~ 9,000 tonnes annually (ICES 2013). Underwater TV surveys show consistently high *Nephrops* burrow densities i.e. with a modal density ~1.0 burrows/m² (Doyle *et al.* 2013). In fact the densities observed in the Western Irish Sea are the highest of any ground currently surveyed and the mean size of *Nephrops* caught is amongst the smallest of any ground commercially fished (Johnson *et al.* 2013). A mud content of > 50 % is also evident in the important Smalls and Aran grounds but these areas are clearly not as muddy as the Western Irish Sea. Both grounds also appear relatively homogeneous with muddier sediments towards the centre of the patches. The mean sizes of *Nephrops* in these areas are larger

and the observed burrow densities are moderate 0.3 - 0.8 burrows / m² (ICES 2013). Data from Bantry Bay, the Porcupine Bank and in Donegal Bay although less numerous also identify muddy substrate in the range of what is suitable for *Nephrops*.

The distribution of the observed benthic sediment arises from a complex interplay of topography, bathymetry and local hydrodynamics, on various timescales. For example, deposition of finer particulate material would be expected in lower energy environments or areas with retention mechanisms such as gyres. However much of the mud sediment on many of these *Nephrops* grounds originated during the last de-glaciation and prevailing hydrodynamic conditions simply act to retain the mud *in situ*. There are concerns in the literature about re-suspension of sediment due to trawling which could have the potential to modify the habitat and in turn impact on productivity and sustainability of the fishery (Kaiser *et al.* 2002, Hily *et al.* 2008). Mapping and monitoring the sediment characteristics and distributions should be continued into the future.

The different sediment characteristics within and between the grounds can have a big impact on the biology of *Nephrops*. The results here support the findings of previous studies that density and size is strongly linked to sediment (e.g. Johnson *et al.* 2013). Integrating density and individual size data with the sediment data on a broad geographical scale is beyond the scope of the present study but this is something which should be investigated further in the future. If muddier sediment, such as that observed in the western Irish Sea, is better for adult standing stock (burrow construction), this could explain the higher densities of individuals and reduced mean size of juveniles and adults through intra-specific competition. The sediment characteristics therefore could be a key constraint on growth and size of individuals in the fishery. However, population density is also dependent on the degree of successful larval settlement which is investigated further in the second part of this study.

Because larval *Nephrops* are thought to develop in warmer waters between the thermocline and the surface, gyres are considered the classical retention mechanism for *Nephrops* larvae (Hill *et al.* 1996). Gyres can be established when bottom fronts form at the edge of water masses with strong horizontal gradients. This occurs primarily in temperature but sometimes in salinity. Water circulation is weakest in the centre of

these gyres contributing to the accumulation of finer sediment. The timing and persistence of cyclical gyres over *Nephrops* mud-patches can be a key factor in the recruitment dynamics and population connectivity for this species.

The use of a coupled hydrodynamic and larval-tracking model in the present study allowed for a detailed investigation into the environmental conditions simulated *Nephrops* larvae are likely to encounter at the time of hatching. The output of the ROMS and particle tracking model was parameterised as accurately as possible using 2011 data. Due to computational and time constraints 500 particles from only a few indicative release sites could be simulated. Nevertheless the output provides evidence for the occurrence of a number of gyres in 2011. The presence of a gyre in the western Irish Sea *Nephrops* gyre, as identified by Hill *et al.* (1996) was apparent in June and July since larvae were advected in an anti-clockwise circular direction. The circulatory systems to the west and south of Ireland are complex and to date poorly understood (White *et al.* 1998). The ROMS model predicts strong currents which follow local bathymetry in association with up-wellings and local flow patterns along the shelf slope as would be expected with this topography. There is also good evidence of cyclical gyres in the larger Labadie and Smalls grounds in most months as hypothesised by Bailey *et al.* (1995). There is clockwise circulation around the Porcupine Bank but at a fairly broad spatial scale in most months. There is little evidence of retention gyres on the Aran grounds or on the small patches along the south coast (FU19). In those areas the shelf currents have the potential to advect larvae considerable distances.

Temperature regimes in particular have an important effect on larval *Nephrops* influencing the duration of the larval stages and thus potential exposure to prevailing hydrodynamic conditions (Dickey-Collas *et al.* 2000b). Data extracted from the ROMS model indicate that a temperature increase of just 1° C can reduce the duration of the larval phase by over 9 days in some instances. Temperatures in the Irish Sea peak in July and August which influence local hydrodynamics and encourage rapid larval development (a little over three weeks). Larval duration over the Aran grounds may be twice as long if hatched in April. Larvae are thought to ascend rapidly following hatching and are predominantly found in surface waters (Dickey-Collas *et al.* 2001b). The benefits of a quick vertical migration are two-fold. Favourable surface currents may

ensure larval retention above suitable sediments for burrow construction, while warmer surface waters encourage a faster larval developmental rate and thus limit the amount of time spent in the potentially dangerous planktonic phase. The regression equations used to formulate larval duration times are reasonably robust but they are also based on very limited data (especially for Phase III larvae). Further research into the developmental rates of these larvae could provide more accurate estimates into metabolic responses to temperature. Like many zooplankton, *Nephrops* larvae are capable of limited independent movement (Hill 1990). LTRANS accounts for this by introducing a swimming speed that increases as a function of age. However, the direction of this movement is modelled randomly which may have little overall effect on ultimate dispersal patterns. Due to computational constraints the present study did not model natural mortality as a factor in the loss of larvae from the system but this is a crucial consideration for future work. The combined effects of starvation, predation and disease may result in > 90% of larvae dying before maturation (stage IV), and the search for suitable habitat commences, with important implications for the recruitment success of this species (Marta-Almeida *et al.* 2008).

Our analysis of local hydrodynamic regimes on *Nephrops* fishing grounds has highlighted the potential for variable environmental conditions to influence the recruitment and ultimate larval dispersal of this species. For example, our study shows that larvae hatched within the east or west Irish Sea fishing grounds are more likely to be retained over a suitable mud patch than if hatched from any other grounds in Irish waters. Furthermore, Irish Sea larvae are also more likely to be retained if hatched in June which agrees with the formation of seasonal gyres as retention mechanisms proposed in previous studies (Hill *et al.* 1996). Both Irish Sea grounds (east and west) were shown to be 100% self-recruiting in 2011. This implies complete stock isolation even between each other. However, this potential disadvantage is offset by the large geographical area of potential habitat in the western Irish Sea which can support a large population of *Nephrops* thus increasing genetic variability (Hillis 1988).

In the Celtic Sea, the multiple smaller grounds in the southwest FU19 i.e. Galley Grounds and Helvick have limited self-recruitment. Three grounds (Galley, Cork Channels and Helvick) donate larvae to at least four other grounds in the vicinity and

this stock inter-connectivity could also buffer against localised depletion. It is not surprising given the spatial scale of the mud patches, which are significantly smaller than the dispersal field in the simulations, that retention rates are low. To remain sustainable these grounds must interact at a meta-population level with different grounds acting as sources and sinks of larvae. The FU19 grounds are also probably linked to the Smalls and the Labadie. Outputs from the ROMS model suggest that surface water flow above the Labadie is strongest during the summer months. However retention is also quite high (33.4%) which indicates that some gyre formation may be in effect entraining the larvae within the area. This is most apparent in April and May with surface water adopting a south-westerly orientation about the domain during June. Retention rates over the Smalls are also relatively high (19.7%) and there may well be connectivity with the Labadie and FU19. On the west coast the Aran ground in FU17 also retains a high percentage of larvae and the smaller Slyne and Galway Bay grounds are net donators to the Aran ground. There is also evidence of some larval transfer between Celtic Sea stocks to the south and Clew Bay and Donegal Bay to the north if larvae are hatched in April.

Many of our results agree well with Hill (1990) who used an advection-diffusion-mortality model to study *Nephrops* dispersal. The author found that surface advection, possibly wind-forced had the greatest effect on larval dispersal and that even low levels of mean advection ($0.04 - 0.05 \text{ m s}^{-1}$) are enough to reduce retention over most mud-patches. The present study observed average velocities between $0.15 - 0.23 \text{ m s}^{-1}$ over the Porcupine and Southwest Slope during peak hatching in April and May resulting in potential larval losses of 87.7 % and 98.9 % respectively. Similar water speed in the Celtic Sea was also observed but as shown, a network of smaller grounds in close proximity has the potential to produce more viable larvae. Relatively high advection rates in the Irish Sea are offset within a gyre which increases retention however increased stratification brought about by warmer waters could result in a greater export of larvae from this area (Olbert *et al.* 2012). Hill (1990) also describes a relationship between the size of the mud-patch and retention with larger grounds retaining more larvae. Our study has shown that larger homogenous mud-patches do retain more larvae, as seen in the Western Irish Sea, the Smalls and the Aran Grounds for example.

As an exception, the Porcupine Bank and, to a lesser degree the Southwest slope only retained low percentages of larvae and also had very little larval exchange with the other fishing grounds. This is unsurprising considering the water depth, the influence of Atlantic currents, upwellings and the physical isolation from other fishing grounds. Recruitment in this stock is known to be variable and the stock has been severely depleted in the recent past ~2008 (ICES 2013). This study found some evidence of a cyclical gyre over the Porcupine Seabight to the south of the fishing ground and the suggestion of a Taylor column in June over the Porcupine Bank, which might enable larvae entrainment over the mud-patch. However, hatching events are thought to be concluded during April – May in this area. The formation of these domes in deeper waters is less predictable, as is their relative strength, which probably leads to the variable recruitment observed. The findings here reinforce the need to lightly exploit the stock and keep female biomass at levels that can buffer against prolonged periods of weak recruitment due to unfavourable hydrodynamic conditions.

Our exploration of larval drift and dispersal is an important first study into the possible environmental drivers of *Nephrops* recruitment around Ireland. The work illustrates a complex interplay between local physical hydrodynamics and *Nephrops* larval development although some caveats remain. The accuracy of the ROMS model should be validated further through direct and indirect comparisons with observations. Larval release sites could be expanded to allow a more accurate quantitative evaluation of retention and exchange rates. The current analysis only provides first a qualitative estimate of these because the number and timing of release sites were so limited. Future release sites could be informed by UWTV abundance estimates and density surfaces. More realistic larval production schedules should be also used in the future. The months of probable larval release used here, although informed by re-emergence patterns of females into the fishery, is a crude simplification. In practice larval production is likely to occur over a more limited 5 or 6 week period and follow a Gaussian shaped distribution (Briggs *et al.* 2002). To do this may require some experimental larval surveys or other observations to identify periods of peak hatching. For example, on-going research within the NEPHROPS project has observed hatching

along the west coast of Ireland to begin on 10th April and concluded by May 12th (Pers. Comm.).

All model simulations present here are forced by environmental data from 2011. Further research could establish methodologies to predict the likelihood of recruitment success in any given year based on annual environmental regimes from ROMS. This could be used to predict future recruitment and stock population dynamics and inform management accordingly. This would be particularly relevant for stocks, such as FU16 and FU20-21, where recruitment variability or impairment has occurred in the past (ICES 2013). Additionally, modelling future climactic trends could enable forecasting on the possible effects of climate change on *Nephrops* and other species. Ocean warming, as predicted by the Intergovernmental Panel on Climate Change (IPCC 2007), has the potential to alter winds, vertical mixing, oxygen, salinity and pH, thus affecting physiology, developmental rates, indirectly food availability and overall survival (Olbert et al. 2012). A better understanding of larval dynamics and hydrography is key to predicting the effects of global warming on commercially important species such as *Nephrops*.

The information base on *Nephrops* stocks around Ireland has improved significantly in the last decade. The challenge now is to integrate data across a number of sources; UWTV surveys, groundfish surveys, sampling of the fishery, fishing activity, habitat sampling and oceanographic models to achieve a better overall understanding of stock dynamics and drivers. The current study is an important contribution in that regard. The ultimate goal is for ecosystem based fishery management (EBFM) of this valuable resource.

Tables and Figures

Table 1. Number of sediment samples taken during Underwater TV surveys from three important *Nephrops* fishing grounds. Data were interpolated in ArcMap 10 to map sediment characteristics.

	Aran	Celtic Sea	Irish Sea
2002	60		
2003	29		128
2004	30		102
2005			91
2006	74	110	75
2007		107	

Table 2. Regression parameters for ln (stage duration) versus temperature relationship for *Nephrops* larvae in this study.

Stage	Slope	SE (slope)	Intercept	SE (Intercept)	Source
I	-0.163	0.006	4.283	0.064	Dicky - Collas et al. (2000a)
II	-0.161	0.013	4.51	0.17	Dicky - Collas et al. (2000a)
III	-0.113	-	4.188	-	Smith (1987)

Table 3. Mean monthly SST's (April – August) as predicted by ROMS in 2011 and the resultant pelagic larval phase duration (days) used in the present study to parameterise the larval transport model (LTRANS).

	Irish Sea		Celtic Sea		Aran Grounds		Porcupine Bank	
	Mean C°	Duration	Mean C°	Duration	Mean C°	Duration	Mean C°	Duration
April	-	-	10.1	52.9	10.4	50.7	11.4	44.0
May	-	-	11	46.5	10.9	47.2	11.8	41.6
June	12.7	36.6	13.1	34.6	13	35.1	13	35.1
July	14.3	29.2	-	-	-	-	-	-
August	15.6	24.4	-	-	-	-	-	-

Table 4. Connectivity matrix to describe the distribution of *Nephrops* larvae over Irish fishing grounds following pelagic dispersal. The matrix describes the percentage of viable larvae that are retained over the same ground from which they are hatched (red); are transported to adjacent grounds (pink) following the pelagic larval phase or are lost from the system entirely (bold).

Fishing Ground	% Loss	Porcupine	Southwest	Slyne	Aran	Galway Bay	Bantry Bay	Galley	Labadie	Banana	Cork	Helvick	Smalls	W. Irish Sea	E. Irish Sea
Porcupine	87.7	12	0.3												
Southwest	98.9		1.1												
Slyne	93.7			5.4	0.9										
Aran	83.4			0.4	15.8	0.4									
Galway Bay	90.5			0.4	1.5	7.6									
Bantry Bay	99						0.2	0.3	0.5						
Galley	77		0.1	0.3	2.5	0.2	0.1	1.6	18.2						
Labadie	66.6							0.9	32.5						
Banana	84.6							0.1	12.7	2.3			0.3		
Cork	92.9						1.1	4.1	1.5	0.2	0.2				
Helvick	92.9						1.3	4.9		0.3	0.5	0.1			
Smalls	80.2								2	0.3			17.5		
W. Irish Sea	66.3													33.7	
E. Irish Sea	68														32

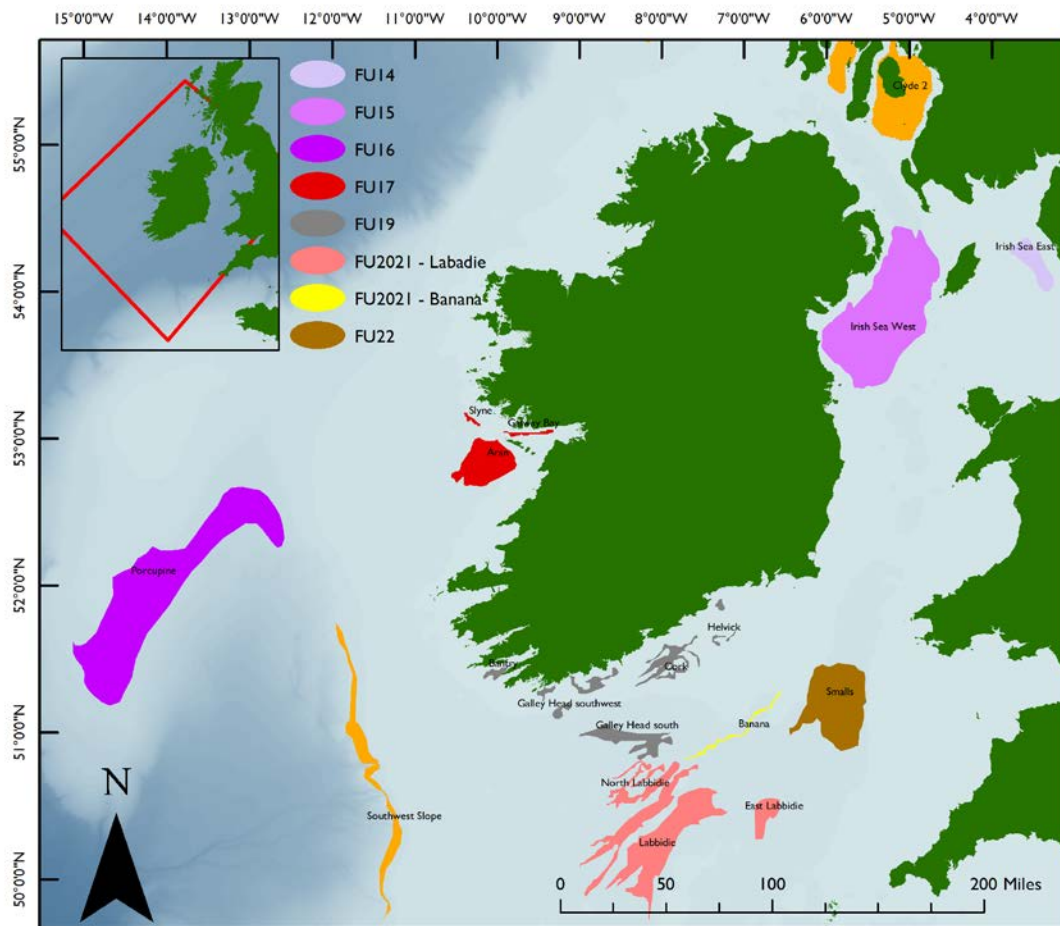


Figure 1. Spatial extent of primary *Nephrops* fishing grounds (named) in Irish waters. Individual grounds are coloured by relevant Functional Units (FUs). Smaller grounds are grouped as one Functional Unit in some cases i.e. Cork, Helvick, Galley and Bantry Bay grounds along the south coast are all FU 19. The Southwest slope is not an FU but was modelled in the present study. The Clyde, a Scottish fishing ground, is also shown but was not considered in the study. Inset – Boundary (red) of LTRANS model domain used in this study to track *Nephrops* larval dispersal.

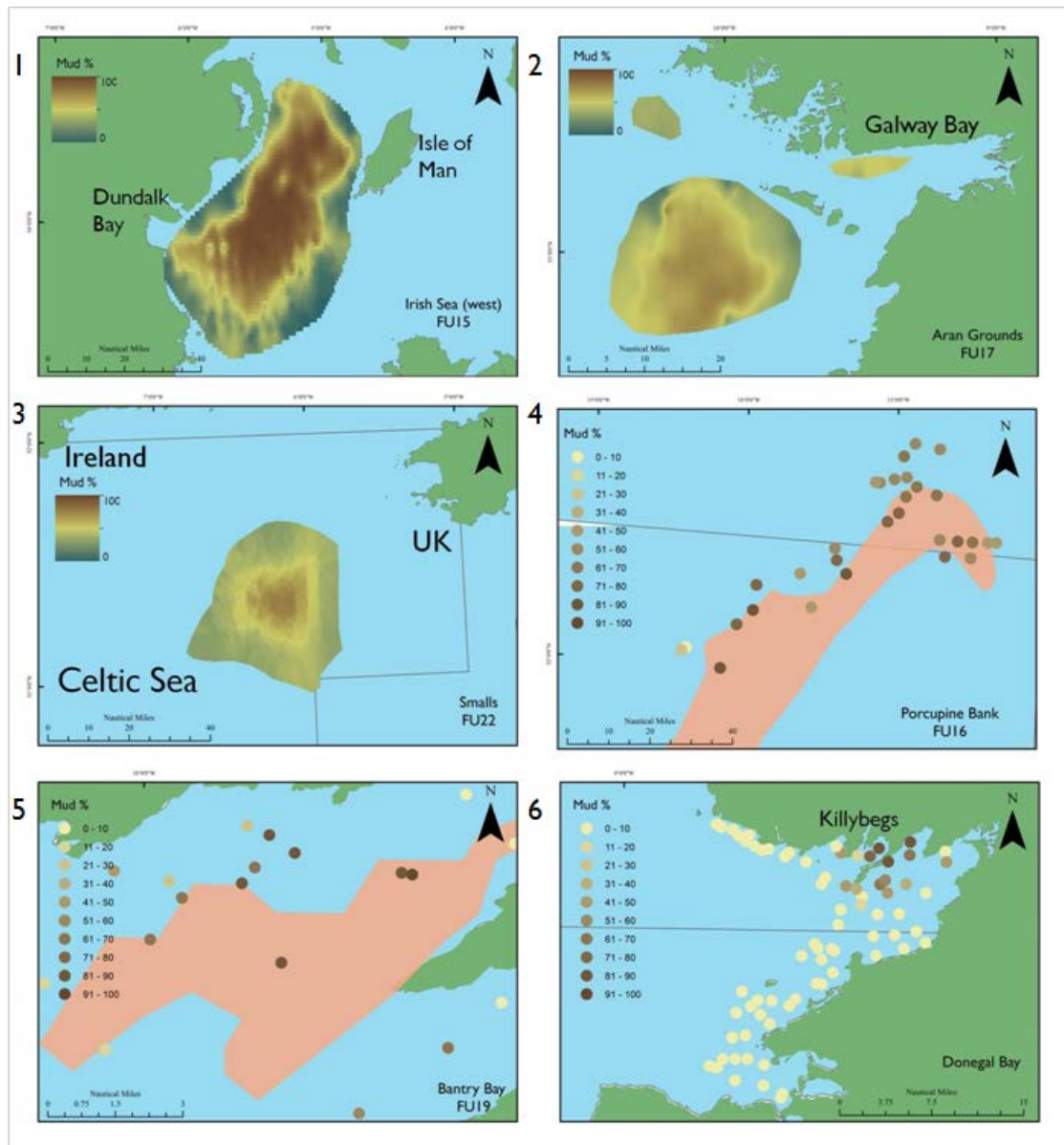
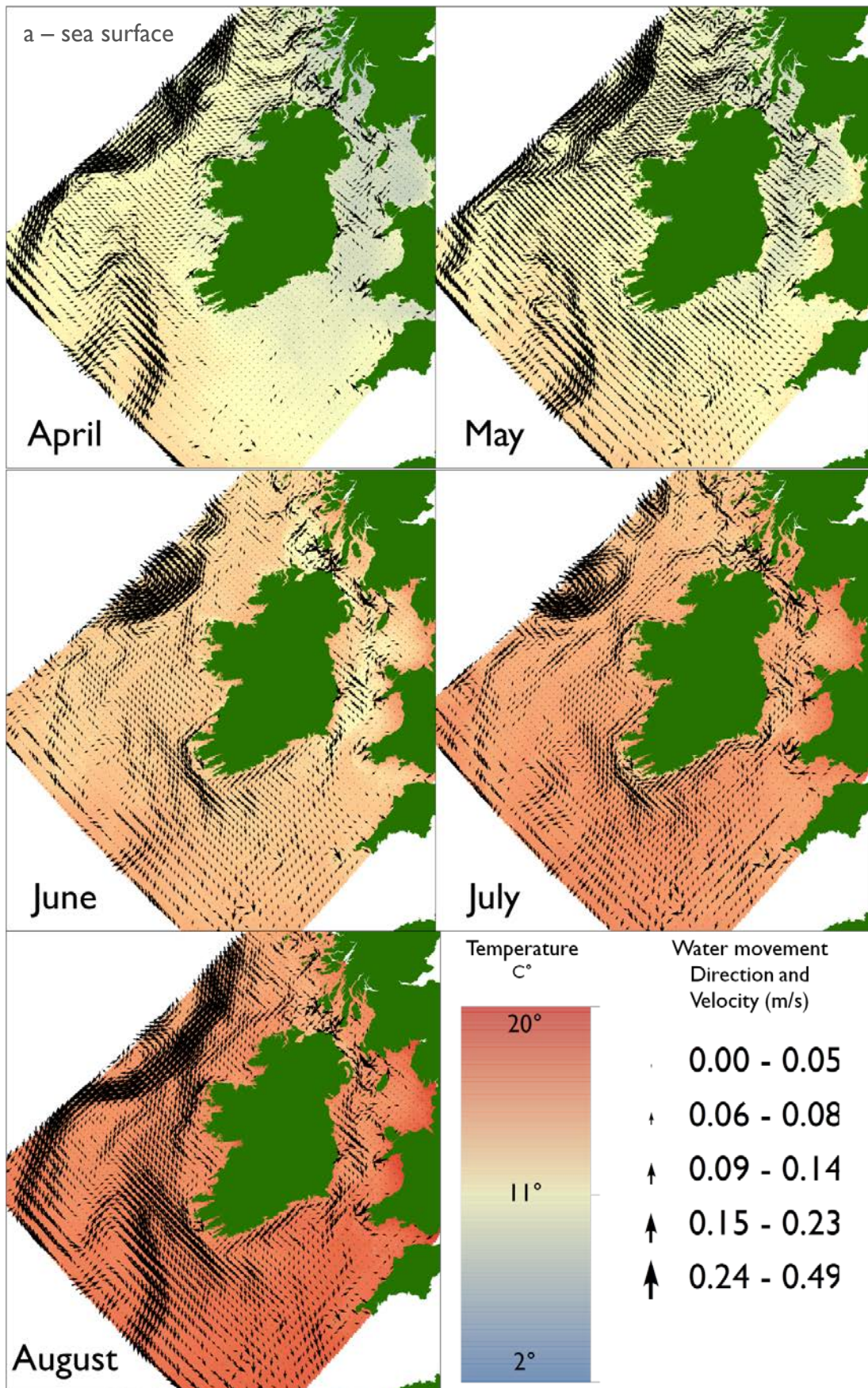
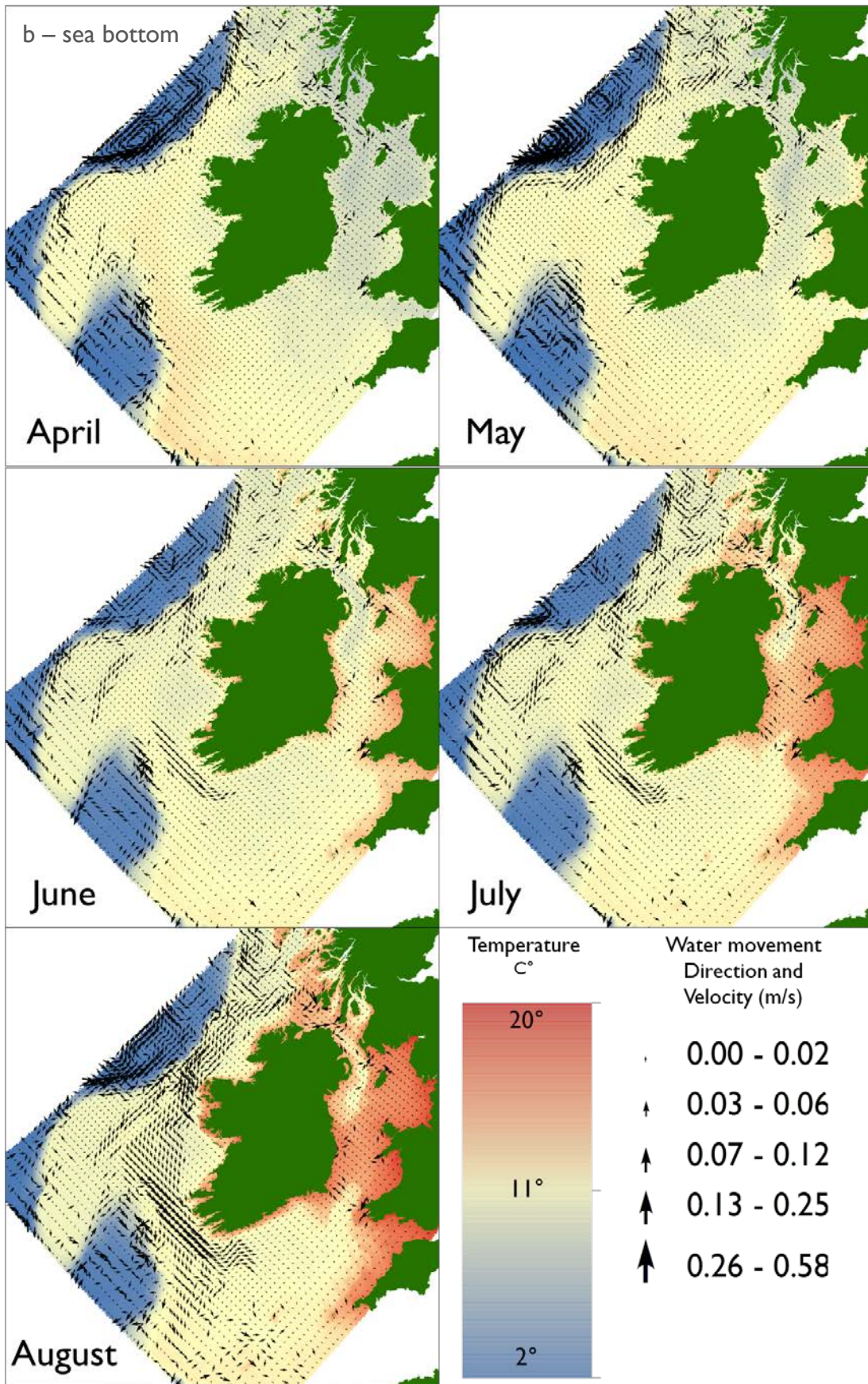


Figure 2. Sediment characteristics of three *Nephrops* fishing grounds. Data are interpolated in ArcMap10. Additional sediment data from INFOMAR seabed mapping programme provide additional information for the Porcupine Bank, Bantry Bay and Donegal Bay but data are too few to interpolate. Colour code is applicable across panels.

Figure 3. Mean monthly surface (a) and sea-bed (b) velocity vector maps describing water speed (m/s^{-1}) and movement around the model domain in conjunction with interpolated temperature regimes extracted from ROMS model.





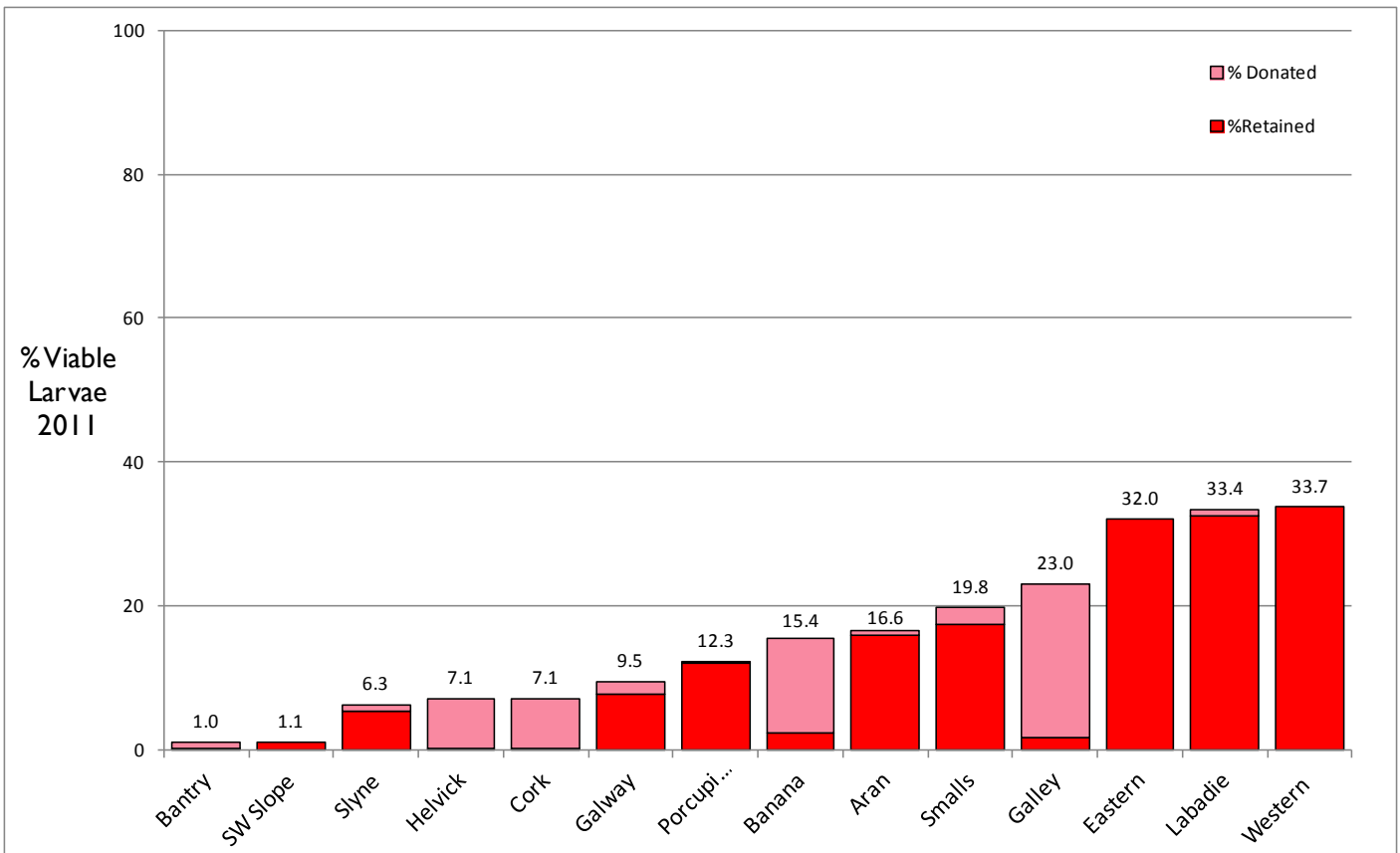
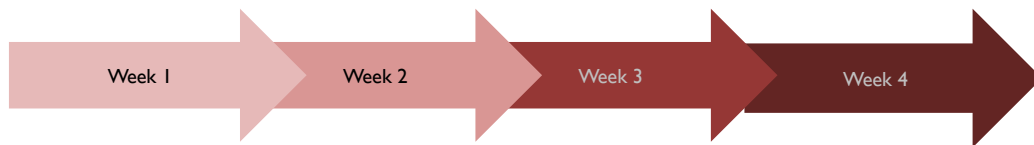
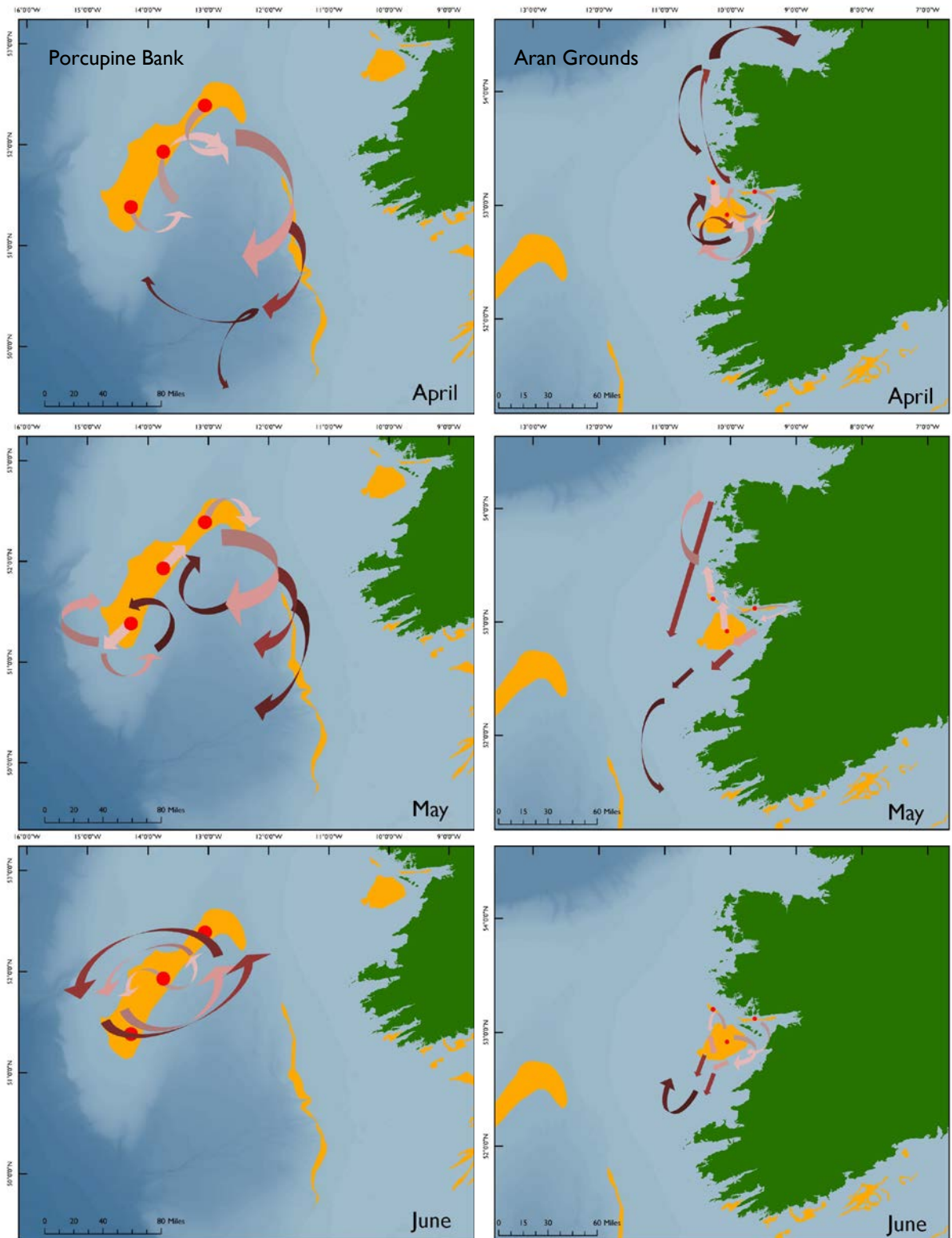


Figure 4. Percentage of viable *Nephrops* larvae that hatched from each fishing ground, Larvae have the potential to either re-seed the same (red), or adjacent (pink), grounds following dispersal. The remainder are considered lost from the system. All simulations per ground are grouped and are based on 2011 data.

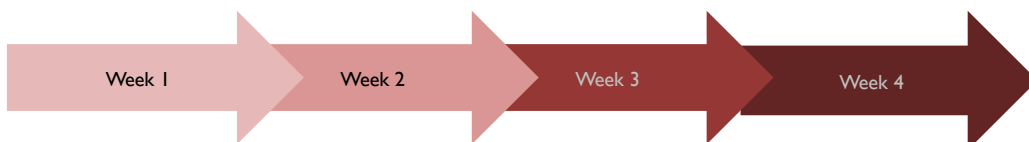
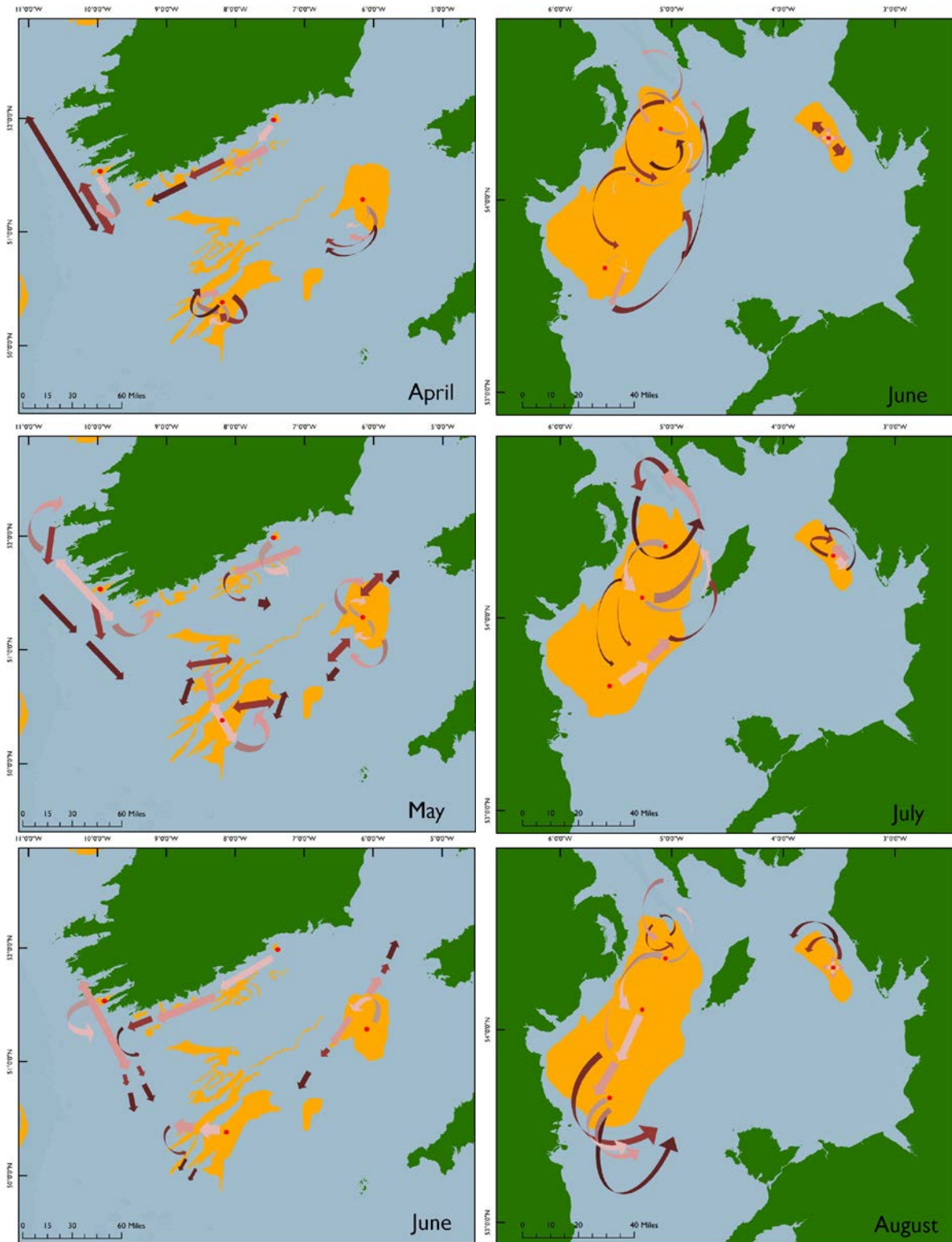
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Figure 5. A representation of larval dispersal over time from four *Nephrops* fishing areas; a) Porcupine Bank, b) Aran Grounds, c) Celtic Sea and d) the Irish Sea. Reading each panel from top to bottom indicates the general pattern of dispersal from each ground over time. Arrow lengths correspond to respective dispersal distance per week. Red dots indicate locations of hatchings on the 1st of each month.

Nephrops – Sediment characteristics and local hydrodynamics



Nephrops – Sediment characteristics and local hydrodynamics



Acknowledgements

Thanks to those in the Marine Institute of Ireland who contributed to this study, including Oceanography, Advanced Mapping Services and the UWTV survey team. This study was funded in part by INFOMAR the national seabed mapping programme. UCC and Plymouth Marine Laboratory who contributed to the collection and analysis of the sediment samples. Finally, we are grateful to those who proof read and/or reviewed this paper and offered advice as to its content.

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ISSN 1649 5055

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