

# Metapopulation connectivity via larval transport of the Norway lobster *Nephrops norvegicus* in waters around Ireland: a modelled approach

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**ABSTRACT:** Many marine invertebrates exist as metapopulations comprised of disparate local populations whose persistence depends on rates of larval delivery and recruitment, and thus connectivity, between populations. For commercially exploited species, predicting connectivity of the metapopulation would enable estimates of potential annual recruitment and help inform fisheries managements in their decisions to ensure sustainable exploitation. The Norway lobster *Nephrops norvegicus* is the second most valuable commercial species landed from Irish waters. Its distribution depends on the presence of suitable sediment and larval supply. The aim of this study was to improve understanding of *N. norvegicus* metapopulation connectivity in waters around Ireland and between disparate fished populations in the wider northeast Atlantic. We employed hydrodynamic and larval transport models to describe spatial and temporal changes in oceanographic conditions and quantitatively predict the degree of connectivity between populations. The simulations suggested that there are 3 isolated populations (Porcupine Bank, Southwest Slope and Irish Sea), whereas a network of populations along the south coast of Ireland are likely interconnected and act as a metapopulation.

**KEY WORDS:** Hydrodynamics · Larval dispersal · Metapopulation · *Nephrops norvegicus*

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## INTRODUCTION

The Norway lobster or Dublin Bay prawn *Nephrops norvegicus* exhibits the classical characteristics of a marine invertebrate metapopulation. Geographically isolated populations of juveniles and adults are confined to patches of muddy habitat suitable to construct their characteristic burrows. These populations are connected during a short larval pelagic planktonic phase typical of many decapod crustacean species (Bell et al. 2006). The extent to which the disparate populations are open or closed can depend on the size of the natal habitat and its proximity to others, the survival of individuals over time and their ability to successfully re-colonise suitable habitats (Hill 1990). Persistence is fundamentally linked to rates of larval delivery and recruit-

ment, and thus connectivity, between the populations (Cowen & Sponaugle 2009).

Decapod crustaceans undergo a pelagic larval stage before metamorphosis and eventual recruitment into the adult population (Bell et al. 2006). The planktonic larvae are subject to certain physical controls in a fluid marine environment, particularly horizontal advection, random turbulent diffusion, wind-forcing, salinity and temperature. Equally, several biological factors influence larval survival rates including maternal condition (quality of the individual), food availability/feeding ability, growth and development, natural predation and vertical migrations (Hill 1990, Cowen & Sponaugle 2009). Therefore, oceanographic variability plays an integrated role in governing the population dynamics of many decapods by influencing larval survival and

dispersal patterns over variable spatial and temporal scales.

*N. norvegicus* (hereafter *Nephrops*) is the second most valuable commercial species landed from Irish waters, worth €80 million at first sale in 2013 (Lordan et al. 2013). *Nephrops* are widely distributed around the east, west and south coasts of Ireland and on the continental shelves of the northeast Atlantic. Overall distribution is discontinuous as the species is dependent on disparate variable-sized patches of muddy seabed sediment. 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<sup>-1</sup>. *Nephrops* construct and occupy burrows within the muddy sediment at depths from 800 m up to the 15 m contour (Bell et al. 2006). 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). Following spawning, larvae are hatched into the water column, and the pre-zoea migrate vertically to the warmer surface layer, passing through 3 temperature-dependent stages of development (Cobb & Wahle 1994, Dickey-Collas et al. 2000a). Post-larvae, which resemble adult *Nephrops* after metamorphosis, descend to resume a benthic existence and either construct new burrows or opportunistically occupy vacant ones. Settlement upon soft muddy sediment and the construction of burrows is crucial as post-larvae dispersed to unsuitable substrate are unlikely to survive (Bell et al. 2006). Growth rate into mature adults likely reflects resource availability, predation pressure and habitat characteristics (Queiros et al. 2013). Adult *Nephrops* are not thought to migrate over large distances (>200 m), and the only opportunity for transfer within populations is during the pelagic larval phase. It is thus important to consider the degree of connectivity between individual mud-patches (Phelps et al. 2015).

*Nephrops* populations are subject to prevailing environmental conditions that influence annual patterns of recruitment (Hill 1990, Lordan et al. 2013). For example, temperature is an important driver determining the larval stage durations of planktonic Crustacea with considerable variation in the developmental rate observed at various temperature regimes (Smith 1987). *Nephrops* larvae develop in warmer waters between the thermocline and the surface, and surface currents are likely to produce the biggest influence on dispersal patterns (Dickey-Collas et al. 2000a). The timing and persistence of surface currents over *Nephrops* mud-patches is thus a key factor in the re-

cruitment dynamics and population connectivity for this species (Hill et al. 1996). In waters around Ireland, fished mud-patches are assessed within 8 functional units (FUs) (ICES 2013). Catch composition analysis reveals consistent differences in population structure between fishing grounds which is correlated with population densities observed on underwater television (UWTV) surveys (Johnson et al. 2013). Time series of catch length distributions on trawl surveys in some areas show variable recruitment levels (ICES 2013) and are thus considered separate stocks (Marine Institute 2013, Queiros et al. 2013). Predicting the degree of connectivity, or isolation between sub-populations within a meta-population should inform harvesting strategies (Marta-Almeida et al. 2008).

The aim of this study is to improve our understanding of the *Nephrops* metapopulation structure and assess the degree of connectivity between disparate populations in waters around Ireland and in the wider northeast Atlantic. Previous studies have identified the importance of hydrodynamics on the population biology of this species. We employ a numerical-based model to quantitatively predict the degree of retention or connectivity between these commercially important fishing grounds and the potential extent of dispersal. A hydrodynamic model developed by the Marine Institute was used to simulate spatial and temporal changes in oceanographic conditions. This data was coupled with a larval transport model, LTRANS, to predict larval trajectories from some of the most important *Nephrops* grounds in 2011 and 2012. Improving our understanding of the environmental drivers and their inter-annual variability will ultimately lead to better informed management.

## METHODS

### Hydrodynamic model

In order to replicate the physical environment an online hydrodynamic model, the Regional Ocean Modelling System (ROMS), was used to simulate the spatial and temporal changes in oceanographic conditions in the areas of interest. ROMS is a member of a general class of 3-dimensional, free-surface, terrain-following numerical models involving certain hydrostatic and Boussinesq assumptions (Haidvogel et al. 2008). The Marine Institute developed a user-defined ROMS model for a portion of the northeast Atlantic that encompasses all of Ireland's territorial waters, parts of the Celtic Sea and the Porcupine Bank. The model includes variables for surface ele-

vation, temperature, salinity and velocity and is forced with operational atmospheric and oceanographic data at the perimeter of the domain and at the air–sea boundary. The domain extent and set up is the same as described in Dabrowski et al. (2014) but with a higher horizontal resolution, ranging from 1.1 to 1.6 km in Irish coastal waters to 3.5 km in the south of the domain, with a mean horizontal resolution of 1.9 km. 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 varies in accordance with bathymetry. The model is run operationally and validated using numerous data sources (e.g. ARGO profile data, satellite sea surface temperature [SST], *in situ* temperature and water level data). These demonstrate that the modelled temperature, salinity and water level fields agree well with observed data. Limited validation of the model current field using Acoustic Doppler Current Profiler (ADCP) data exists while Berry et al. (2012) successfully simulated surface currents by reproducing the fate of an oil spill in the Celtic Sea in February 2009. The present study uses environmental data for both 2011 and 2012 to produce hydrodynamic conditions in the domain for both years.

### Larval transport model

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 neutrally bouyant larvae throughout the model domain and track them in 3 dimensions as they are forced by stored environmental data (2011 and 2012). 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. This approach allows maximum dispersal to be investigated following Robins et al. (2013). 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 & North (2012).

### Data extraction

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 were used to overcome this bias and negate the effect of tidal cycles, providing a reasonable estimation of monthly net water speed ( $\text{m s}^{-1}$ ) and direction of movement about the study domain. Data were interpolated using geo-statistical methods (Inverse Distance Weighting, IDW) within ArcMap 10. Temperature data was similarly extracted to describe changing regimes and to parameterise LTRANS run times.

### Release locations and dates

The spatial extent of *Nephrops* populations in the waters around Ireland have been mapped in high resolution using a combination of fishery-dependent data, i.e. integrated Vessel Monitoring Systems (VMS) and logbook data (Gerritsen & Lordan 2011) and fishery-independent data. These include multi-beam backscatter available from the Irish National Seabed Survey and INFOMAR project ([www.infomar.ie](http://www.infomar.ie)), sediment samples, *Nephrops* density estimates (burrows  $\text{m}^{-2}$ ) from UWTV surveys and trawl catch data from Irish Groundfish surveys. These maps were used to determine release locations of larvae within the model domain. For stock monitoring and assessment purposes, *Nephrops* populations have been divided into notional stocks or FUs shown in Fig. 1 in relation to the extent of the ROMS domain. Some FUs contain multiple discrete mud-patches in close proximity whereas other larger contiguous mud-patches encompass an entire FU, e.g. Porcupine Bank (FU16). In the case of FUs with multiple discrete grounds, a subset of representative grounds were selected for study. For example, 4 separate grounds (Bantry Bay, Helvick Head, Cork Channels and the Galley grounds) were studied within FU19 along the south coast. In larger mud-patches, multiple-release sites were selected (generally north, south and central depending on orientation) to better capture local hydrodynamic variation. These were the Porcupine Bank (FU16), Irish Sea west (FU15) and the Smalls (FU22). A single central location was chosen in the Irish Sea east (FU14) and

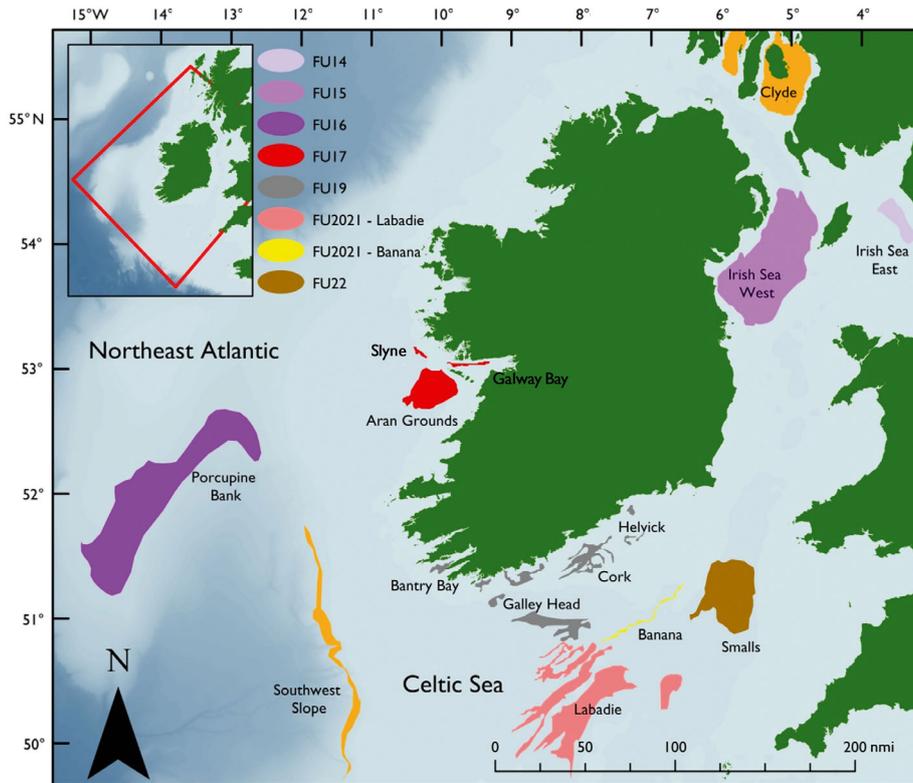


Fig. 1. Spatial extent of primary *Nephrops norvegicus* fishing grounds (coloured) in waters around Ireland. Individual grounds are indicated with their relevant functional units (FUs). Orange areas: the Southwest Slope is not an FU, but potential dispersal was modelled from it. The Clyde, a Scottish fishing ground, is also shown but was not considered in the study. nmi: nautical miles. Inset: boundary (red) of the Regional Ocean Modelling Systems (ROMS) domain

the Labadie and Banana grounds (both within FU2021) 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 FU. In total, larval dispersal was examined from 21 release sites within *Nephrops* fishing grounds around Ireland. The Clyde, a fishing ground on the west coast of Scotland was not studied as it straddled the domain boundary and thus offered less confidence in predictive ability. Within the model specifications, larvae can be released at any time of year. In this analysis hatching events occurred on the first day of the month in April and May for mud-patches in the northeast Atlantic (FU16 and FU17) and May and June for the Celtic Sea (FU19, FU2021 and FU22) and Irish Sea (FU14 and FU15) following Hill (1990) and Bell et al. (2006).

### Larval duration

Previous experimental studies on the relationship between temperature and developmental rates of reared *Nephrops* larvae were used to determine larval duration (Table 1). Dickey-Collas et al. (2000a) proposed an exponential regression equation

that described Stage I and Stage II larvae. Difficulties successfully rearing larvae through to Stage III resulted in those authors adopting an alternative Stage III regression equation based on Smith (1987). The current study employs regression equations used in both former studies. The results for all 3 stages were summed to give total larval duration. As *Nephrops* larvae generally remain in surface waters (Dickey-Collas et al. 2000b), only SSTs were used to parameterise the model. Larvae had no swimming ability for the duration of Stage I and were passively dispersed during this time (Marta-Almeida et al. 2008). Larvae swimming speed was specified to increase as a function of time when the larvae reached Stage II until the larvae metamorphosed to post-larvae, from 0.0001 to 0.0015 m s<sup>-1</sup> (Smith 1987, Dickey-Collas et al. 2000a). Larval swimming behaviour was modelled as a random walk function.

Table 1. Regression parameters for ln(stage duration) vs. temperature for *Nephrops norvegicus* larvae in this study. n.a.: not applicable

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

Table 2. Mean monthly sea surface temperature (SST) (April–July) as predicted by ROMS for 2011 and 2012 and the resultant pelagic larval phase duration used to parameterise the larval transport model (LTRANS) in the present study

	— Irish Sea —		— Celtic Sea —		— Aran Grounds —		— Porcupine Bank —	
	Mean SST (C°)	Duration (d)	Mean SST (C°)	Duration (d)	Mean SST (C°)	Duration (d)	Mean SST (C°)	Duration (d)
<b>2011</b>								
April	–	–	10.1	52.9	10.4	50.7	11.4	44.0
May	12.7	36.6	11	46.5	10.9	47.2	11.8	41.6
June	14.3	29.2	13.1	34.6	13	35.1	13	35.1
July	15.6	24.4	–	–	–	–	–	–
<b>2012</b>								
April	–	–	10.3	48.8	10.3	50.1	11.6	42.0
May	12.8	33.2	11.5	39.6	10.9	43.7	12	38.4
June	14.6	26.3	13.6	32.2	12.7	36.6	13.1	34.6
July	15.9	23.4	–	–	–	–	–	–

### Simulation

500 larvae per simulation were apportioned to each population and were tracked in 3D for the relevant larval duration. This number was determined by the computational power of a desktop computer and not the relevant size of each population. The integrated particle-tracking/hydrodynamic model used in this study was not written to take advantage of parallel computing power. On completion of the simulation, the end position was recorded. We hereby refer to 'viable' larvae as those which metamorphosed into post-larvae over areas of suitable sediment following pelagic dispersal and the remainder as being lost from the system entirely. Actual larval settlement upon the seabed was not simulated. Larvae were only considered to be viable if their end position was within the defined mud-patch boundary of their natal ground or any other. The analysis grouped all simulations undertaken per ground to determine the average number of hatchlings that were retained, donated or lost from the system. The distance of each larval trajectory was measured in a GIS to establish potential dispersal from each mud-patch studied.

## RESULTS

### Larval duration

Average monthly temperature predicted by ROMS in 2011 and 2012 for different sea areas and the resultant pelagic larval phase durations are shown in Table 2. In 2011 *Nephrops* hatched on Porcupine Bank on April 1 potentially remained in the water column for 44 d, decreasing to 35.1 d if hatched on June 1. The difference in temperature regimes expe-

rienced 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 d from April to June. Larval durations in the Celtic Sea between April, May and June lasted 52, 46 and 34 d. Warmer SSTs in the Irish Sea indicated a uniform increase between May and June. The temperature rose from ~1 to 12°C in April and May to between 16 and 19°C in the third quarter of the year. This reduced larval duration from 36.6 d in June to 26.3 d in July. In 2012, SST around Ireland increased slightly in all studied FUs except in the Aran Grounds. As a result, larval durations were slightly shorter in 2012 but only differed by a maximum of 6.9 d, as observed in the Celtic Sea in May.

### Dispersal distance

In Fig. 2, dispersal patterns for larvae hatched in April and May (2011 and 2012) from Porcupine Bank are compared. Larvae hatched from all 3 release locations over Porcupine Bank in April 2011 have the potential to be advected >600 km. This represents the greatest dispersal distance measured in this study. Potential dispersal distance in April 2012 decreased. For example, maximum potential dispersal from the centre of the mud-patch in 2011 was 658.2 km, dropping to 390.5 km in 2012. Mean potential dispersal from Porcupine Bank was 357.4 km in 2011 and 227.6 km in 2012.

Annual patterns of larval dispersal within the Irish Sea are shown in Fig. 3. In the western Irish Sea, larvae were advected greater distances in 2012

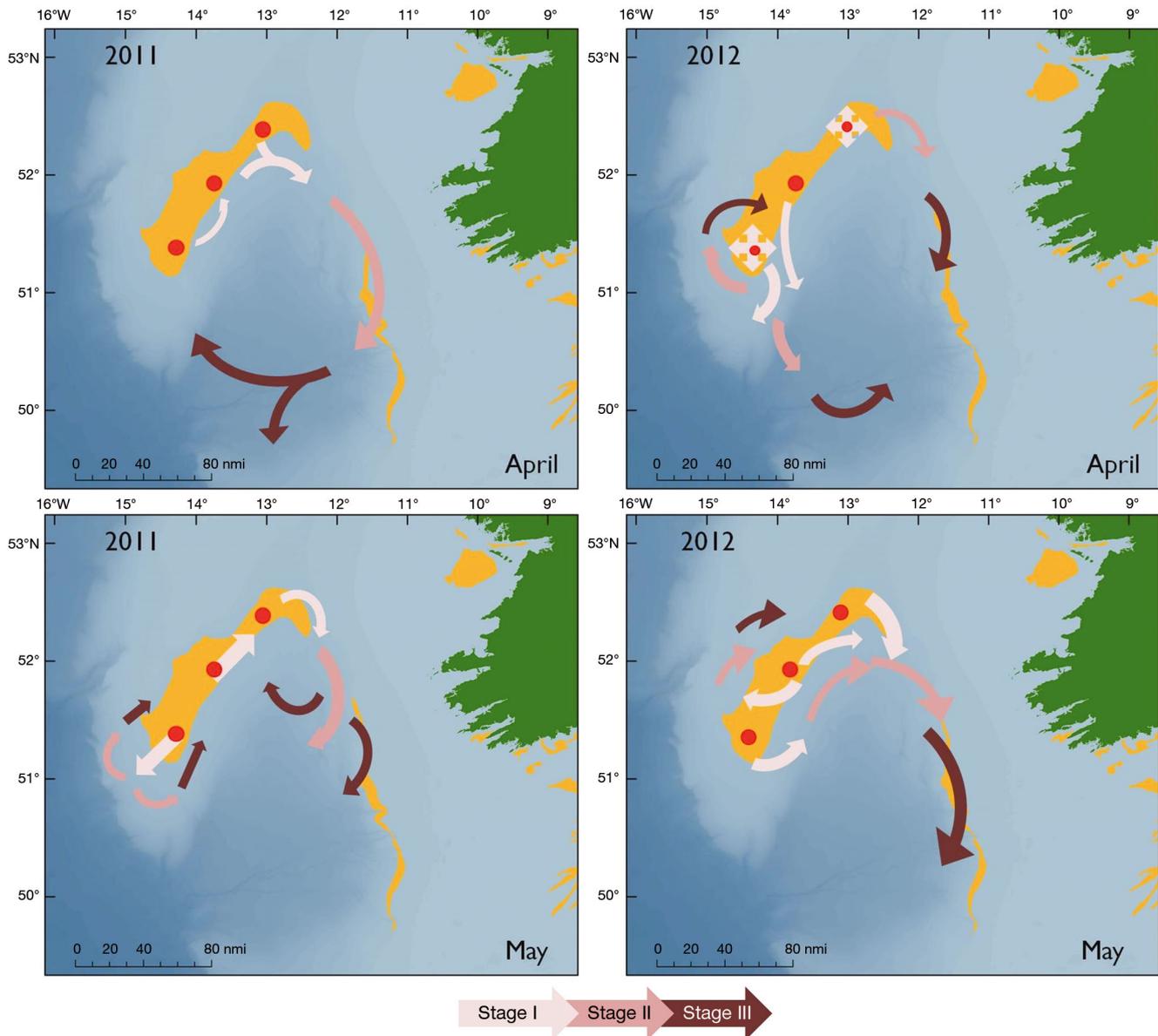


Fig. 2. Predicted dispersal patterns of *Nephrops norvegicus* larvae hatched on Porcupine Bank (FU16; see Fig. 1) in April and May in 2011 and 2012. The patterns are a qualitative visual interpretation of the patterns observed in the simulations. Colour-coded arrows indicate general patterns of movement for 3 larval stages. Arrow size does not indicate relative concentrations of larvae. Red dots are release locations

(mean larval trajectory was 153.8 km in 2011 and 187.6 km in 2012). June hatchlings were transported the greatest distance in both 2011 (183 km) and 2012 (192.7 km). Mean advection rates in the eastern Irish Sea (FU14) were 51.4 km in 2011 and 64.9 km in 2012.

Fig. 4 highlights the difference in monthly dispersal patterns from mud-patches in the Celtic Sea area (FU19, FU2021 and FU22) and Ireland's west coast (FU17). Advection measured from Aran Grounds was higher in 2011, with larvae having the potential to be transported 224.3 km compared with 118.5 km in

2012. Similar dispersal distances were measured in both years on Smalls ground (131.1 km in 2011 and 137.1 km in 2012) and from the Cork Channels mud-patch (219.4 km in 2011 and 218.9 km 2012).

### Loss

Overall, the percentage of viable larvae produced was low, <10% at 6 fishing grounds in both 2011 and 2012, indicating significant larval loss from those systems (Fig. 5). In 2011 for example, 98.9% of larvae

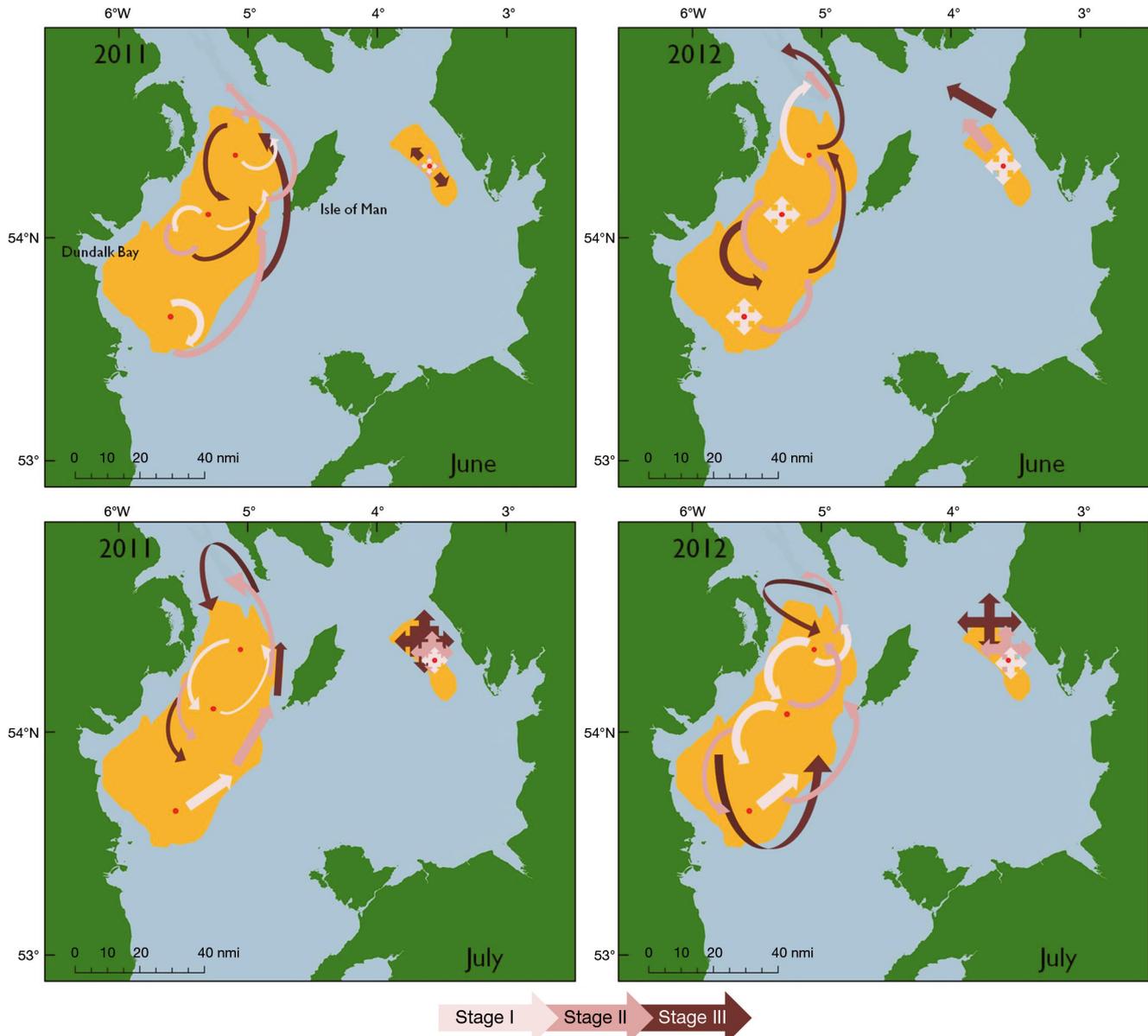


Fig. 3. Predicted dispersal patterns of *Nephrops norvegicu* larvae hatched from 2 mud-patches in the Irish Sea (eastern FU14 and western FU15, see Fig. 1) in June and July in 2011 and 2012. The patterns are a qualitative visual interpretation of the patterns observed in the simulations. Colour-coded arrows indicate general patterns of movement for 3 larval stages. Arrow size does not indicate relative concentrations of larvae. Red dots are release locations

produced on the Southwest Slope were lost. Four fishing grounds (Porcupine Bank, Banana, Aran Grounds and Smalls) produced between 10 and 20% viable larvae in 2011, 5 did so in 2012. In total, 89.2% of larvae hatched from Aran Grounds in 2011 were lost from the system, but there is evidence that some larvae hatched in FU17 were dispersed northward along the west coast of Ireland. More larvae were lost from Bantry Bay than any other fishing ground, 99% in 2011 and 98.4% in 2012. The highest percentage of viable larvae were produced in the western Irish Sea both in 2011 (33.7%) and 2012 (36.4%).

### Retention vs. donation

Retention was highest in the western Irish Sea in 2011 where 33.7% of all hatched larvae remained above that fishing ground following metamorphosis (Fig. 5). This ground did not donate any larvae to nearby grounds in 2011, but there is evidence that 5.7% of larvae hatched here in 2012 were transported over the Clyde fishing ground in Scottish waters. Of larvae hatched in the western Irish Sea in 2012, 30.7% were retained. Only 2 other grounds, Labadie (33.4%) and the eastern Irish Sea (32%)

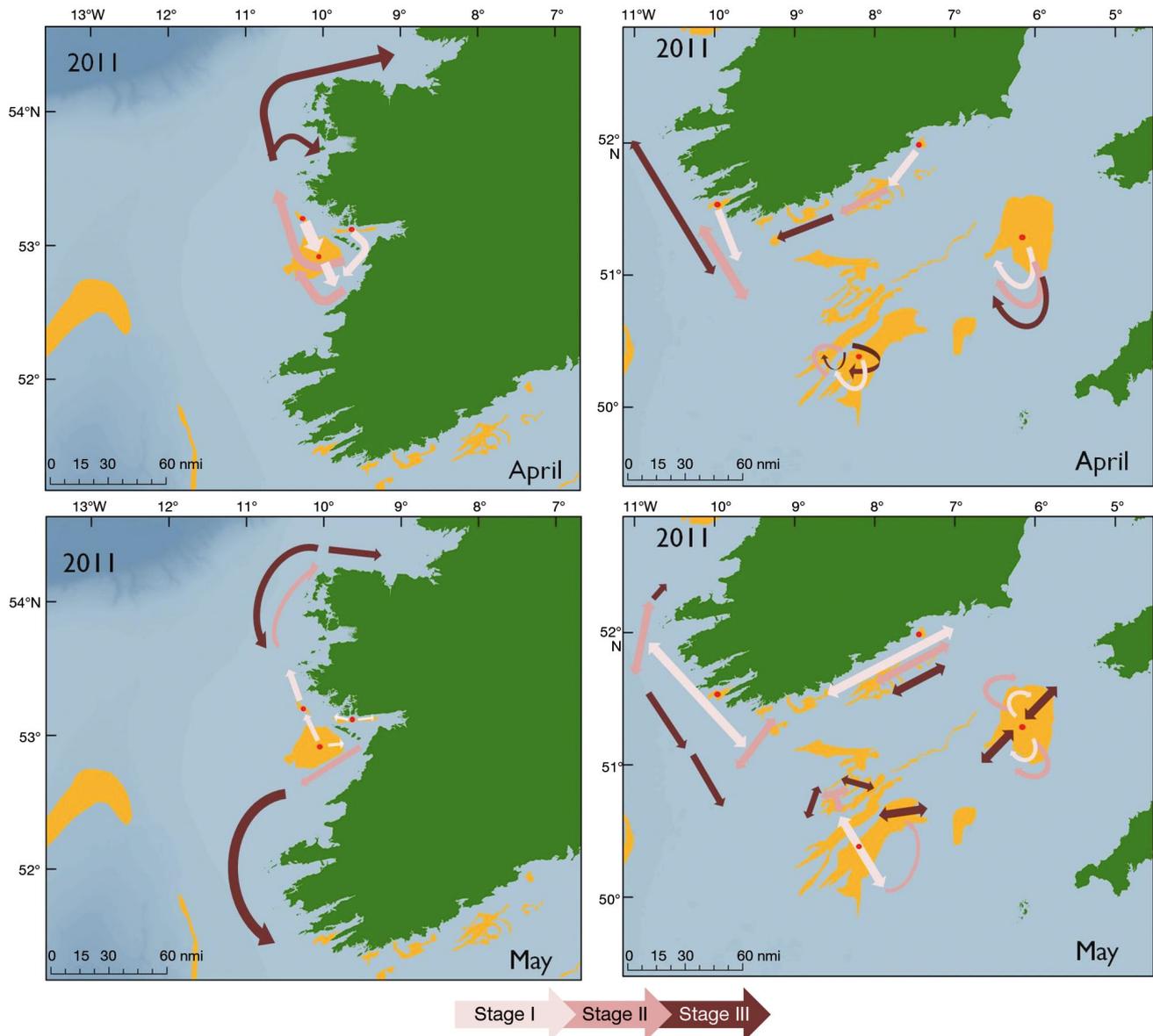


Fig. 4. Predicted dispersal patterns of *Nephrops norvegicu* larvae hatched on the west (left) and south (right) coast of Ireland in April and May 2011. The patterns are a qualitative visual interpretation of the patterns observed in the simulations. Colour-coded arrows indicate general patterns of movement for 3 larval stages. Arrow size does not indicate relative concentrations of larvae. Red dots are release locations

retained >30% of viable larvae in 2011. Labadie retained >30% of viable larvae in 2012 whereas retention fell to 10.1% in the eastern Irish Sea. Retention on Porcupine Bank rose to 30.2% in 2012 from 12% in 2011.

There was more connectivity between the mud-patches in 2011 than 2012 as described in Fig. 5. The eastern Irish Sea did not contribute larvae to any other grounds in 2011 or 2012. In 2011 the Celtic Sea grounds of Bantry Bay, Galley Grounds, Banana Grounds, the Cork Channels and Helvick Grounds all contributed more larvae to adjacent mud-patches than were retained. There were 4 such grounds in

2012 (Slyne Grounds, Galway Bay, Cork Channels and Helvick Grounds). The Banana ground contributes larvae to 3 other adjacent grounds; Cork Channel and Helvick grounds both contribute larvae to 4 others while the Galley Head ground contributes larvae to 6 other mud-patches covering the Celtic Sea and the northeast Atlantic as far as the Southwest Slope. In 2012, Galley Ground only contributed larvae to Bantry Bay (0.1%) and Labadie (0.4%). Only 1 ground, Banana, contributes larvae to 3 or more nearby grounds in 2012. These are the Galley (4.8%), Labadie (2.4%) and Smalls grounds (0.1%) in the Celtic Sea. The average loss from the combined sys-

2011 Release	% Loss	Porcupine	Southwest Slope	Slyne	Aran	Galway Bay	Bantry Bay	Galley	Labadie	Banana	Cork Channels	Helvick	Smalls	Irish Sea west	Irish Sea east	Clyde
Porcupine	87.7	12	0.3													
Southwest Slope	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 Channels	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			
Irish Sea west	66.3													33.7		
Irish Sea east	68														32	
2012 Release	% Loss	Porcupine	Southwest Slope	Slyne	Aran	Galway Bay	Bantry Bay	Galley	Labadie	Banana	Cork Channels	Helvick	Smalls	Irish Sea west	Irish Sea east	Clyde
Porcupine	69.7	30.2	0.1													
Southwest Slope	97.1	0.1	2.8													
Slyne	94.5			0.6	4.9											
Aran	84.4			0.8	14.4	0.4										
Galway Bay	89.9			0.6	7	2.5										
Bantry Bay	98.4						1.6									
Galley	87.6						0.1	11.9	0.4							
Labadie	68.9							0.1	31							
Banana	91.6							4.8	2.4	1.1			0.1			
Cork Channels	97.1						1.8	1.1			0					
Helvick	92.3						2.6	5.1				0				
Smalls	80.5									0.1			19.4			
Irish Sea west	63.6													30.7		5.7
Irish Sea east	89.9														10.1	

**Fig. 5.** Connectivity matrices to describe the distribution of *Nephrops norvegicularvae* over Irish fishing grounds following pelagic dispersal in 2011 and 2012. Rows represent release sites and the columns are recipient sites. The matrices describe retention (dark grey), donation (light grey) and loss of viable larvae. Note that larvae were not released from Clyde in Scottish waters in this study, but we provide evidence of larval transfer to this mud-patch in 2012 from the western Irish Sea

tems is 84.4% in 2011 and 86.1% in 2012. Aran Grounds donated 0.4% of its larvae to both the Slyne and Galway Bay grounds in 2011, and these adjacent grounds contributed to the larger Aran Ground (0.9 and 1.5% respectively). In 2012, both the Slyne and Galway Bay grounds donated more larvae to Aran Grounds than they retained themselves. To better understand larval dispersal over time, a 4D visualization tool (Eonfusion v2.3) was used. The software allows clear visualization and a better understanding of potential dispersal from each mud-patch. A short movie clip visualizing this aspect of the work is available at: <https://vimeo.com/107145708>.

## DISCUSSION

The use of a hydrodynamic and larval-tracking model in the present study allowed for a detailed investigation into the environmental conditions pelagic *Nephrops* larvae were likely to encounter during 2011 and 2012. The analysis finds that variable environmental conditions and circulation patterns influence the annual dispersal distance of pelagic larvae with subsequent effects on the degree of larval transfer between separate populations. We find evidence of isolated *Nephrops* populations in the Irish Sea and Porcupine Bank, moderately connected areas in the south Celtic Sea, and an interconnected meta-population along Irelands' south coast.

Environmental conditions exert a strong influence on the population dynamics of *Nephrops* during both the adult and larval phases. For example, much of the mud sediment in which adults construct burrows originated during the last de-glaciation and prevailing hydrodynamic conditions retain the mud *in situ* (Bailey et al. 1995). Following hatching from these mud-patches, *Nephrops* larvae ascend rapidly to the surface waters, where they generally remain for the remainder of the pelagic phase (Emsley et al. 2005). Warmer surface waters encourage a faster larval developmental rate and limit the amount of time spent in the potentially dangerous planktonic phase (Dickey-Collas et al. 2000b). For example, data extracted from the ROMS model indicate that an increase of 1°C can reduce the duration of the larval phase by over 9 d. Cowen & Sponaugle (2009) suggest faster-growing larvae generally experience a higher degree of survival and are more likely to be transported to a suitable settlement habitat. The present study finds that increasing temperature through May and June in the Irish Sea encouraged rapid larval development, resulting in increased

viable larvae with the potential to re-settle as the season progressed.

Gyres are considered the classical retention mechanism for *Nephrops* larvae (Hill et al. 1996) and 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 deposition of finer sediment (Bailey et al. 1995). The presence of a gyre in the western Irish Sea, as identified by Hill et al. (1996) was apparent in May and June, with larvae being advected in an obvious anti-clockwise circular direction. There is also some evidence of cyclical gyres in the larger Labadie and Smalls grounds as hypothesised by Bailey et al. (1995) and Brown et al. (1995).

Gyre speed and strength is primarily influenced by water temperature and seasonal stratification patterns (White et al. 1998). In the present study, May was identified as the onset of the Irish Sea gyres in both 2011 and 2012, but a higher mean temperature in 2012 contributed to a more powerful gyre with longer dispersal trajectories. However, overall larvae loss from the western Irish Sea was the lowest of all grounds studied, indicating that the strength of the gyre is not as important in influencing *Nephrops* hatching events as the time it appears, an idea supported by Hill (1990). We suggest a closed population that exhibits coupling between local production and recruitment in agreement with Irish Sea retention rates identified in this study. Cowen et al. (2000) describe a similar mechanism which is more apparent in larger mud-patches, resulting in increased genetic homogeneity. Comparable Irish Sea larval retention rates were also described by Phelps et al. (2015) in a recent study in which the authors also identified the potential for the gyre to 'leak' particles northward. The present study demonstrated the same (in 2012 data). Taking both studies together suggests that while there is occasional larval transport towards the Clyde, the large mud-patch in the western Irish Sea is entirely self-recruiting.

In contrast, the circulation systems to the west and south of Ireland are complex and poorly understood (White et al. 1998). ROMS indicates that strong currents follow local bathymetry along the shelf slope, resulting in low retention rates on the Porcupine Bank and the Southwest Slope in 2011 and limited larval exchange with adjacent fishing grounds. However, there was evidence of a cyclical gyre to the south of the fishing ground, and the suggestion of a Taylor Column in May/June. Broad circular gyres were again observed in 2012 that enabled larvae

entrainment over the mud-patch resulting in higher retention. Although a longer time series is needed, the formation of these columns and their relative strength appears less predictable in deeper waters (White et al. 1998). This is unsurprising, considering the water depth, the influence of Atlantic currents and the physical isolation from other fishing grounds. Recruitment is known to be variable here, and the stock has been severely depleted since 2008 (ICES 2013). White et al. (1998) provides evidence of increased phytoplankton abundance and primary production directly over Porcupine Bank as opposed to either side of it. This could suggest that *Nephrops* hatching events in the Atlantic benefit from optimal primary production rather than relying on irregular local hydrodynamics.

Hill (1990) used an advection-diffusion-mortality model to study *Nephrops* dispersal and found that low levels of mean advection ( $0.04$  to  $0.05$   $\text{m s}^{-1}$ ) were enough to reduce retention over most mud-patches. We observed predicted velocities between  $0.15$  and  $0.23$   $\text{m s}^{-1}$  over Porcupine Bank and Southwest Slope during peak hatching periods with resultant dispersal trajectories  $>500$  km and poor retention. Similar water speed in the Celtic Sea also resulted in low retention but a high degree of larval transfer between the grounds. This process is facilitated in part by the nearshore anti-clockwise Irish coastal current. Its effect on nearshore south coast mud-patches (FU19) is clearly evident as larvae are quickly advected northward around the coast. Hydrodynamic conditions over the Labadie and Smalls fishing grounds in the Celtic Sea appear to be more stable. Dispersal patterns are comparable in both years, the dispersal distances are the shortest (after the eastern Irish Sea) and retention rates are high. This may be related to the size of the natal ground as Hill (1990) suggests bigger areas of habitat lead to higher rates of retention, and in the present study, larger homogeneous mud-patches such as the western Irish Sea, Aran Grounds, Smalls and Labadie retain more larvae than they donate, with the obvious exception being Porcupine Bank.

Some biological simplifications and assumptions were necessary to parameterise ROMS/LTRANS during this study. For example, mortality was not modelled even though the combined effects of starvation, predation and disease may result in  $>90\%$  of larvae dying before metamorphosis (Marta-Almeida et al. 2008). However, mortality reduces the number of particles available for analysis within LTRANS, and instead larvae remain alive throughout the simulations. A similar approach is described in Robins et al.

(2013). Diel vertical migration (DVM) is a predator-avoidance mechanism whereby larvae shelter in the deep by day and rise to the surface at night to feed (Emsley et al. 2005). However, those authors did not parameterise *Nephrops* larvae with DVM in a biophysical model of the Irish Sea, and Dickey-Collas et al. (2000b) concluded that *Nephrops* larvae generally remained in surface waters throughout their 3 planktonic stages. Thus, our study assumes larvae are neutrally buoyant and are without DVM behaviour, only moving vertically through diffusion or hydrodynamic flow.

Larval release dates are more likely to occur over a more limited 5 or 6 wk period and follow a Gaussian-shaped distribution (Briggs et al. 2002). The regression equations used to formulate larval duration times are based on limited data (especially for Stage III larvae) and require further research into the metabolic response of *Nephrops* to temperature. Finally, the present study simulates the release of a fixed number of larvae (500 ind.) from each area. Apportioning release numbers to reflect individual population size may deliver a clearer understanding of dispersal trajectories and larval interconnectivity.

Although some simplifications exist, the study is a good first attempt to describe dispersal patterns of larvae from *Nephrops* fishing grounds in waters around Ireland and the degree of connectivity between the grounds. There is clockwise circulation around Porcupine Bank in April and May at a broad spatial scale but little evidence of retention gyres on 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. Hatching on the Porcupine Bank coincides with peak primary production, which is more likely to maximise larval survival than irregular circulation patterns. In the Irish Sea, peak hatching events coincide with the onset of regular seasonal gyres that increase retention. The Smalls and Labadie populations in the Celtic Sea are well-mixed. We find that a network of smaller grounds, in close proximity to each other, along the south coast of Ireland potentially share and donate larvae and thus act as a more resilient metapopulation.

Beyond fisheries interest and ecosystem functioning, knowledge of metapopulation connectivity is essential for applied environmental problems including marine reserve designation, coastal and offshore management and climate change (O'Sullivan & Emmerson 2011, Olbert et al. 2012). The use of a coupled hydrodynamic model in this capacity has the potential to predict future population trends, assist in eco-

system-wide management decisions and contribute to a more sustainable fishery. The findings also reinforce the need to lightly exploit *Nephrops* populations in the waters around Ireland to buffer against prolonged periods of weak recruitment due to unfavourable hydrodynamic conditions.

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