Larval transport dynamics in *Nephrops norvegicus*

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Table of Contents

Declaration III
Acknowledgements IV
Abstract V

Chapter 1 - General Introduction 1
1.1. Introduction 2
1.2. Habitat and Distribution 2
1.3. Reproduction 4
1.4. Pelagic Larval Phase 5
1.5. Phenology 7
1.6. Fishery 9
1.7. Management 10
1.8. Assessment Methods 11
1.9. Underwater Television (UWTV) 12
1.10. Irish Population Trends 13
1.11. Biophysical Larval Transport Model 15
1.12. Research Objectives 17
1.13. References 19
1.14. Figures 28

Chapter 2 - Twilight Migrators: Factors Determining Larval Vertical Distribution in *Nephrops norvegicus* with Implications for Larval Retention 31
2.1. Abstract 32
2.2. Introduction 33
2.3. Materials and Methods 36
2.4. Results 41
2.5. Discussion 44
2.6. References 52
2.7. Tables 59
2.8. Figures 62

Chapter 3 - Shift in the Larval Phenology of a Marine Ectotherm Due to Ocean Warming with Consequences for Larval Transport 69
3.1. Abstract 70
3.2. Introduction 71
3.3. Materials and Methods 74
3.4. Results 79
3.5. Discussion 83
3.6. References 90

3.7. Tables 95
3.8. Figures 97
3.9. Appendix 104

Chapter 4 - Larval Transport and Connectivity of the Norway Lobster (*Nephrops norvegicus*) Around Ireland 108
4.1. Abstract 109
4.2. Introduction 110
4.3. Materials and Methods 113
4.4. Results 118
4.5. Discussion 121
4.6. References 129
4.7. Tables 135
4.8. Figures 137
4.9. Appendix 145

Chapter 5 - General Discussion 153
5.1. Discussion 154
5.2. Future Work 160
5.3. References 167

Declaration

I, Ryan McGeady, certify that this thesis is my own work and I have not obtained a degree in the National University of Ireland, Galway, or elsewhere, on the basis of the work described in this thesis.

Signed: 

Ryan McGeady

Date: 13/11/2020

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Abstract

Transport of meroplankton larvae in the ocean is a crucial process as it enables connectivity between populations and determines larval supply for species with narrow habitat requirements and sedentary adult stages. The Norway lobster (*Nephrops norvegicus*), Europe's most important commercial crustacean, has a patchy distribution across the Northeast Atlantic Ocean and Mediterranean Sea. Adults inhabit areas of muddy substrate where they excavate and spend most of their time within burrows. The pelagic larval phase enables connectivity between populations separated by uninhabitable substrate. Larvae rely on settlement on suitable mud habitat for survival. Therefore, larval settlement, driven by local hydrography, may act as a constraint on recruitment. Biophysical models offer a method of simulating larval transport, which is extremely difficult to observe *in-situ* due to the inherent difficulties in tracking miniscule larvae in vast areas of the ocean. In the current study, a biophysical larval transport model was used to estimate larval retention, dispersal distance and connectivity for *N. norvegicus* grounds around Ireland. Models parameters were supported by empirical data in order to accurately represent the biological and behavioural processes of larvae.

In Chapter 2, the vertical distribution and occurrence of a Diel Vertical Migration (DVM) in *N. norvegicus* larvae was examined. Larval vertical distribution was influenced by the vertical temperature differential in the water column, zooplankton biomass and the potential energy anomaly. A twilight DVM was identified and involved two ascents and two descents per day. In Chapter 3, historical zooplankton datasets were used to identify an earlier larval phenology shift in *N. norvegicus* by 19.1 days from 1982 - 1995 to 2000 - 2010. Ocean warming was identified as the most likely cause as increasing temperatures led to a contraction of the embryo incubation period and earlier hatching of larvae. The phenology shift appeared to have a limited effect on larval duration and transport. Only large variations in modelled larval retention and dispersal distance were observed between larvae released very early and very late in the season. In Chapter 4, a 20-year time series of modelled larval retention, dispersal distance and connectivity estimates for 6 *N. norvegicus* Functional Units (FUs) demonstrated their capacity to retain, import and export larvae. Smaller FUs had a decreasing trend in retention over the time series which appeared to be as a result of

strengthening currents. On the Aran grounds, a link between modelled larval retention and dispersal distance and empirically observed burrow densities from underwater television with a 3-year lag was observed.

The findings indicate that larval transport may act as a constraint on recruitment for *N. norvegicus* populations like the Aran grounds with low and variable larval retention and limited larval imports due to spatial isolation from other grounds. It demonstrates the potential of using larval transport estimates to identify instances of poor recruitment, due to low larval settlement, early in the life cycle before its effects manifest in the adult population. It can also be applied to similar species with defined habitat and planktonic life stages and may assist in limiting overexploitation for commercial species, particularly in the face of climate change and the likely impacts on oceanography.

Keywords: *Nephrops*, larvae, transport, simulation, connectivity, global warming

Chapter 1

General Introduction

1.1. Introduction

The Norway lobster (*Nephrops norvegicus*; Linnaeus 1758), also known as the Dublin Bay prawn, langoustine, scampi and cigala, is a marine decapod crustacean and the only extant species of the genus *Nephrops* (Phylum: Arthropoda, Subphylum: Crustacea, Class: Malacostraca, Order: Decapoda, Class Suborder: Pleocyemata, Infraorder: Astacidea, Family: Nephropidae). *Nephrops* means "kidney eye" and describes the shape of its dark coloured eyes. The benthic dwelling species is distributed across muddy habitat in the Northeast Atlantic Ocean and Mediterranean Sea. Its distribution is closely coupled with the presence of mud habitat in which it excavates and shelters within a burrow. It is commercially harvested across its distribution and is considered one of the most economically valuable fisheries in Europe (Ungfors et al. 2013). Unlike the relatively sedentary benthic adult that spends most of its time in the burrow, the pelagic larvae enable connectivity between populations separated by uninhabitable substrate (Figure 1). Due to the crucial requirement for larval settlement on suitable mud habitat, oceanography may play an important role in determining larval supply and therefore, recruitment.

1.2. Habitat and Distribution

N. norvegicus are distributed across the continental shelf and upper slopes of the Northeast Atlantic Ocean and Mediterranean Sea. It has been recorded at depths between 4 - 754 m (Johnson et al. 2013). Individuals construct burrows approximately 30 cm deep with two or more crescent-shaped openings on soft muddy substrate (Rice and Chapman 1971). Unlike other habitat types such as rock, natural cover for refuge is scarce in muddy areas. Instead, burrows offer an adequate means of protection from predators. Tagging studies have demonstrated that adults are relatively sedentary and do not undertake extensive migrations (Chapman 1982; Merder et al. 2020). Burrow emergence is nocturnal with crepuscular peaks in continental shelf areas and diurnal in deeper slope populations (Aguzzi et al. 2003). A strong requirement for mud habitat and relative lack of adult movement mean that population boundaries are easily defined. At least 30 populations separated by uninhabitable substrate are known to exist (Bell et al. 2006). Despite the inability of adults to migrate between grounds, Atlantic populations exhibit relatively low levels of genetic differentiation reflecting gene flow potential

during the pelagic larval phase (Maltagliati et al. 1998; Stamatis et al. 2004). However, genetic differences have been recorded between Atlantic and Mediterranean populations (Gallagher et al. 2019).

Adult burrow densities have a dome-shaped relationship with sediment particle size, highest densities are associated with medium-grained mud in which stable burrow systems can be constructed (Alfonso-Dias 1998; Campbell et al. 2009). In coarser sandy substrates, burrows are unstable and collapse easily. Whereas, in very fine muds, extensive burrow systems cover larger areas, resulting in higher competition for space. Burrow densities have an inverse relationship with *N. norvegicus* size (Johnson et al. 2013). For example, underwater television (UWTV) surveys from 2018 indicate that on the Western Irish Sea (WIS) ground (Figure 2), burrow densities were high (0.73 burrows m^{-2}) but mean weight (16.1 g) from landings was low (ICES 2019; Lundy et al. 2019). In contrast, on the Porcupine Bank ground, to the west of Ireland (Figure 2), burrow densities were low (0.15 burrows m^{-2}), but weight was high at 41.6 g (Aristegui et al. 2019b).

High recruitment and subsequent competition for resources may suppress growth of *N. norvegicus* at high densities. The semi-enclosed WIS ground is known to exhibit high larval retention (O'Sullivan et al. 2015; Phelps et al. 2015), perhaps aided by a seasonal circular gyre thought to enhance larval retention (Hill et al. 1996). Consequently, high densities lead to increased competition for limited food resources and space. *Nephrops norvegicus* are also known to exhibit agonistic behaviour with bouts of fighting often resulting in burrow eviction (Chapman and Rice 1971). The formation of dominance hierarchies result in lower ranked animals being evicted from their burrows more often and covering larger distances when outside the burrow (Katoh et al. 2008; Sbragaglia et al. 2017). Furthermore, density-dependent growth suppression has been observed in males, with slow-growing individuals being most impacted (Merder et al. 2020). In contrast, low densities mean less encounters and thus fewer occurrences of aggressive behaviour as territoriality is diminished (Rice and Chapman 1971).

1.3. Reproduction

Mature female *N. norvegicus* moult after egg hatching and their soft postmoult condition elicits a response from males that initiates copulation (Farmer 1974). Mature females only moult between hatching and spawning, therefore, copulation can only occur during this time period. Fertilisation is thought to take place internally as eggs pass over the thelycum before being extruded onto the underside of the abdomen (Powell and Eriksson 2013). Spawning occurs at night with the female laying on her back as eggs are emitted from the genital apertures to the abdomen as the egg mass is then held in place by the pleopods.

Several methods of estimating fecundity have been attempted, including using potential, actual and realised fecundity. Potential fecundity is determined by counting oocytes in the ovary and is exponentially related to female body size and ranges from 600 - 1200 oocytes in females of 25 mm Carapace Length (CL) to 3200 - 4800 oocytes in 45 mm CL females (Bell et al. 2006). Effective fecundity, derived from counting eggs close to hatching, is significantly lower due to egg loss. Potential reasons for egg loss are stress from fishing, extrusion failure, lack of fertilisation, detachment, infection, parasites, predation and cannibalism (De Figueiredo and Thomas 1967; Powell and Eriksson 2013). Egg loss can range from 18 - 75% over the duration of the incubation period (Powell and Eriksson 2013). However, most estimates are derived from trawl caught females and method of capture appears to be important as creel caught females lose fewer eggs (Tuck et al. 2000; Briggs et al. 2002). Geographical differences have also been recorded in both egg loss and fecundity (Tuck et al. 2000; McQuaid et al. 2009).

Embryos are sustained by the yolk during the incubation period. Females remain in the burrow and display brooding behaviour by elevating pleopod activity when carrying late-stage eggs; the behaviour is also displayed for early-stage eggs in hypoxic conditions (Eriksson et al. 2006). A 9-stage egg development classification was outlined by Dunthorn (1967) and details the early dark green stages, up to the late pink/orange stages, with the ready-to-hatch larva visible. Eggs grow in size during incubation and in the Firth of Clyde, eggs increased in diameter from 1.20 mm to 1.55 mm (Smith 1987). In the North Tyrrhenian Sea (western Mediterranean), Mori et al. (2001) noted differences in egg volume between shallow (1.55 mm^3; 200 - 300 m) and deeper (1.41 mm^3; 500 - 550 m) areas, possibly due to contrasting feeding conditions. Female size

appears to have no influence on egg volume, indicating that females invest energy into producing more eggs rather than larger eggs, potentially to compensate for losses (Mori et al. 2001; McQuaid et al. 2009).

Embryo incubation is strongly influenced by ambient temperature with warmer temperatures reducing the incubation period (Dunthorn 1967; Farmer 1974). Farmer (1974) demonstrated a 50% reduction in incubation duration due to a 10 °C increase in temperature. Incubation duration was 240 days for ovigerous females kept in 10-12 °C and 120 days when kept at 20 - 22 °C. In warmer conditions, embryo yolk consumption, heart rate and oxygen consumption increase (Styf et al. 2013). Incubation duration varies by population and tends to have a positive relationship with latitude, with longer incubations at higher latitudes and cooler temperature regimes (Powell and Eriksson 2013). Populations in the Mediterranean Sea tend to incubate for ~6 months while in the North Atlantic Ocean it can last from 7 - 9 months (Farmer 1974; Mori et al. 1998).

1.4. Pelagic Larval Phase

Egg hatching occurs at night over several successive days (Farmer 1974). The female raises the abdomen above the substrate by standing on the tips of the pereiopods and beats the pleopods, while rocking the abdomen backwards and forwards, to help disperse newly hatched larvae. In laboratory conditions, females left their artificial shelters, indicating that females exit the burrow for larvae to escape more easily (Farmer 1974; Smith 1987). Newly hatched larvae in the prezoeal stage are unable to swim, and moult into the first swimming larval stage within minutes (Farmer 1974; Smith 1987). This first swimming stage (Stage I) immediately swims towards the surface of the water column with its telson facing upwards to commence the pelagic phase of the life cycle (Farmer 1974).

Newly hatched larvae swim up through the water column and display positive photoaxis towards 400 - 600 nm and high barokinesis (Smith 1987). Larvae progress through three developmental stages (Stage I - III) by moulting. The larval stages are primarily distinguished by size and differences in the tail, abdomen and appendages. Stages I-III possess extended abdominal spines, likely used to deter predators (Phillips et al. 2006). At Stage III, larvae become increasingly photonegative and begin to descend through

the water column (Smith 1987). The postlarval stage settles on the seabed and settlement on suitable mud habitat is crucial to survival. Postlarvae often enter an existing adult burrow and excavate their own small tunnel (Tuck et al. 1994).

Larval development is strongly influenced by temperature, with higher temperatures leading to more rapid development and earlier settlement. Pelagic Larval Durations (PLDs) can last 1 - 2 months at average temperatures of 8.5 - 14 °C (Smith 1987; Thompson and Ayers 1989; Dickey-Collas et al. 2000b). As temperature increases, metabolic activity and food demand also increases (Jones 2009). Therefore, optimal feeding conditions are important to larval development. *Nephrops norvegicus* larvae are carnivorous, and under high densities, become cannibalistic (Farmer 1975). Starved newly hatched larvae exhibit slower development and longer PLDs (Smith 1987). One day of starvation has little effect on survival; however, periods of more than one day significantly increase mortality (Smith 1987). Laboratory studies have demonstrated that diet composition is important to survival and growth (Rotllant et al. 2001). Moreover, larvae exhibit a plasticity in feeding behaviour by increasing consumption of prey when abundant and following periods of starvation (Pochelon et al. 2009). Such a strategy may mitigate the harmful effects caused by short periods of low food availability.

Peak densities of *N. norvegicus* larvae are found in the upper 40 m of the water column (Hillis 1974; Smith 1987; Lindley et al. 1994). A small ascent at dusk indicates the potential occurrence of a Diel Vertical Migration (DVM); however, studies to date have not adequately tested for the presence of DVM behaviour (Hillis 1974). Larval swimming speeds range from 21.2 mm s^{-1} at Stage I to 30.0 mm s^{-1} at Stage III (Smith 1987). However, horizontal transport is primarily dictated by the local hydrodynamic regime. Even low levels of mean advection (40 - 50 mm s^{-1}) can limit larval settlement on large mud patches (Hill 1990). In the WIS, a cyclonic near-surface gyre forms in spring and is thought to act as a larval retention mechanism by retaining larvae over the mud ground (Hill et al. 1996). In the Celtic Sea, several closely situated grounds promote larval exchange and act as a metapopulation (O'Sullivan et al. 2015). Further afield, off southern Portugal, retention in the Algarve stock was estimated at 0.2 - 0.5%, indicating potential recruitment issues (Marta-Almeida et al. 2008). Due to the non-migratory and sedentary nature of *N. norvegicus* adults, the larval phase enables the

colonisation of new areas and connectivity between populations separated by unsuitable habitat. Also, due to the crucial requirement for larval settlement on mud habitat, oceanography may be an important advective control on recruitment (Hill and White 1990).

The postlarvae are similar in appearance to the juvenile and adult stages. Despite retaining some swimming behaviour, postlarvae are mostly benthic and prefer fine-grained mud substrates (Powell and Eriksson 2013). Small tunnels inside adult burrows suggest that postlarvae enter and reside in existing burrows (Cobb and Wahle 1994; Tuck et al. 1994). Furthermore, postlarvae showed less interest in artificial hand constructed burrows in laboratory conditions, suggesting their attraction to adult burrows is driven by a chemical stimulus (Powell and Eriksson 2013). Burrowing speed increases with age, it takes 4.5 days for a 2-day old postlarva (Stage I) to construct a u-shaped burrow, 2.5 days for a 6-day old postlarva (Stage I) and only 1 day for a Stage II postlarva (Eriksson and Baden 1997). Juveniles seldom leave the safety of the burrow in the first year (Cobb and Wahle 1994). The occurrence of fragmented polychaetes and lower biomass inside the burrow compared to at its entrance, suggest that juveniles feed while inside the burrow (Chapman 1980).

Growth in juveniles is fast and moulting can occur once per month in the first year. Moulting frequency decreases to 3 - 4 per year in the second and third year and after sexual maturity, decreases to 0 - 1 times per year for females which slows their growth, and 1 - 2 per year for males (Sardà 1995; Bell et al. 2006; Haynes et al. 2016). Sexual maturity in females occurs between 22 - 36 mm CL and varies within and between populations (Tuck et al. 2000; Bell et al. 2006). However, age at sexual maturity tends to be more consistent, between 3 - 4 years (Tuck et al. 2000; Bell et al. 2006). In males, an appendix masculina, used in copulation, is developed at three years of age, although spermatophores may be produced earlier (Farmer 1975; Bell et al. 2006).

1.5. Phenology

Phenology, the seasonal timing of recurring life cycle events, of larval hatching varies depending on population. Incubation is strongly temperature-dependent; therefore, the timing of larval hatching varies with latitude and the breeding cycle changes from

annual to biennial in northern populations (Dunthorn 1967; Farmer 1974). For annual breeding populations, mating occurs in winter or spring subsequent to larval hatching and spawning takes place in late summer or early autumn (Bell et al. 2006). Females remain in their burrows during the incubation period until larvae hatch, after which they moult, mate again and the cycle is repeated. For populations in warmer regions such as the Mediterranean Sea, incubation is approximately 6 months, with larvae hatching in winter (Mori et al. 1998). Whereas, in cooler waters around the British Isles, incubation periods are more prolonged at 7 - 10 months (Farmer 1974; Powell and Eriksson 2013). At the northern limits of its distribution, off the coast of Iceland and the Faroe Islands, the breeding cycle is biennial and incubation can last up to 13 months (Eiríksson 2014). Therefore, incubation overlaps with the spawning period, meaning that females can no longer participate in the years breeding cycle and must wait until the following year.

The WIS population, off the east coast of Ireland, is well studied and spawning occurs between August and September (Farmer 1974). The larval season extends from March to June and peak hatching of Stage I larvae takes place between late April and early May (Nichols et al. 1987; Dickey-Collas et al. 2000a; Briggs et al. 2002). On the small coastal Galway Bay ground off the west coast, the larval season is from February to May with peak hatching between March and April, indicating an earlier larval phenology in comparison to the cooler waters of the Irish Sea (de Bhaldraithe 1976). Less is known about larval phenology on other Irish grounds; however, due to similar temperature regimes, grounds to the west of Ireland and in the Celtic Sea are likely to be similar.

As embryo and larval development rates are heavily influenced by temperature, *N. norvegicus*, like many other ectotherms, are prone to phenology changes due to ocean warming (Farmer 1974; Dickey-Collas et al. 2000b). Between the 1980s and 2010s, surface temperatures in the North Atlantic Ocean have increased at a rate of 0.1 - 0.5 °C decade^{-1} and further warming is predicted for the future (Olbert et al. 2012; Dye et al. 2013). In Iceland, an increased ratio of post-hatching to pre-hatching females in May from the 1970 - 1990s to the 2000s indicates an earlier larval phenology (Eiríksson 2014). Similarly, the onset of hatching in the American lobster advanced by 5 weeks from 1989 - 2014 in response to increased temperatures (Harr et al. 2020). Despite many examples of changing phenology in the ocean, less is known on how it affects

recruitment dynamics (Edwards and Richardson 2004; Poloczanska et al. 2013) . A larval phenology shift may result in changes to larval transport, particularly in regions with seasonal oceanographic processes and/or a match/mismatch with optimal food conditions or high predation risk (Philippart et al. 2003; Edwards and Richardson 2004; Fuchs et al. 2020). Therefore, it is important to identify phenology shifts and investigate potential negative impacts to recruitment, particularly for species of commercial or conservation importance.

1.6. Fishery

N. norvegicus is exploited throughout its range and is considered the most important commercial crustacean in Europe with landings of 44,000 tonnes valued at approximately €360 million in 2016 (EUROSTAT, ec.europa.eu/eurostat/web/fisheries/data/database). Despite low landings relative to other species, its high unit value make it an important fishery in many countries. Annual landings increased from 1950 - 1985 and have been relatively stable since (Ungfors et al. 2013). The UK takes most of the landings (43.9%), followed by Ireland (22.2%), France (10.3%), Denmark (9.2%), Netherlands (3.8%), Iceland (3.2%), Italy (2.9%) and Spain (1.4%; EUROSTAT). In 2019, the *N. norvegicus* fishery was the most valuable in Ireland with the Irish quota valued at approximately €58.5 million (Marine Institute 2019). Fishing is primarily conducted using trawling gear; however, off the west coast of Scotland and in the Skagerrak, off Sweden, creels are increasingly being used, with higher values attained for creel-caught *N. norvegicus* (Ungfors et al. 2013).

The burrow emergence patterns of *N. norvegicus* strongly influence their catchability. Factors affecting emergence include reproductive state, light levels and tidal cycle (Bell et al. 2006). Ovigerous females rarely emerge from the burrow, therefore, the catch is dominated by males during the incubation period, although ovigerous females have been caught by creels, indicating they will leave the burrow for easily available food (Ungfors et al. 2013). On the continental shelf (100 m depth), peak burrow emergence occurs at sunset and sunrise, whereas, in deeper (400 m depth) continental slope areas, emergence peaks during the day, in phase with the light cycle (Aguzzi et al. 2003). Higher catch rates have also been recorded at spring tides in comparison to neap tides (Bell et al. 2008).

1.7. Management

Commercial harvests of *N. norvegicus* are managed by several different authorities, for example Norway, Iceland and the Faroe Islands independently manage their own fisheries. In the European Union, fisheries are managed under the Common Fisheries Policy using a Total Allowable Catch (TAC) system. TACs are set according to International Council for the Exploration of the Seas (ICES) subareas, meaning a quota may be shared over several separate populations, also known as Functional Units (FU). FUs are individual or closely situated *N. norvegicus* grounds of which there are 34 in the Northeast Atlantic, ranging from Iceland to Portugal. Stock assessments are conducted at FU level, to obtain an estimate of abundance, harvest rate, and to calculate catch advice. Management at the TAC level allows vessels to fish whichever grounds are most productive, often resulting in concentrated exploitation, and can lead to overfishing. Therefore, ICES recommends that TACs should be set at the FU level to ensure each stock is sustainably exploited and to reduce localised stock depletion (Marine Institute 2019).

The FUs around Ireland are situated inside the ICES subarea VII, these are FU14 (eastern Irish Sea) and FU15 (WIS) in the Irish Sea, FU16 (Porcupine Bank), FU17 (Aran), FU18 to the west of Ireland and FU19 (South Coast), FU2021 (Labadie, Jones & Cockburn Banks) and FU22 (Smalls) in the Celtic Sea (Figure 2). Fishing is primarily conducted from vessels using bottom otter trawls. The TAC is set for the whole of ICES subarea VII, with a separate catch limit on FU16 (Porcupine Bank) since 2011. Since 2016, *N. norvegicus* fisheries in ICES subarea VII are covered under the landings obligation, requiring all catch to be landed. The landings obligation is hoped to result in improvements to selectivity and a reduction in discards which will lead to increases in catch weight and decreases in mortality, and therefore, increased future catch rates. A high survivability exemption applies to creels and bottom trawls with mesh size greater than 100 mm, as well as highly selective gear features such as square mesh panels, seltra panel, sorting grid or separation panel (Marine Institute 2019).

FU15 (WIS) is one of the most productive *N. norvegicus* fisheries across its distribution, with landings of 5756 t in 2018 (Marine Institute 2019). On FU16 (Porcupine Bank), large individuals attain high market values. Landings peaked in the 1980s (~4,000 t) but have declined since then, landings in 2018 were 2,079 t at an estimated value of

approximately €20 million (Aristegui et al. 2019b). A seasonal fishery closure between May-July was in place from 2010 to 2012 and the fishery has been closed for the month of May since 2013 (Marine Institute 2019). On FU17 (Aran), abundance has had a significant decline since 2004 and has been close to or below Maximum Sustainable Yield (MSY) biomass trigger (the biomass at which management procedures are implemented to halt further stock decline) since 2012 (Aristegui et al. 2019a). Catch rates have fluctuated in recent years and landings of 494 t in 2018 were valued at approximately €3.2 million (Aristegui et al. 2019a).

In the Celtic Sea, FU19 (South Coast) consists of 9 discrete mud patches around the south coast of Ireland. In recent years, landings have declined from 957 t in 2007 to 219 t in 2018 valued at €1.5 million, and abundances were below MSY biomass trigger in 2016, 2018 and 2019 (Doyle et al. 2019a; Marine Institute 2019). FU2021 (Labadie, Jones & Cockburn Banks) are relatively low density grounds and had landings of 1,997 t at a value of €8.5 million in 2018. Stock abundance in FU22 (Smalls) was below MSY biomass trigger in 2016 and 2018 and landings in 2018 were 1975 t valued at €11.5 million, down from 3560 t the previous year (Doyle et al. 2019b)

1.8. Assessment Methods

Several assessment methods have been applied to *N. norvegicus* populations, including Catch-Per-Unit-Effort (CPUE), Length Cohort Analysis (LCA), Virtual Population Analysis (VPA), annual larval production method and UWTV. Due to strong diurnal and seasonal effects on emergence patterns and therefore, catch rates, CPUE is limited in estimating stock trends (Bell et al. 2006). LCA uses catch length composition data along with mortality and growth information; though, it can only be applied to stable stocks and fails to identify recruitment overfishing (ICES 2003). VPA requires catch at age data, which is problematic due to difficulties in aging crustaceans as hard structures are lost during moulting (Hartnoll 2001). 'Slicing' is used to convert length data to ages using von Bertalanffy growth parameters. However, issues pertaining to growth variability between individuals and year classes cause problems when identifying age classes (ICES 2004). The annual larval production method is used to obtain a fishery-independent estimate of female spawning stock biomass and involves collecting larvae and using estimates of larval mortality and female fecundity to calculate total quantities

of produced larvae (Briggs et al. 2002; Bell et al. 2006). However, it is too labour and time intensive to use as a regular stock monitoring routine (Bell et al. 2006).

1.9. Underwater Television (UWTV)

UWTV as a means of counting *N. norvegicus* burrows has been used as a survey method for several years on many FUs. UWTV provides a fishery-independent estimate of size, exploitation levels and catch rates of individual stocks (ICES 2009; Leocádio et al. 2018). Early work in the 1980s showed the potential of UWTV to quantify burrows identified in video footage (Chapman 1985). It has since been used to assess stocks across the Northeast Atlantic Ocean and Mediterranean Sea (Bell et al. 2006). It is assumed that one burrow corresponds to one adult and occupancy is 100%, although juveniles are known to excavate their own tunnel within an adult burrow (Tuck et al. 1994; Bell et al. 2006). Non-occupied burrows are thought to collapse soon after abandonment, and therefore, are not counted in UWTV footage. However, time before burrow collapse can also depend on sediment composition, activity of other species, hydrography and fishing activity (Ungfors et al. 2013). Surveys provide an absolute abundance estimate which is used to calculate fishery catch advice, subsequent to bias correction, e.g. edge effect, burrow detection and identification rates (Leocádio et al. 2018).

On UWTV surveys, a camera-mounted sledge is lowered and once stable on the seabed, the vessel slowly tows the sledge while ensuring ground contact is maintained and a 10-minute video is recorded. Vessel position and sledge position are recorded regularly and the area covered by the sledge is calculated using the width of the camera frame or laser points. Trained burrow counters quantify the number of burrow systems observed in the recording. *Nephrops norvegicus* burrows have several distinctive characteristics which assist in their identification, such as a crescent-shaped opening, the presence of excavated sediment at the entrance and tracks left by burrow occupiers as they exit and enter. At the beginning of a survey, counters are usually re-trained using UWTV footage from a previous survey and counts are validated to ensure re-familiarisation prior to counting (ICES 2009). Burrow counting data is screened for unusual counts using Lin's Concordance Correlation Coefficient (CCC; Lin 1989). Lin's CCC enables comparisons of counts with a scale ranging from -1 to 1, with 1 signifying perfect

concordance. In UWTV surveys, a threshold of 0.5 is used and values below the threshold mean a third counter reviews the footage and provides an additional count.

Mean burrow density is calculated as the number of burrow systems divided by the survey area observed. Abundance estimates are obtained by multiplying mean burrow density (burrow m^{-2}) by the area of the mud ground. UWTV surveys also obtain ancillary information such as *N. norvegicus* activity outside the burrow, co-occurring species, trawl marks and temperature data. Recently, high definition cameras have been used on Irish surveys, producing digitalised still images (12 frames per second) rather than video, which allows image annotation (ICES 2020). This development, coupled with progress in building deep learning models which detect and count burrows automatically indicate positive advances in relation to survey improvements, particularly in terms of accuracy, efficiency and validity (ICES 2020).

1.10. Irish Population Trends

The UWTV survey in Ireland has been conducted since 2002 on the Aran (FU17) grounds (ICES 2020). Burrow density estimates have fluctuated widely with a general decline since 2002 (Figure 3). Initially, between 2002 and 2005, densities were at a high level (0.79 - 1.08 burrow m^{-2}). However, from 2004 - 2012 densities fluctuated with a general decline before beginning to stabilise at a lower level (0.28 - 0.40 burrows m^{-2}) from 2012 - 2019. Since 2012 the total abundance estimate for FU17 has been below the MSY biomass trigger of 540 million burrows in all but two years, signifying potential issues with recruitment (ICES 2020). The vast majority of burrows are observed on the large Aran ground (~93%), with ~5% and ~2% from the smaller Galway Bay and Slyne grounds, respectively. The mean lengths of male and female *N. norvegicus* on the Aran grounds, from beam trawl surveys (2006 - 2018), have also shown an increasing trend, suggesting limited recruitment (Doyle et al. 2018).

On the WIS (FU15) ground, the time series of burrow estimates began in 2003 and the ground exhibits high burrow densities with small adult sizes (Johnson et al. 2013). Burrow estimates have remained relatively stable since 2003 with densities of 0.7 - 1.0 burrow m^{-2} (Figure 3; Lundy et al. 2019). Abundance estimates have remained between 4.5 - 6 billion burrows and have always well exceeded the MSY biomass trigger of 3

billion burrow (Lundy et al. 2019). A decline was observed, between 2005 - 2008 and 2013, although increases followed in subsequent years. Overall, the WIS population is in a stable healthy condition.

On the Porcupine Bank (FU16) ground, UWTV surveys have been conducted since 2012, except in 2015. It is characterised by low densities of large adults and burrow densities have ranged from 0.10 - 0.16 burrow m^{-2} (Figure 3) and abundance from 722 - 1117 million (Aristegui et al. 2019b). Since 2012, burrow abundance has had a general increasing trend over time, despite a small decrease in the most recent 2019 survey (Aristegui et al. 2019b). The Spanish groundfish survey has been conducted since 2001 on the Porcupine Bank ground and provides biomass and abundance indices, length frequency and distributions of commercial species, including *N. norvegicus* (Ruiz-Pico et al. 2019). Biomass of *N. norvegicus* was below 1 kg $haul^{-1}$ from 2001 - 2015 in every year except 2010 and increases in biomass were observed from 2016 - 2019 with a peak in 2018 (Ruiz-Pico et al. 2019). Low numbers of small *N. norvegicus* (<21 mm CL) were recorded from 2001 - 2012; however, in 2013 a large increase in small individuals was evident and from 2013 - 2019 it has remained above 0.5 ind. $haul^{-1}$, indicating good recruitment in recent years (Ruiz-Pico et al. 2019).

In the Celtic Sea, the longest time series of UWTV burrow estimates is for the Smalls (FU22; 2006 - 2019). Burrow densities have ranged from 0.31 - 0.55 burrow m^{-2} and abundance from 866 - 1622 million burrows (Doyle et al. 2019b). Abundance has fluctuated widely since 2015 (Figure 3) and has been below the MSY biomass trigger of 990 million burrows in 2016 and 2018 (Doyle et al. 2019b). On FU19, the earliest UWTV survey was carried out in 2006 on a section of the grounds, although most of the grounds have been surveyed since 2011. Abundance for FU19 has had a general decline from approximately 665 million burrows (0.34 burrow m^{-2}) in 2011 to a historical low of 176 million burrows (0.09 burrow m^{-2}) in 2018 and abundance has been below the MSY biomass trigger of 430 million burrows in 2016, 2018 and 2019 (Doyle et al. 2019a). Finally, the large Labadie, Jones and Cockburn Banks (FU2021) grounds have the shortest time series of UWTV burrow estimates (2013 - 2019). Densities have ranged from 0.06 - 0.44 burrow m^{-2} (Figure 3) and abundance has ranged from 617 - 4428 million burrows (White et al. 2019). Abundance was quite stable from 2013 -

2016 until a large increase in 2017, followed by subsequent declines in 2018 and 2019 (White et al. 2019).

1.11. Biophysical Larval Transport Model

Due to the inherent difficulties in monitoring larval transport *in-situ*, biophysical larval transport models are increasingly being used as a method of estimating larval retention, dispersal distance and connectivity between populations. Biophysical larval transport models typically involve an ocean circulation model coupled with a Lagrangian particle tracking tool which enable simulations of larval transport. Understanding larval transport dynamics is particularly important for species with sedentary and non-migratory adult stages that rely on the larval phase for gene flow and colonisation of new habitats. *Nephrops norvegicus* is a good example, as adults spend the majority of their time in the burrow, only leaving in search of food and to mate (Sardà 1995). Due to their requirements for mud habitat, populations separated by uninhabitable substrate are only connected via larval migration. Also, larvae depend on settlement on suitable habitat for survival, therefore, larval supply influenced by local hydrographic processes, may constrain recruitment.

Several physical and biological factors affect larval transport; therefore, to obtain accurate larval transport estimates, models must be correctly parameterised (Metaxas and Saunders 2009). Planktonic larvae are primarily transported by currents due to weak swimming abilities. Due to depth-varying currents, vertical swimming can enable larvae to regulate horizontal transport (Paris and Cowen 2004; Queiroga and Blanton 2005). Vertical movements are influenced by several cues, the most important appear to be light, pressure and gravity; however, temperature, salinity, turbulence and currents also affect behaviour (Queiroga and Blanton 2005). DVMs are common in meroplankton larvae, believed to be a predator avoidance mechanism. Such behaviour can also influence transport, for example, when a circular gyre is present, a vertical migration can move larvae away from peak gyral flows (Phelps et al. 2015). Due to its importance to horizontal transport, a good knowledge of DVM behaviour and vertical distribution is needed before modelling larval transport.

Seasonal oceanographic processes may affect larval transport patterns, therefore, the timing and duration of modelled larval release must coincide with that of egg hatching *in-situ*. Phenological variability between populations often exists, empirical observations are required so that modelled larvae are released at the right time of year to correctly estimate PLD and obtain settlement dates (Bell et al. 2006). The development of planktonic larvae is frequently temperature-dependent (Dickey-Collas et al. 2000b; O'Connor et al. 2007). Therefore, an accurate estimation of PLD depends on knowledge of the relationship between temperature and PLD. Increased temperatures tend to reduce planktonic dispersal duration and dispersal distance which can potentially affect the ability of larvae to settle successfully (Shanks 2009).

The distribution of breeding females in a population may vary from year to year. In *N. norvegicus* populations, it is common for burrow distributions to differ quite significantly from one year to the next (Aristegui et al. 2019b; Lundy et al. 2019; White et al. 2019). Retention likelihood may also vary depending on the release location, with certain areas having enhanced retention probability. Ospina-Álvarez et al. (2013) observed differences in the larval trajectories of European anchovy when using a realistic spatial distribution, from acoustic surveys, compared to a randomly-generated distribution. This observation demonstrates the importance of incorporating empirical information on the spatial distribution of the spawning stock to recreate the initial distribution of hatching larvae.

Several ocean models with increasing resolution have become available in recent years. The ocean model plays a crucial role in recreating the hydrodynamic conditions experienced by larvae and ultimately, coupled with the biological and behavioural component, dictating larval transport, connectivity and settlement patterns. In Ireland, a high resolution, Regional Ocean Modelling System (ROMS) model is operated by the Marine institute (Dabrowski et al. 2016). The model has a horizontal resolution of 1.1 - 1.6 km in coastal waters, 40 depth layers and 3- or 1- hourly temporal resolution. The global Hybrid Coordinate Ocean Model (HYCOM; Chassignet et al. 2007) model has been used in many larval transport studies worldwide and is available from 1994 to present with a 3-hourly temporal frequency and a 1/12° (~9 km) horizontal resolution between 40 °S and 40 °N and 1/24° (~4 km) resolution poleward of these latitudes. Despite the availability of alternative models, ROMS and HYCOM are the most

commonly used in larval transport studies (Swearer et al. 2019). Striking a balance between resolution and temporal availability is important to satisfy the particular objectives of a study.

In summary, biophysical larval transport models are increasingly being utilised as a tool to study larval transport dynamics of species with pelagic larval stages. For sedentary species with specific habitat requirements, larval transport is crucial to connectivity and settlement patterns and may constrain recruitment. Therefore, larval transport models have great potential as tools in the monitoring and management of species, particularly when recruitment is difficult to estimate, e.g. due to the lack of an ageing criteria. However, biological and behavioural components of the model must be supported by empirical observations to ensure correct model parameterisation and confidence in model results (Metaxas and Saunders 2009).

1.12. Research Objectives

The research conducted in this study concerns the larval stages of *N. norvegicus* with a strong emphasis on larval transport. For *N. norvegicus*, the larval phase enables migration between populations and because of its strong requirement for mud habitat, larval settlement rates may be an important constraint on recruitment. The primary hypothesis of the study is whether modelled larval transport estimates (retention/dispersal distance) can be used to explain variation in empirical *N. norvegicus* population densities. To test this hypothesis, empirical observations of vertical distribution and migratory behaviour were required to correctly parameterise models and are reported in Chapter 2. Historical data in the Irish Sea were used in Chapter 3 to examine long term trends in larval phenology and test the hypothesis if ocean warming has led to a larval phenology shift. A novel long term (2000 - 2019) time series of larval transport estimates for 6 Irish FUs in Chapter 4 provides information on each FUs capacity for larval retention and exchange with other FUs. Using burrow density estimates from the UWTV survey, the main hypothesis of whether modelled larval transport indices can predict empirical population density fluctuations is tested.

The objectives of the study were:

- To examine the vertical distribution of *N. norvegicus* larvae, identify biotic and abiotic factors that influence vertical distribution, investigate whether larvae perform a DVM and explore the implications of a DVM to larval transport. A dedicated research cruise was conducted to achieve these aims, with larvae being sampled on both the Aran grounds, off the west coast of Ireland, and the WIS ground, off the east coast. Spatially separated sampling stations on both grounds were used to examine vertical distribution, whereas, a fixed station was used to examine the occurrence of a DVM, in order to control for environmental factors that influence depth preference. In addition, several different vertical migration behaviours were tested to examine the influence of DVM on larval transport. These results are presented in Chapter 2.

- To test the hypothesis if ocean warming has led to a contraction of the embryo incubation period and therefore, earlier larval phenology in *N. norvegicus*. This hypothesis was tested using two complementary approaches, the first used previous experimental parameters combined with historic temperature data from the Irish Sea to build a predictive model of larval release timing. The second used zooplankton datasets as far back as the 1980s to examine the temporal distribution of larvae. Larval transport modelling was also conducted to examine the effect of a shifting phenology (and inter-annual variability) on larval transport patterns on the WIS ground. These results are presented in Chapter 3.

- To test the primary research hypothesis of whether modelled larval transport estimates can be used to explain fluctuations in empirical population densities observed in UWTV surveys. To ensure that larval release dates were correct for the data scarce Aran grounds population, a light trap survey from March-June was conducted to examine larval temporal distribution. For 6 FUs off the coast of Ireland, a long term time series of larval transport indices (retention, dispersal distance, exports) was created to examine FU characteristics and trends. UWTV density estimates were available since 2002 and 2003 for the Aran and WIS grounds, therefore, these were chosen to test if modelled larval transport estimates and UWTV burrow densities are linked. These results are presented in Chapter 4.

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1.14. Figures

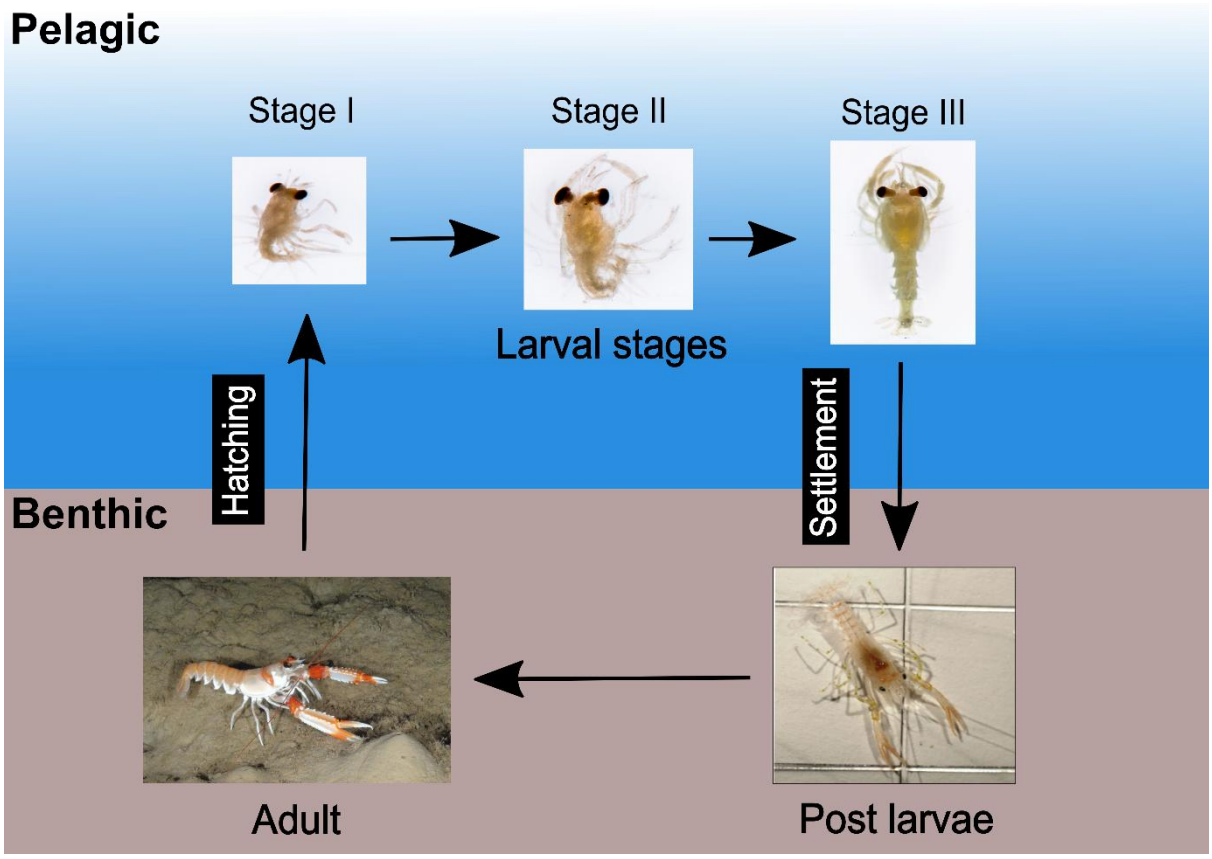

Figure 1. Life cycle of *N. norvegicus* indicating benthic and pelagic life stages.

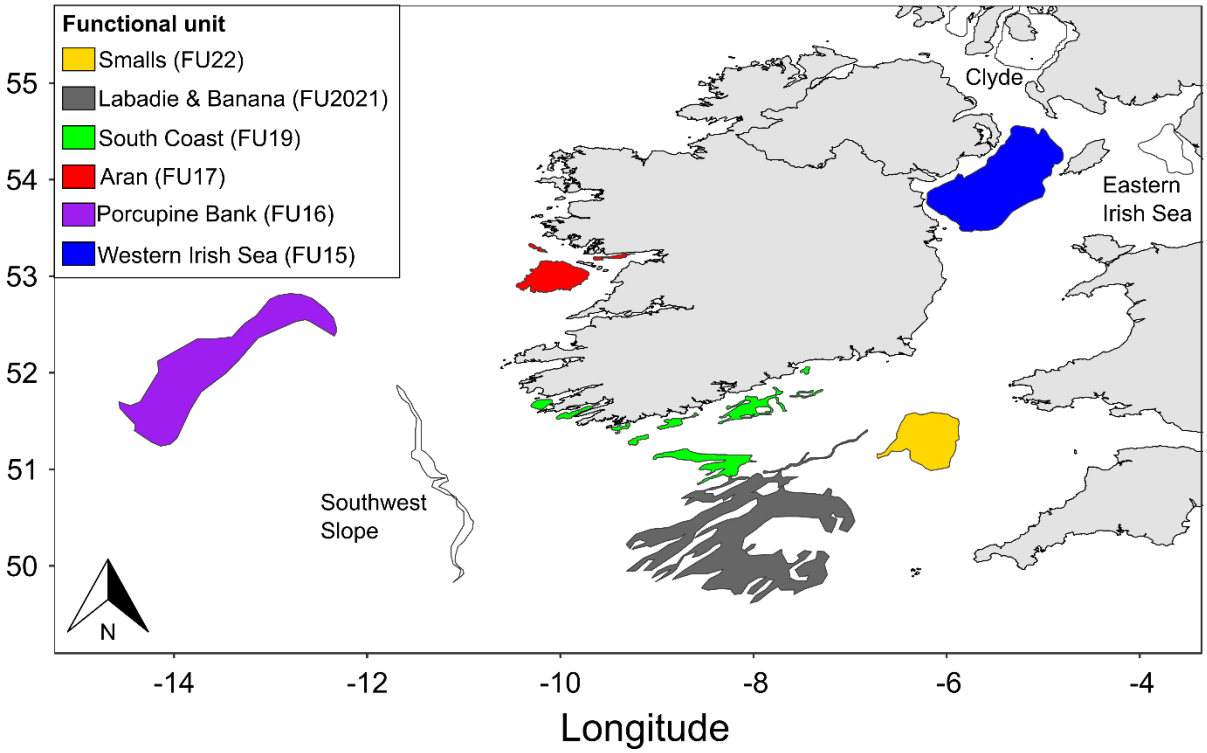

Figure 2. Map of *N. norvegicus* Functional Units (FU) in Irish territorial waters. Nearby grounds that are outwith Irish waters (Eastern Irish Sea & Clyde) or do not represent a FU (Southwest Slope) are also represented.

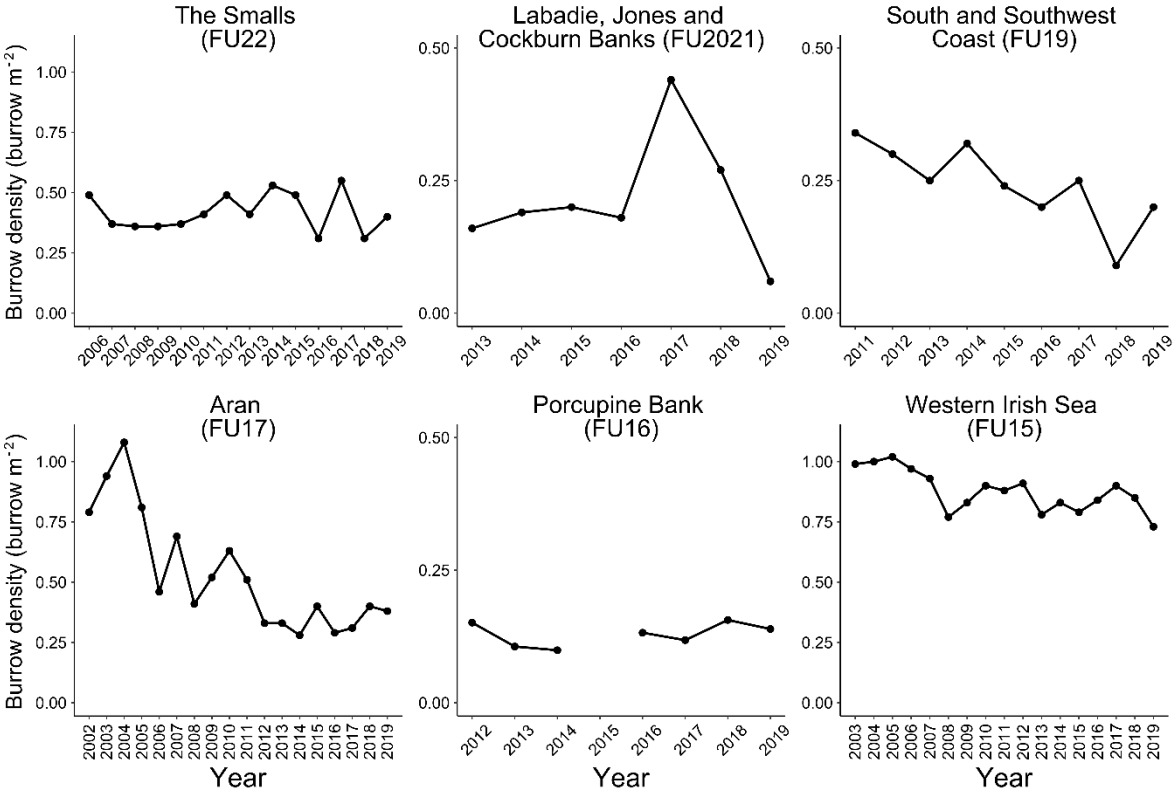

Figure 3. Time series of burrow density estimates (burrow m^{-2}) obtained from underwater television surveys on Irish Functional Units (FU). Please note changes to y-axis.

Chapter 2

Twilight Migrators: Factors Determining Larval Vertical Distribution in *Nephrops norvegicus* with Implications for Larval Retention

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Contribution to published paper: Fieldwork, sample processing, statistical analysis, larval transport modelling, figure generation and writing manuscript.

2.1. Abstract

The vertical distribution of pelagic marine larvae can greatly influence their dispersal due to depth-varying currents, which can determine larval retention or transport away from critical habitat. Vertical distribution of commercially important lobster *Nephrops norvegicus* larvae was examined over fishing grounds off the west and east coasts of Ireland. Larval vertical distribution for both grounds was significantly influenced by the temperature differential between the surface and 60 m depth, zooplankton biomass, and to a lesser extent, stratification, measured using the Potential Energy Anomaly (PEA). Fixed station sampling was conducted over three days in the Western Irish Sea (WIS) to investigate the occurrence and extent of a Diel Vertical Migration (DVM). Larvae performed a twilight DVM with a ~10 m ascent prior to sunset and sunrise and a descent at midnight and after sunrise. Larval transport model simulations were used to examine the effect of DVM behaviour on larval retention over mud habitat. The presence of a DVM actually reduced the likelihood of retention on both the Aran and WIS grounds. Predicted larval retention was unusually low over the Aran grounds in 2018, which is potentially significant in the context of historic stock fluctuations in this area. These findings suggest that understanding larval dynamics could be crucial in managing *N. norvegicus* stocks on fishing grounds, in particular those with variable inter-annual oceanography and a low rate of larval imports from other grounds.

Key words: Vertical distribution, diel vertical migration, larvae, particle-tracking, larval retention, *Nephrops norvegicus*

2.2. Introduction

Nephrops norvegicus (Norway lobster) is a benthic crustacean found in the Northeast Atlantic Ocean and Mediterranean Sea. Adults are restricted to mud habitats where they construct and reside in burrows. Like many other decapod crustaceans, after embryo hatching, *N. norvegicus* undergo a pelagic larval phase prior to settlement and eventual recruitment into the adult population. Free swimming larvae pass through three stages by a series of moults prior to re-joining the benthic phase as postlarvae (Farmer 1974).

Both embryonic and larval development are dependent on temperature. Therefore, the duration of embryo incubation, timing of larval hatching and Pelagic Larval Duration (PLD) varies with latitude (Sardà 1995, Dickey-Collas et al. 2000). In warmer waters of the Mediterranean Sea, the duration of embryo incubation can last between 120 - 180 days (Orsi Relini et al. 1998). In contrast, populations situated off Iceland that experience cooler temperatures incubate for longer periods, ~380 days (Eiriksson 1970). Efforts to describe the relationship between temperature and larval development have been met with limited success due to the difficulties of captive rearing to postlarval stage. Observed developmental rates of Stage I and II larvae (combined) range from 33 days at 9 °C to 13 days at 15 °C (Thompson & Ayers 1989, Dickey-Collas et al. 2000). However, the larval period is further prolonged when the PLD of Stage III is accounted for. On the Western Irish Sea (WIS) ground, larvae are present in the water column between March and June with peak densities in May (Nichols et al. 1987). Larvae appear earlier off the west coast in a small population in Galway Bay where the larval season lasts from February to May with a peak from March to April (de Bhaldraithe 1976). However, the seasonality of larval timing at the much larger population on the Aran ground (Figure 1) was unknown, until now.

N. norvegicus fisheries are among the most economically valuable in Europe (Ungfors et al. 2013). Landings from Irish waters in 2017 had a value of €54 million at first sale (Doyle et al. 2018a). Underwater television (UWTV) is used as a method of estimating stock size by calculating burrow density. The UWTV surveys are well-established in Ireland and surveys have been conducted annually since 2002 on the Aran grounds and since 2003 on the WIS ground. Observed burrow densities have remained relatively stable over time at the densely-populated WIS ground (Clements et al. 2018). However, the Aran and Porcupine Bank grounds, off Ireland's west coast, have experienced

marked fluctuations, making the sustainability of the respective fisheries a concern (Doyle et al. 2018a, b).

Several factors such as recruitment, exploitation, predation or other sources of natural mortality determine *N. norvegicus* population size (Johnson et al. 2013). It is thought that local oceanographic conditions can play a significant role in the recruitment success of this species because of the potential for larvae to be transported beyond the boundary of mud habitat, which can be patchy and spatially isolated (Bell et al. 2006). In certain instances, localised oceanographic features can aid in larval retention, such as a seasonal gyre that coincides with the larval season in the WIS, which is suggested to entrain larvae over the WIS mud patch (Hill et al. 1996, Olbert et al. 2012). However, off the west coast of Ireland, where stock size is more likely to fluctuate, no obvious retention mechanism exists (O'Sullivan et al. 2015).

Weak swimming capabilities prevent *N. norvegicus* larvae from counteracting the force of horizontal currents; however, larvae can have more influence over their vertical position in the water column. Because currents vary with depth, larvae may ultimately control horizontal dispersal by regulating vertical distribution (Queiroga and Blanton 2005). Vertical position also has major consequences for feeding and predation exposure (Huntley & Brooks 1982, Bollens & Frost 1989). Many factors are known to influence the vertical distribution of pelagic decapod larvae such as light, pressure, temperature, salinity, currents and endogenous rhythms (Roberts Jr 1971, Hughes 1972, Ennis 1975, Ennis 1986, Kelly et al. 1982, Forward 1987). Diel Vertical Migration (DVM) is widespread amongst decapod larvae, with predator evasion thought to be one of the main reasons for the behaviour (Hays 2003, Queiroga & Blanton 2005, Dos Santos et al. 2008). Three main types of DVM are known to exist, nocturnal DVM, when an ascent to shallower depths occurs between dusk and dawn, reverse DVM, when ascent occurs during the day, and twilight DVM, when two ascents and descents are performed in a 24 hour period, i.e. a first ascent at dusk, followed by a descent at midnight and then a second ascent to the surface before a descent after sunrise (Forward 1988).

Several modelling studies have highlighted the importance of vertical distribution to horizontal dispersal by examining distinct migratory behaviours (Emsley et al. 2005, Marta-Almeida et al. 2006, Marta-Almeida et al. 2008). A downward migration and

overall deeper vertical distribution was favourable to settlement and retention of coral reef fish larvae in the Straits of Florida (Huebert et al. 2011). Similarly, migrating copepods exposed to near-bottom onshore flow during the day had a greater likelihood of retention than those at the surface (Batchelder et al. 2002). Meanwhile, Phelps et al. (2015) examined the retentive properties of the WIS gyre and concluded that retention was maximised when *N. norvegicus* larvae remained at the depth of peak gyral flow and was reduced when a DVM behaviour was introduced. If thermoclines are present, larvae in warmer waters above the thermocline develop faster and settle earlier and less time spent in the pelagic larval phase is linked to shorter dispersal distances for near-surface meroplankton (Shanks 2009). Thus, to fully comprehend the horizontal transport of planktonic larvae, an understanding of vertical distribution is essential.

Few studies have examined the vertical distribution of *N. norvegicus* larvae in great detail. Peak densities of larvae have been observed in the upper 40 m of the water column (Hillis 1974, Smith 1987, Lindley et al. 1994). A small ascent was observed from daytime to dusk suggesting the possible occurrence of a DVM (Hillis 1974). In addition, Lindley et al. (1994) observed a shallower distribution during the spring bloom in April compared to afterwards in May. However, in most cases, information on this subject has been indirect, with many studies primarily focused on horizontal distribution, collecting samples at insufficiently high temporal resolution, or not obtaining adequate numbers of larvae to thoroughly examine DVM. As a result, little is known about the environmental drivers that influence vertical distribution or their relative influence in this species.

The principal aims of the present study were to (1) provide the first information on larval seasonality on the Aran grounds off the west coast of Ireland, (2) explore biotic and abiotic factors that influence vertical distribution, (3) investigate the potential occurrence and extent of DVM behaviour in *N. norvegicus* larvae and (4) determine the effect of DVM behaviour on larval transport and retention.

2.3. Materials and Methods

Sample collection

Larvae were sampled at two *N. norvegicus* grounds from 4th - 15th April 2018 on-board the *RV Celtic Voyager*. At the Aran grounds, situated off the west coast of Ireland, sampling was conducted at a total of 24 stratified random stations chosen using a randomisation process, whereby 12 randomly generated stations were allocated on the outer boundary of the *N. norvegicus* mud patch and 12 stations were chosen towards the centre of these grounds (Figure 1). During the second day of sampling on the Aran grounds, work was discontinued due to poor weather and three opportunistic stations were sampled on the Galway Bay ground before continuing on the Aran ground. After a 48 hour transit period to the east coast of Ireland, sampling continued on the WIS ground, from 9th - 15th of April with a further 24 stratified random stations sampled. Again, 12 of the stations were on the boundary and 12 were situated towards the centre of the WIS ground.

In addition to the sampling conducted above, fixed station sampling was performed during three consecutive days on the WIS ground in an area with historically high densities of *N. norvegicus* larvae in April (data.cefas.co.uk/#/View/2620, accessed 13th December 2016). At the fixed station, zooplankton samples were collected every three hours (00:00, 03:00, 06:00, 09:00, 12:00, 15:00, 18:00 & 21:00; UTC + 1). Fixed station sampling commenced precisely at the indicated hour to ensure sampling times were identical across three diel cycles. In total, 24 sampling events were completed over a total of 69 hours. Zooplankton samples were collected using a multinet (Hydrobios type Midi, 0.25 cm^{-2} aperture size, 300 µm mesh size). All of the following depth strata were sampled: 10 m from bottom to 40 m, 40 - 30 m, 30 - 20 m, 20 - 10 m and 10 - 0 m. Increased sampling intensity took place in surface layers due to evidence that *N. norvegicus* larvae are concentrated in the upper 40 m of the water column (Hillis 1974, Smith 1987, Lindley et al. 1994). To ensure that adequate numbers of larvae were caught in each depth stratum, a minimum seawater volume of 100 m^{-3} was filtered. The plankton sampler was deployed on an oblique haul and speed was carefully controlled to ensure equal sampling of each depth stratum. Once aboard, samples were retrieved and preserved in buffered 4% formaldehyde solution for processing in the laboratory. For each sample, larvae were counted and sorted according to larval stage. Zooplankton

biomass (ml m^{-3}) associated with each sample was measured using the volume displacement method (Beers 1976). Before measuring the displacement volume, zooplankton samples were filtered and blotted for a minimum of 5 minutes to remove excess interstitial water and zooplankton measuring >3 cm were removed to avoid bias associated with large individual organisms.

Vertical profiles of temperature were measured from the surface of the water column to within 10 m of the seabed using a multinet-mounted CTD. Profiles of salinity, density & fluorescence were collected using a Seabird SBE 911 CTD with mounted ECO FLNTU fluorometer. To examine the association between water column characteristics and larval vertical distribution, the difference between the surface and 60 m was calculated for temperature and salinity at every station, termed 'Δ Temperature' and 'Δ Salinity', respectively.

The Potential Energy Anomaly (PEA; J m^{-3}) was calculated for each station to provide a measure of stratification of the water column. The PEA is defined as the amount of energy needed to fully homogenise the water column, described according to Simpson et al. (1977) by the equation:

$$PEA = \frac{1}{D}\int_{-H}^{n} gz(\bar{p} - p)dz \qquad (1)$$

where *g* is the gravitational acceleration, *z* is the vertical coordinate from *–H* (deepest measurement) up to the sea surface *n* and *p(z)* is the density profile in a water column of depth *D*.

A hyperspectral irradiance sensor (Trios Ramses ACC; spectral accuracy: 0.3 nm) was deployed prior to collection of zooplankton samples to measure underwater down-welling irradiance (mW m^{-2} nm) in the upper 40 m of the water column. The sensor had a wavelength range between 320 - 950 nm and logged one measurement per second. Tidal height data were extracted from the Irish National Gauge Network (data.marine.ie/geonetwork/srv/eng/catalog.search#/metadata/ie.marine.data:dataset.2774, accessed 15th January 2019). Tidal data were taken from the Inishmore gauge for stations on the Aran grounds and from the Port Oriel gauge for the WIS ground.

The Weighted Mean Depth (WMD) of *N. norvegicus* larvae was calculated for all stations as follows:

$$WMD = \frac{\sum_{i=1}^{5} n_i d_i}{\sum_{i=1}^{5} n_i} \quad (2)$$

where n_i is individuals per m^{-3} of larvae at the ith stratum and d_i is the mean depth of the ith stratum. WMD provides a single measure of depth, integrated across depth strata at a particular station, i.e. at the fixed station in the current study. One WMD value represents the 'average' vertical distribution of *N. norvegicus* larvae across all 5 strata at a particular time of day. This value enables different times of day to be compared. WMDs were also used to allow comparisons across sampling stations to investigate horizontal patterns of preferred larval depth. When the total number of larvae was <10 individuals, stations were excluded from analyses. The WMD metric was also used to determine 'average' depth of zooplankton biomass per station.

Analysis

Larval densities were compared between grounds for each larval stage using Mann-Whitney U tests. Comparisons between stages within grounds and day/night larval densities were made using Wilcoxon signed rank tests. These tests were chosen due to non-normality of data after transformation.

To examine the association between biotic/abiotic factors and WMD of Stage I larvae as a response variable, a multiple linear regression was performed across horizontally sampled stations on the Aran and WIS grounds. Stage I larvae were used in these analyses due to their relatively high densities in comparison to later larval stages. The initial maximal model included the following variables: average zooplankton biomass (across 5 depth strata), WMD of zooplankton biomass, depth of maximum fluorescence, tidal height, bottom depth, PEA, Δ temperature (surface temperature - temperature at 60 m), Δ salinity, irradiance at 15 m, time of day and location of grounds (Aran or WIS). Prior to running analyses, correlations between explanatory variables were examined by obtaining Variance Inflation Factors (VIFs). When a VIF of >10 was observed, one of the correlated variables was excluded from the analysis. A correlation between PEA and Δ salinity was detected and the latter was removed. A model simplification process was followed using a stepwise forward selection of variables. The optimal model was identified using Akaike's Information Criterion (AIC), when the addition of further variables did not bring a reduction in AIC, the model was considered optimal. The AIC

method allows the user to fit the optimal model by balancing complexity in contrast to goodness-of-fit (Akaike 1974).

To examine the relative importance of each predictor in the optimal model, the respective amount of explained variance was assessed. The metric 'lmg' in the R package *relaimpo* was used to decompose the overall R^2 into non-negative contributions for each predictor that sum to the total R^2 (Johnson & LeBreton 2004, Grömping 2006).

Predictive performance of the final model was evaluated using leave-one-out cross validation. Leave-one-out cross validation fits the model using all but one observation in the dataset and is then repeated for all observations (Efron 1983, Jain et al. 1987). To evaluate model performance, predicted versus observed values from the leave-one-out procedure were compared using Spearman's rank correlation.

To investigate the occurrence of a DVM, the effect of time of day on WMD of Stage I larvae was examined across three daily cycles (69 hours) at the fixed station, using analysis of variance (ANOVA) with Tukey's honestly significant differences (HSD) post-hoc tests. In addition, a simple linear regression was used to examine the association between down-welling irradiance at 15 m during daylight hours and Stage I larval WMD. All analyses were performed using the statistical software R version 3.5.1 (R Core Team 2018).

Larval transport

To investigate the effect of DVM on larval retention and dispersal distance, particle-tracking model simulations were carried out using a 3D hydrodynamic model. Output from the Regional Ocean Modelling System (ROMS) was used to replicate hydrography around Ireland. The ROMS model is a free-surface hydrostatic primitive equations model that uses orthogonal curvilinear coordinates on an Arakawa-C grid for the horizontal dimension and a prognostic terrain-following coordinate for the vertical dimension (Shchepetkin and McWilliams 2005). A ROMS model encompassing a large area of the northwest European continental shelf including Irish territorial waters was used (i.e. 'Northeast Atlantic model', Dabrowski *et al.*, 2016). The model has a resolution of 1.1 - 1.6 km in Irish coastal waters and has 40 terrain-following vertical

layers (Dabrowski et al. 2016). Hourly current velocity output produced by the ROMS model was used in particle-tracking.

Model output from ROMS for the relevant period in 2018 was coupled with an individual-based model (Ichthyop v3.3; Lett et al. 2008) to simulate larval transport originating from the Aran and WIS grounds. Larval transport simulations were conducted using hourly ROMS current output using a Runge-Kutta 4th order numerical scheme and a 5 minute time step. In total, 10,000 particles were released on each ground for each of the scenarios and particles were released with a uniform spatial distribution across the respective grounds. The simulation began on 15th March for the Aran grounds and 1st April for the WIS ground to reflect the predicted timing of larval hatching from observed larval stages and densities (see Results). Simulation duration was set at 60 days which was in close agreement to PLDs estimated from regression parameters obtained from previous experiments of temperature-dependent development (Smith 1987; Thompson and Ayers 1989; Dickey-Collas et al. 2000) combined with 60 day average sea surface temperature from the ROMS model on the Aran grounds (64 days at 8.8 °C) and WIS ground (62 days at 9 °C).

Three DVM behaviour scenarios were simulated for both grounds: (1) No DVM, (2) Twilight DVM and (3) Nocturnal DVM. In the No DVM scenario, particles remained fixed at a depth of 30 m for the Aran grounds and 20 m for the WIS throughout the simulation, in line with observations of average larval WMD from empirical data in the present study. Twilight DVM particles made two ascents and descents over a 24 hour period, an ascent at dusk followed by a descent at midnight and another ascent before a daytime descent. Nocturnal DVM particles were programmed to make one ascent at dusk and one descent at dawn over the diel cycle. For the Twilight DVM and Nocturnal DVM scenarios, particles ascended and descended between 15 m and 30 m for the Aran grounds and 10 m and 20 m for the WIS to reflect empirical observations of WMD. The percentage of particles within the boundaries of the grounds in which they originated (retention) and straight line distance from initial to final position after 60 days were calculated for each of the three scenarios on each ground.

2.4. Results

Horizontal distribution of larvae

Average densities of Stage I *N. norvegicus* larvae on the Aran grounds were 0.14 ± 0.09 ind. m^{-3} (mean ± SD), with lowest densities observed to the west and northeast boundaries (Figure 2a). Stage I larvae were significantly more abundant than Stage II larvae (0.03 ± 0.03 ind. m^{-3}) on the Aran grounds (Wilcoxon signed rank test, $n_1 = n_2 = 24$, $Z = -4.1$, $p < 0.001$) and maximum Stage II densities were observed to the south of the grounds (Figure 2b). Stage I (0.04 ± 0.02 ind. m^{-3}), II (0.05 ± 0.05 ind. m^{-3}) and III (0.02 ± 0.01 ind. m^{-3}) larvae were observed at each of the three stations on the Galway Bay ground. The presence of Stage III larvae indicated that seasonality was further advanced in this coastal area compared to the nearby Aran grounds.

Densities of Stage I (0.11 ± 0.09 ind. m^{-3}) and II (0.01 ± 0.02 ind. m^{-3}) larvae were also significantly different in the WIS (Wilcoxon signed rank test, $n_1 = n_2 = 24$, $Z = -4.1$, $p < 0.001$). Highest densities of Stage I larvae in the WIS were observed at southern and central parts of the ground with stations on the southeast boundary either lacking larvae or containing very low densities (Figure 2c). Several stations on the southeastern boundary were lacking Stage II larvae and highest densities of this stage were observed to the south (Figure 2d). Densities of Stage I larvae between the WIS and Aran grounds were similar (Mann-Whitney U test, $n_1 = n_2 = 24$, $U = 239$, $p = 0.31$). However, significantly lower densities of Stage II larvae were observed in the WIS compared to the Aran grounds, indicating later seasonality in the WIS (Mann-Whitney U test, $n_1 = n_2 = 24$, $U = 134$, $p < 0.01$).

Drivers of vertical distribution (Aran and WIS grounds)

The optimal (i.e. using AIC) multiple linear regression model explaining larval Stage I *N. norvegicus* WMD contained the following predictor variables: Δ Temperature, average zooplankton biomass, PEA and tidal height (Table 1). The optimal model explained 68% of the variance in larval WMD, with Δ Temperature contributing 40%, average zooplankton biomass contributing 22%, followed by PEA (5%) and finally tidal height (1%; Table 2). Model performance was evaluated using leave-one-out cross

validation, a correlation of observed and predicted values indicated good predictive performance (Spearman rank correlation = 0.78, $p < 0.001$).

There was a highly significant association between Δ Temperature and Stage I larval WMD. Larval WMD appeared shallower when a warmer surface layer was present but WMD was deeper when water was warmer at depth (Table 2; Figure 3a). The significance of this factor was identified due to strong oceanographic differences amongst stations: when a cooler and fresher surface layer was present, as observed at stations on the Aran grounds, larvae were deeper in the water column (Figure 4). However, when temperature was constant through the water column or a warmer surface layer was present, as was seen on the WIS ground, larvae resided closer to the surface (Figure 4).

A significant relationship was observed between average zooplankton biomass (across 5 depth strata) and Stage I larval WMD (Table 2; Figure 3b). Higher zooplankton biomass resulted in larvae inhabiting deeper parts of the water column (Figure 5). By contrast, in the presence of low biomass, larvae appeared closer to the surface. The PEA, an indicator of stratification, explained only 5% variation in WMD, with larvae observed closer to the surface when the water column was more stratified and deeper when it was less stratified (Figure 3c). PEA was lowest to the western and northern areas of the Aran grounds and to the eastern boundary of the WIS ground. Bottom depth was 85 - 115m for stations on the Aran grounds and 68 - 109m on the WIS ground.

Vertical migration of larvae (fixed station)

Fixed station sampling occurred over three consecutive days in the WIS, beginning at 21:00 and samples were collected every three hours thereafter until 18:00 on the third day, resulting in a total of 24 sampling events. Bottom depth at the fixed station was 99m. The vast majority of larvae (94%) resided within the upper 30m of the water column with the highest proportion (45%) observed between 10m and 20m. Larvae were absent from the deepest stratum (>40m) for 50% of sampling events. Stage I larvae were present for each sampling event with average densities of 0.08 ± 0.03 ind. m^{-3} (mean ± SD). Larval densities did not vary significantly from day to night (Mann-Whitney U test, $n_1 = n_2 = 9$, $U = 27$, $p = 0.26$), indicating that catchability remained consistent over the diel cycle. Average Stage I WMD across all three diel cycles was

15.48 ± 4.44m (mean ± SD). Stage II larvae were present in very low numbers at the fixed station (0.002 ± 0.002 ind. m^{-3}).

Larvae consistently ascended and descended through the water column over the diel cycle (Figure 6). The sustained vertical movement of larvae was significantly influenced by time of day (ANOVA, $F_{7, 16} = 4.7$, $p < 0.01$; Figure 6a). Larvae made a significant ascent prior to sunset between 15:30 and 18:30 (Tukey HSD, $p < 0.05$). A descent was observed between 18:30 and 00:30 (Tukey HSD, $p = 0.06$). A second ascent took place before sunrise between 00:30 and 06:30 (Tukey HSD, $p < 0.05$) before another descent after sunrise between 06:30 and 15:30 (Tukey HSD, $p < 0.05$). Larvae were deepest during the day at 12:30 (18.56 ± 2.89m) and 15:30 (20.29 ± 4.29m) and during the night at 00:30 (19.86 ± 3.45m; Figure 6a). In contrast, they were shallowest at sunrise at 06:30 (10.72 ± 3.44m), shortly prior to sunset at 18:30 (11.52 ± 2.55m) and soon after sunset at 21:30 (12.82 ± 2.47m).

Related to time of day, the WMD of larvae was also significantly influenced by light, expressed as down-welling irradiance at 15m ($n = 15$, $p = 0.002$, $R^2 = 0.52$). Larvae were often deepest when irradiance was high, such as at midday (Figure 6b). The midnight descent and subsequent ascent was observed on each of the three nights; however, on the first night it was not as pronounced as the second or third. What was consistent, was the tendency for larval WMD to descend rapidly and return to the same depth again on either side of a 'midnight sink' (this pattern is apparent by comparing near-identical depths at 21.30 and at 03:30 on each of the three nights sampled; Figure 6b).

Implications of DVM for larval transport

Retention was highest for the No DVM scenario and decreased when a Twilight or Nocturnal DVM was introduced. On the Aran grounds, retention was very low, with all three DVM scenarios resulting in <1% larval retention (Table 3). The majority of virtual larvae originating from the Aran grounds were transported north and stayed close to the coast (Figure 7). Dispersal distance was 181.5 ± 102.8 (mean ± SD) for No DVM, 181.2 ± 98.9 for Twilight DVM and 199.5 ± 106.4 km for the Nocturnal DVM scenario. The maximum dispersal distance for all three DVM scenarios on the Aran grounds was over 580 km.

Retention was greater on the WIS ground (Table 3). Again, the No DVM scenario resulted in the highest retention (32.3%) and dispersal distance of 99.8 ± 68.1 km. Retention was reduced by more than half for the Twilight (15.1%) and Nocturnal (15.0%) DVM scenarios. Dispersal distances were 125.0 ± 81.4 km for Twilight and 120.5 ± 80.3 km for Nocturnal DVM behaviours. A large number of virtual larvae were either transported north or a small distance south after release from the WIS ground (Figure 7).

2.5. Discussion

Larval seasonality is one critical element of recruitment success (James et al. 2003, Husebo et al. 2009) and this survey of *N. norvegicus* larvae highlighted substantial differences in larval timing, even across grounds at the same latitude in Ireland. On the Aran grounds, off Ireland's west coast, a high proportion of Stage II larvae indicated that the larval season was underway for some time by the start of April 2018. Stage I larvae were still present in higher densities than Stage II at the Aran grounds, which is likely due to mortality between larval stages (Nichols et al. 1987). On the cooler WIS ground (east coast), the larval season was less advanced with much lower densities of Stage II larvae. The contrast in timing can be explained by a close relationship between temperature and incubation duration (Farmer 1974, Sardà 1995). The variation in larval phenology between grounds was further demonstrated from opportunistic sampling on the Galway Bay ground, where Stage III larvae were observed at each of the three stations, indicating that development was even further advanced in this coastal area off the west coast. Stage I larvae have previously been observed as early as February in Galway Bay with each of the three stages being present in April (de Bhaldraithe 1976).

Sampling larvae from two distinct populations with differing oceanographic regimes on the Aran and WIS grounds allowed the drivers of vertical distribution to be identified. The principal driver of vertical distribution at these spatially-separated stations was a temperature differential through the water column (Δ Temperature) which was expressed as surface temperature minus temperature at 60m (note that this value changes sign, depending on whether it is warmer at the surface or at depth). In the WIS, the water column was mostly homogeneous with a slightly warmer surface layer at

several stations. Meanwhile, many stations on the Aran grounds displayed a fresh cooler surface layer above a more saline warmer bottom layer. Larvae were associated with warmer water, where warmer water was found at depth (i.e. Aran grounds), larvae were deeper and where warmer water was at the surface (i.e. WIS ground), larvae were found shallower (Figure 4). The cool fresh surface layer on the Aran grounds likely originated from the River Shannon, Ireland's largest river, to the south. Huang et al. (1993) described the River Shannon plume as being different to the surrounding coastal water in temperature and salinity as it travels north along the west coast of Ireland. Compared to coastal waters, the plume is cooler in spring and warmer in summer with maximum temperature differences of 1.5 °C. River discharge influences its size and wind affects the direction of the plume (Huang et al. 1993). Overall, these results suggest a preference for warmer water which is a fundamental factor in *N. norvegicus* larval development rates (Thompson & Ayers 1989, Dickey-Collas et al. 1996).

Higher zooplankton biomass resulted in a deeper WMD of Stage I larvae (Figure 3b). Higher densities of zooplankton biomass were observed on the Aran grounds compared to the WIS, reflecting the earlier timing of the spring bloom in the area. The observed tendency to inhabit shallower water when biomass was low may be related to food availability. With insufficient food, larvae may forego the relative safety of deeper water, where protection against visual based predators is enhanced, to spend longer feeding near the surface where food is more abundant. In contrast, when the availability of food is adequate, larvae may occupy deeper waters to avoid predation. *Nephrops norvegicus* larvae consume more prey when food levels are high and will feed for longer if previously starved (Pochelon et al. 2009). Our results suggest that *N. norvegicus* larvae adapt their behaviour as a 'plastic' response to match food availability in their environment. This adaptive response could be of benefit both to larvae hatched before the spring bloom which may be exposed to inadequate feeding conditions as well as those hatched after the bloom with more plentiful food. Indeed, larvae in the WIS were previously observed closer to the surface during the early stages of the spring bloom in April and were deeper later in the season when chlorophyll *a* levels were higher (Lindley et al. 1994). Behavioural changes in response to feeding were also observed in the isopod *Eurydice pulchra* and estuarine crab *Rhithropanopeus harrisi*, whose response to light changes with satiation level (Jones & Naylor 1970, Cronin & Forward 1980).

PEA was used as an index of stratification in the study. The results indicated that larvae were shallower when PEA was high; however, its relative importance was small. PEA increases over the course of the larval season due to surface heating (Simpson et al. 1977). The WIS gyre, which begins to appear in spring with the onset of thermal stratification, has been suggested to aid *N. norvegicus'* larval retention (Hill et al. 1996, Horsburgh et al. 2000, Olbert et al. 2011). Gyral currents are restricted to the upper layers of the water column, therefore larvae in surface waters would be more likely to benefit from the retentive properties of the gyre (Horsburgh et al. 2000). However, in the absence of a known gyre, such as on the Aran grounds, increased current velocities at the surface may lead to a higher probability of transport away from the ground (Fernand et al. 2006, O'Sullivan et al. 2015). A characteristic feature of a highly stratified water column is a thermocline. The cruise took place early in the larval season, when the water column was predominantly mixed. However, in the months that followed, surface heating could be expected to cause greater stratification and, therefore, a steeper thermocline. The current study did not sample later in the season and the potential influence of more intense stratification and a stronger thermocline was not examined. However, our results from earlier in the season suggest that stratification was associated with larvae appearing closer to the surface. Observations when stratification is more intense are needed to further explore this relationship.

Fixed station sampling over the diel cycle revealed a short distance 'twilight' DVM through the water column. Stage I larvae ascended the water column twice daily, prior to both sunrise and sunset, followed by a daytime descent and a rapid 'sink' at midnight. Recall that no significant relationship was observed between larval WMD and time of day at horizontally sampled stations. This may be explained because, at the fixed station, temperature, average zooplankton biomass and PEA remained relatively constant, making it possible to identify the DVM behaviour. However, when greater variation existed in environmental factors between stations, the influence of time of day was not significant (noting also that different times of day within stations were not sampled). It may be that the factors that are significant in horizontal patterns (Δ Temperature, Zooplankton biomass & PEA) govern the vertical distribution from which a DVM is performed.

Larvae of *N. norvegicus* have previously been documented moving closer to the surface at dusk (Hillis 1974, Lindley et al. 1994). But Hillis (1974) also reported a 'vertical dispersion' of larvae at night with increased numbers of larvae appearing deeper in the water column, which may be equivalent to the 'midnight sink' identified in the current study. Anaesthetised Stage I larvae passively sink at a rate of 9mm per second (i.e. 32m per hour; Smith 1987). This sinking rate suggests that in order to descend at the speed observed in the present study, larvae must either sink at a rate that is slowed by active swimming or swim downwards and subsequently stop and maintain their position in the water column.

The 'midnight sink' is a characteristic behaviour in twilight migrators where organisms descend at midnight after the dusk ascent (Cushing 1951). The behaviour has been attributed to satiation, i.e. organisms ascend to the surface to feed and descend at midnight after becoming satiated before a second ascent (Pearre 1973, Simard et al. 1985). Another explanation is the avoidance of vertically migrating predators, which is thought to cause the midnight sink in *Calanus* (avoiding krill; Tarling et al. 2002). Although the vertical migration observed in *N. norvegicus* larvae was relatively short, only ~10m, it is proportionately significant considering 94% of larvae resided within the upper 30m at the fixed station. A vertical migration of this magnitude may be advantageous by increasing exposure to warmer surface waters, leading to faster development, and reducing risks associated with prolonged time in the vulnerable larval phase (Neverman and Wurtsbaugh 1994). Avoiding a long distance DVM that involves moving to cooler depths may also limit associated delays in development.

The vertical migration observed in *N. norvegicus* was closely related to sunrise and sunset, making light, specifically the rapidly changing light levels associated with dawn and dusk, a likely causal factor (Figure 6). Sampling was carried out in mid April when sunrise and sunset times in the Irish Sea were approximately 06:30 and 20:20, respectively. Interestingly, light was also implicated in the observations of a dusk ascent by Hillis (1974) whose observations were in June, when sunset would have occured at least an hour later. *Nephrops norvegicus* adults on the continental shelf also display a crepuscular burrow emergence pattern related to light, with peak emergence at dawn and dusk (Aguzzi et al. 2003). These observations suggest that rapidly changing light

levels are an important cue governing the behaviour of *N. norvegicus* throughout the life cycle.

Finally, larval transport simulations for 2018 indicated that DVM behaviour reduces larval retention. Little difference in retention was observed between the Twilight and Nocturnal DVM scenarios, but retention was lower in both cases compared the No DVM scenario. In the WIS, by remaining fixed at 20m, close to peak gyral flow, larvae may be more likely to become entrained in the gyre and experience its retentive benefits. The upward vertical migrations employed on the WIS ground would have decreased exposure to peak gyral flow and fast flowing near-surface currents increased dispersal away from natal habitat. The presence of a vertical migration has similarly been shown to have a large influence on the transport patterns of European anchovy (Ospina-Alvarez et al. 2012), Northeast Arctic cod (Vikebø et al. 2007) and bicolor damselfish (Paris and Cowen 2004) making it a vital consideration when estimating larval dispersal extent and pathways. Through empirical sampling, the present study has demonstrated that *N. norvegicus* larvae do indeed perform a DVM and larval retention enhancing mechanisms such as the WIS gyre can only partially benefit the retention of larvae since DVM moves them away from optimal gyral flows for part of the 24 hour cycle. Phelps et al. (2015) similarly observed lower retention (and greater dispersal distance) in the WIS when including a DVM component. The results indicate that the observed DVM behaviour in *N. norvegicus* larvae does not improve the likelihood of retention and is, in fact, less favourable for retention, paricularly for the WIS ground.

No gyral retention mechanism has been documented for the Aran grounds, so it is interesting that predicted larval retention rates on the Aran grounds were extremely low (<1%) in each of the DVM scenarios for 2018. At the end of the simulation, many of the virtual larvae had been transported to the northwest coast of Ireland and even further north to Scotland (Figure 7). Survival of *N. norvegicus* is dependent on larvae settling on suitable mud habitat. Therefore, local oceanographic processes provide an important control on recruitment. The fact that all simulations at the Aran grounds resulted in extremely low retention is of significance because of historic fluctuations in adult stock sizes at these grounds (Doyle et al. 2018b). Poor larval retention from unfavourable oceanographic conditions may be a contributing factor, especially as this population may receive few larval imports from other large grounds (O'Sullivan et al. 2015).

O'Sullivan et al. (2015) observed substantially higher larval retention rates of 15.8% for 2011 and 14.4% for 2012 compared to the present study's observations for 2018 (note: in previous simulations no DVM was specified and larvae had a later release and a shorter PLD). However, the vast differences in retention across years suggests that this population may be subject to significant inter-annual variability in larval dispersal. Indeed, inter-annual variability in ocean currents may be more important for retention than other factors such as vertical behaviour (Dickey-Collas et al. 2009; Kvile et al. 2018). This association has obvious implications for fisheries management because variable inter-annual oceanography and a low rate of larval imports from other grounds may be key factors in the decline and fluctuation of stock abundance on the Aran grounds, or other fishing grounds with similar characteristics.

Release date is also an important consideration in larval transport, as larvae released later in the season would be expected to have a shorter PLD due to warmer sea temperatures. Thus, the date of larval release is important in dictating the length of time that larvae spend exposed to local oceanographic conditions, hence their dispersal and likelihood of retention. In the current study, virtual larvae were released in mid March but it would also be interesting to examine the consequences for dispersal of different release times. An extended time series of larval retention estimates which evaluate the role of oceanographic variability and release timing on larval recruitment would be valuable for grounds which have undergone stock fluctuations in the past.

The present study demonstrated that the vertical distribution of *N. norvegicus* larvae was influenced by differential temperature in the water column, average zooplankton biomass and, to a lesser extent, PEA. The findings suggest a complex vertical distribution in *N. norvegicus* that balance the benefits of accelerated development with food availability and potentially predator evasion. Larvae performed a DVM, characterised by a twilight vertical migration with a 'midnight sink'. Larval transport model results indicated that the observed DVM decreases larval retention and the retentive properties of the WIS gyre are less important than previously suggested, due to larvae migrating outside the zone of peak gyral flow for a proportion of the 24 hour period. The results may be applied in further studies to estimate larval transport in *N. norvegicus*, to help predict impacts of low larval retention for fisheries stock

fluctuations as well as impacts from climate-driven changes to oceanography (e.g. Cetina-Heredia et al. 2015).

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2.7. Tables

Table 1. Multiple linear regression model selection process. Response variable: Weighted Mean Depth (WMD) of Stage I *N. norvegicus* larvae. Predictor variables: Δ Temp (temperature at the surface - temperature at 60m), average zooplankton biomass (across 5 depth strata), Potential Energy Anomaly (PEA), tidal height, bottom depth, *N. norvegicus* ground, light (irradiance at 15m), depth of fluorescence maximum, time of day, and WMD of zooplankton biomass. Model 4 (in bold) was selected as the optimal model based on Akaike's Information Criterion (AIC). Δ AIC indicates the change in AIC observed in competing models relative to the optimal model.

Model No.	Structure	AIC	Δ AIC
1	WMD ~ Δ Temp	275.4	9.6
2	WMD ~ Δ Temp + Average Biomass	271.7	5.9
3	WMD ~ Δ Temp + Average Biomass +PEA	266.6	0.8
4	**WMD ~ Δ Temp + Average Biomass + PEA + Tide**	**265.8**	**0.0**
5	WMD ~ Δ Temp + Average Biomass + PEA + Tide + Depth	266.7	0.9
6	WMD ~ Δ Temp + Average Biomass + PEA + Tide + Ground	267.1	1.3
7	WMD ~ Δ Temp + Average Biomass + PEA + Tide + Light	267.3	1.5
8	WMD ~ Δ Temp + Average Biomass + PEA + Tide + Fluor. Depth Max	267.7	1.9
9	WMD ~ Δ Temp + Average Biomass + PEA + Tide + Time of day	267.7	1.9
10	WMD ~ Δ Temp + Average Biomass + PEA + Tide + Biomass WMD	267.7	1.9

Table 2. Multiple linear regression for Weighted Mean Depth (WMD) of Stage I *N. norvegicus* larvae. Predictor variables retained in optimal model: Δ Temperature (temperature at the surface - temperature at 60m), average zooplankton biomass (across 5 depth strata), Potential Energy Anomaly (PEA) and Tidal height, $n = 41$.

Term	Estimate	Standard error	*t* - value	*p* - value	R^2
Intercept	13.64	3.43	3.98	< 0.001	
Δ Temperature	-26.31	4.47	-5.89	< 0.001	0.40
Average Biomass	60.28	17.63	3.42	< 0.01	0.22
PEA	-0.17	0.07	-2.55	< 0.05	0.05
Tide	1.25	0.78	1.61	0.12	0.01
AIC = 265.8				Overall R^2 =	0.68

Table 3. Larval retention (proportion of particles retained on ground) and dispersal distance (average straight-line distance between initial and final particle positions; ± standard deviation) for three Diel Vertical Migration (DVM) behaviour scenarios on the Aran and Western Irish Sea (WIS) grounds obtained from larval transport simulations.

	Aran grounds			**WIS ground**		
	No DVM	**Twilight DVM**	**Nocturnal DVM**	**No DVM**	**Twilight DVM**	**Nocturnal DVM**
Retention (%)	0.9	0.2	0.2	32.3	15.1	15.0
Distance (km)	181.5 ± 102.8	181.2 ± 98.9	199.5 ± 106.4	99.8 ± 68.1	125.0 ± 81.4	120.5 ± 80.3

2.8. Figures

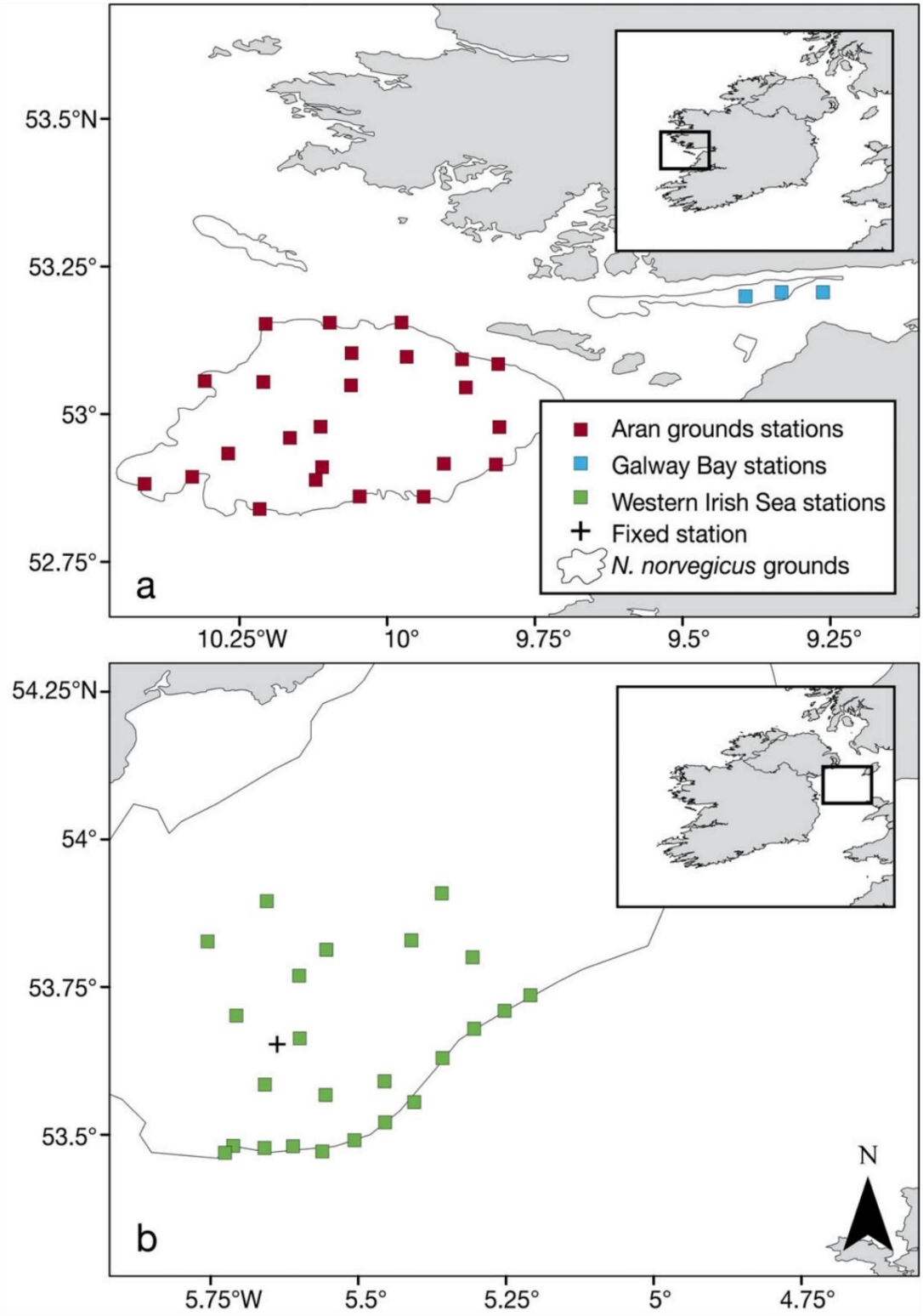

Figure 1. Location of sampling stations on the Aran, Galway Bay (top panel) and western Irish Sea grounds (bottom panel). The outline of *N. norvegicus* mud patches are also indicated.

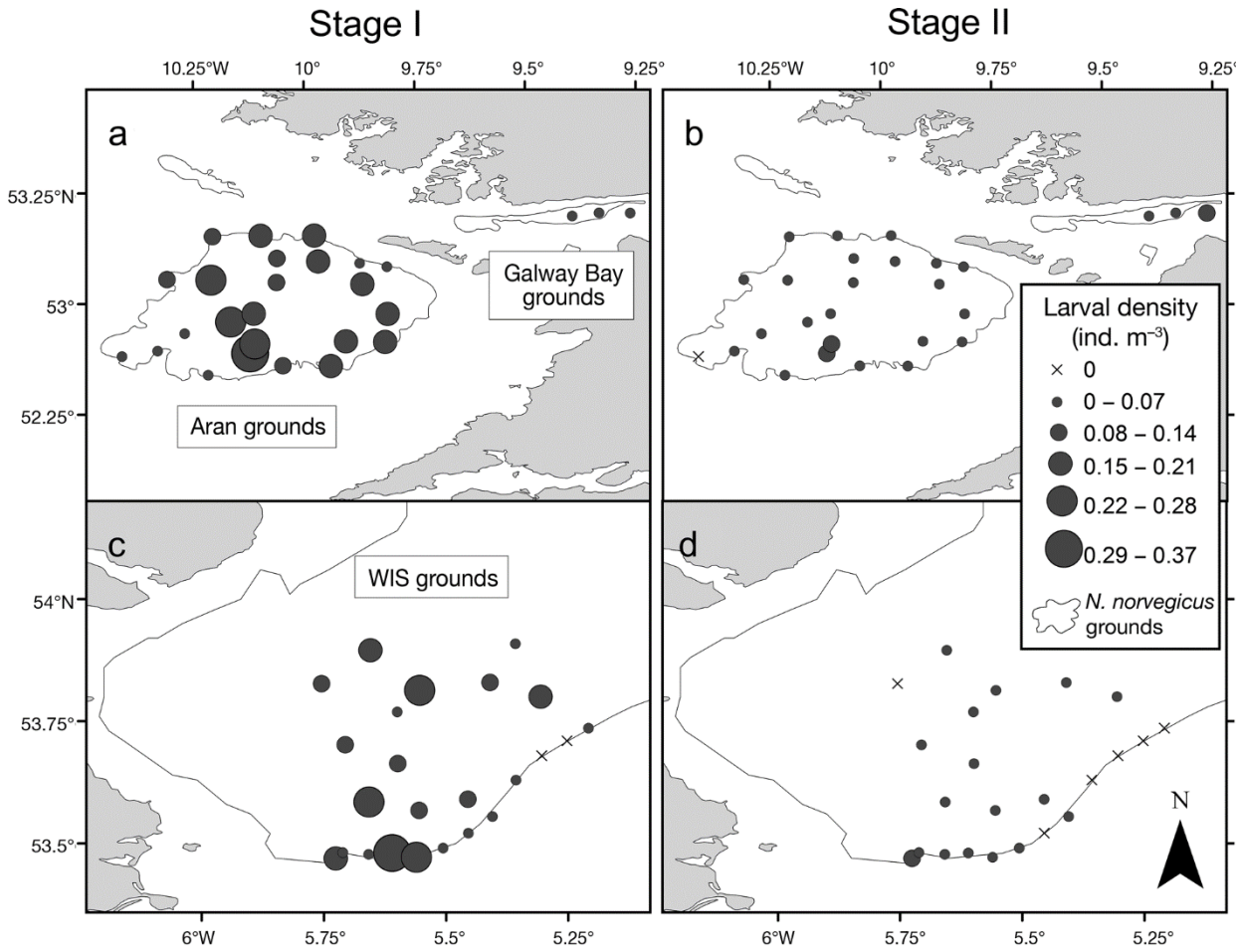

Figure 2. Densities (individuals per m^{-3}) of Stage I and II *N. norvegicus* larvae on the a) & b) Aran and Galway Bay grounds, and c) & d) western Irish Sea ground.

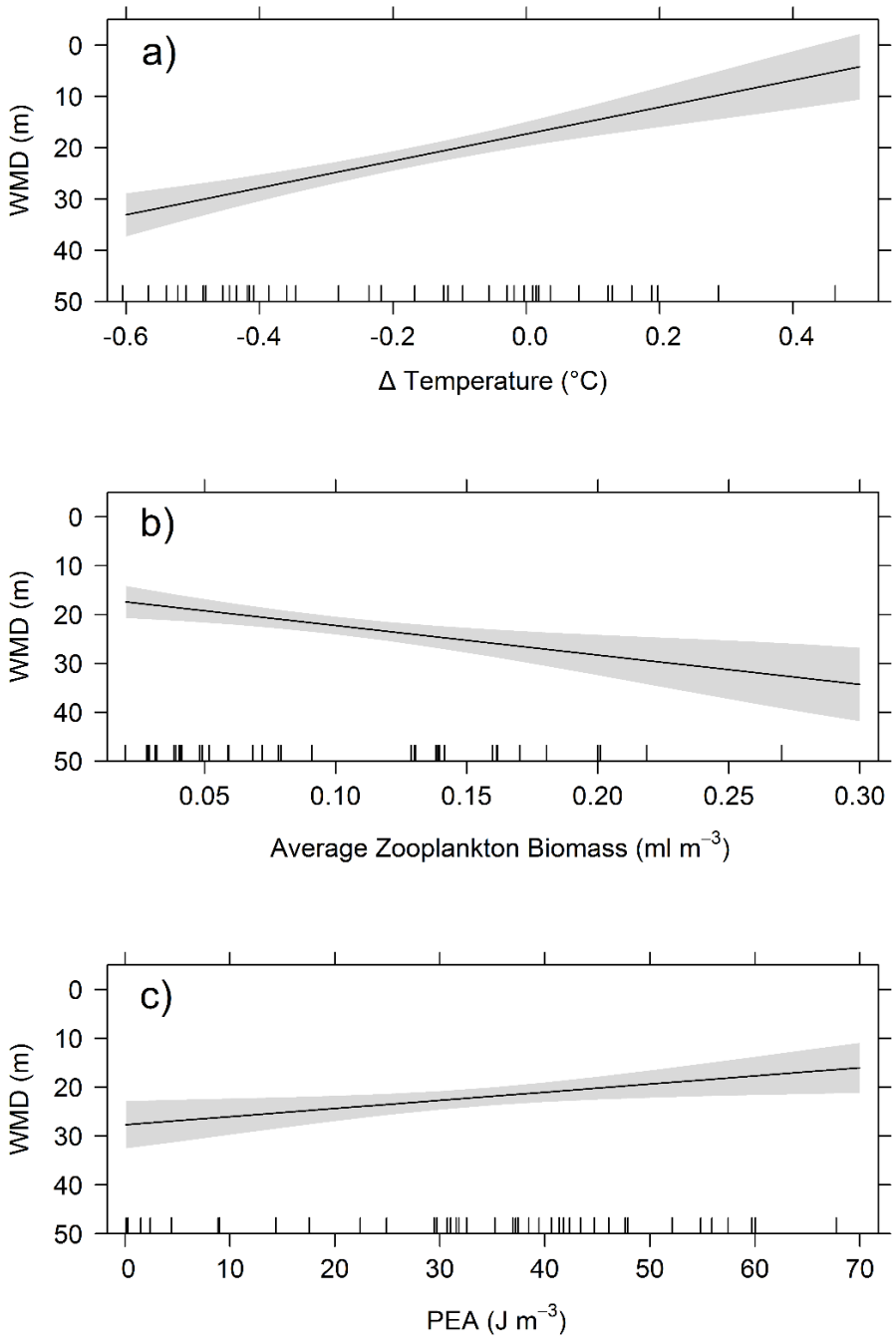

Figure 3. Association between Weighted Mean Depth (WMD) of Stage I *N. norvegicus* larvae and a) Δ Temperature (between surface and 60m; negative values on x-axis indicate a cooler surface layer and positive values represent a warmer surface layer), b) average zooplankton biomass (across 5 depth strata) and c) Potential Energy Anomaly (PEA). Lines and shaded areas indicate significant relationships and 95% confidence intervals from multiple regression analysis. Ticks along x-axis indicate observations for the predictor variable.

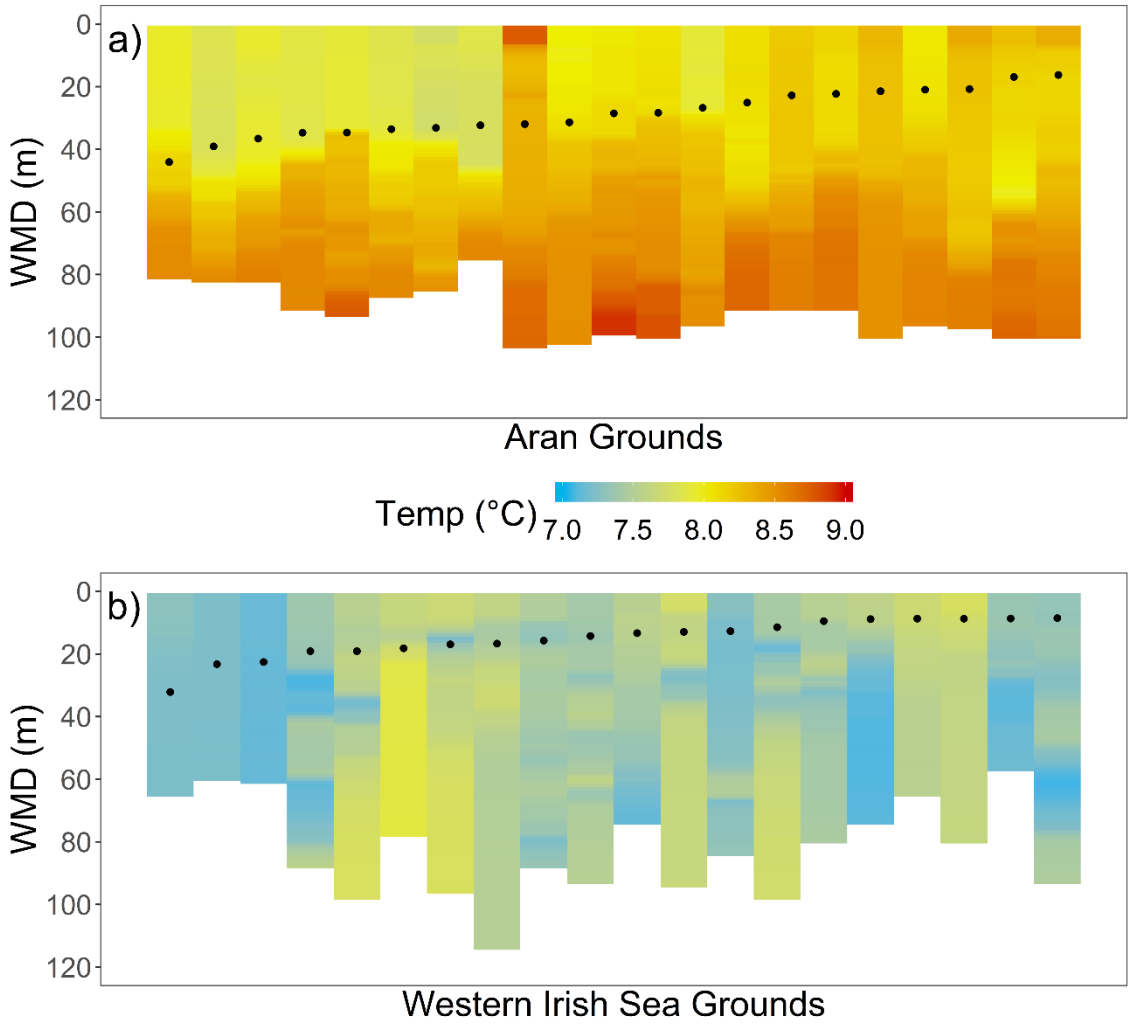

Figure 4. Weighted Mean Depth (WMD) of Stage I *N. norvegicus* larvae (black points), sorted from deepest to shallowest, overlaid on the vertical temperature profile on the a) Aran and b) western Irish Sea grounds. For each station, where data ends on the y-axis indicates bottom depth. Only stations with >10 larvae are included.

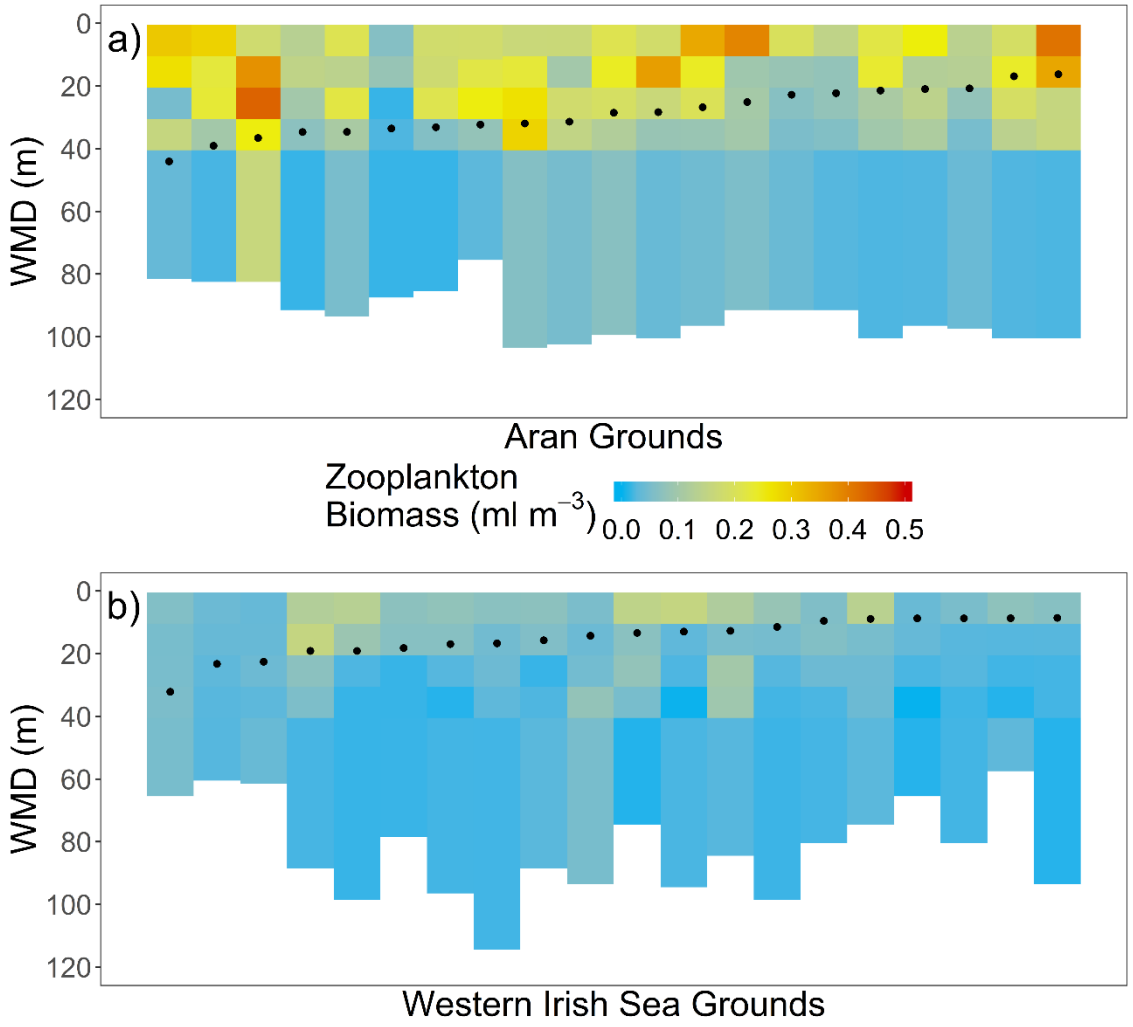

Figure 5. Weighted Mean Depth (WMD) of Stage I *N. norvegicus* larvae (black points), sorted from deepest to shallowest, overlaid on zooplankton biomass at each sampled stratum on the a) Aran and b) western Irish Sea grounds. For each station, where data ends on the y-axis indicates bottom depth. Only stations with >10 larvae are included.

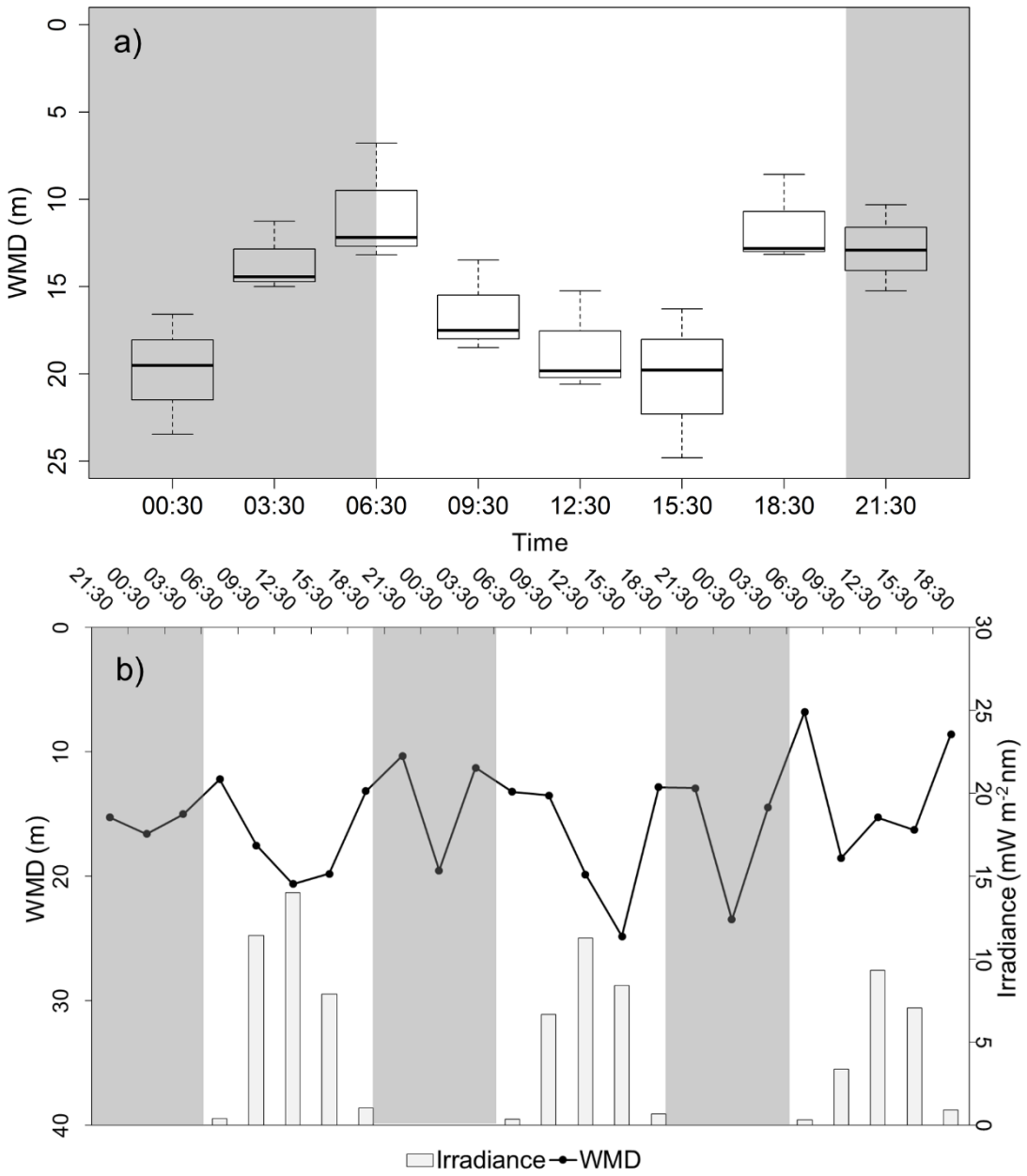

Figure 6. Fixed station Weighted Mean Depth (WMD) of Stage I *N. norvegicus* larvae a) averaged across three days for each sampled time, and b) at each sampling event with irradiance at 15 m indicated by light grey bars. Central lines in boxplots correspond to median depths, box extremities indicate 1st and 3rd quartiles and whiskers specify range. Times represent mid haul and shading indicates sunset to sunrise. Bottom depth at the fixed station was 99 m.

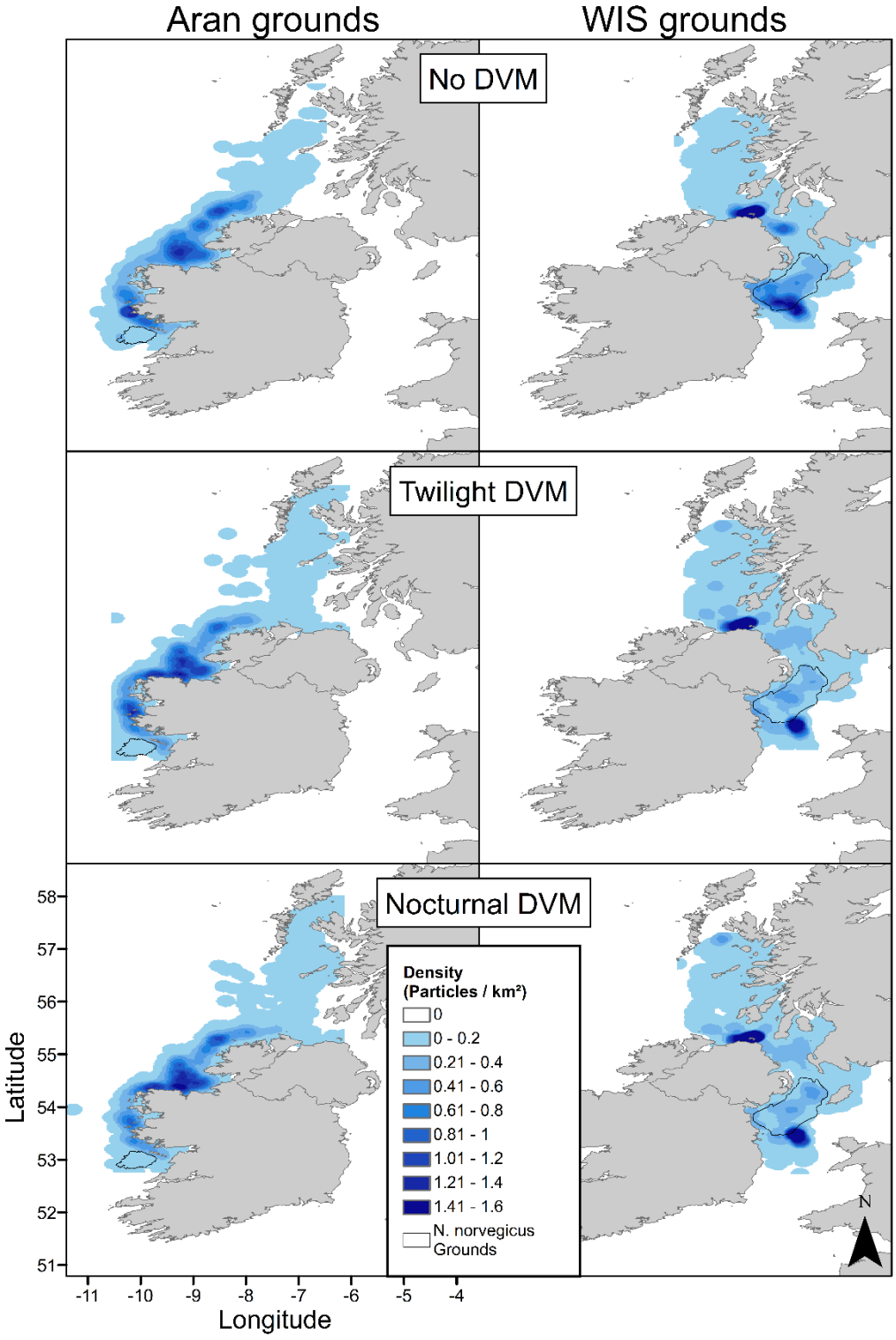

Figure 7. Estimated larval distribution after 60-day simulated transport based on regional oceanographic conditions for the relevant periods in 2018 with three Diel Vertical Migration (DVM) scenarios: No DVM, Twilight DVM and Nocturnal DVM for the Aran grounds and WIS grounds. Beginning of simulation was set at 15th March for the Aran grounds and 1st April for the WIS ground.

Chapter 3

Shift in the Larval Phenology of a Marine Ectotherm Due to Ocean Warming with Consequences for Larval Transport

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Contribution to published paper: Data collation, larval transport modelling, statistical analysis, figure generation and writing manuscript.

3.1. Abstract

Because environmental temperature has an important influence on their developmental rate and physiology, marine ectotherms are vulnerable to phenology changes due to ocean warming. Identifying changes to phenology, the timing of biological events, and understanding their effect on recruitment and abundance is of critical importance to establish potential population effects. We examined the larval phenology of the commercially important Norway lobster (*Nephrops norvegicus*) and used a larval transport model to examine its effect on simulated transport patterns. Using a model to estimate annual larval release dates based on temperature-dependent embryo incubation, an earlier shift of 17.2 days occurred between 1982 - 1995 and 2000 - 2010 in the Irish Sea, similar to an observed empirical shift in phenology of 19.1 days using historical zooplankton datasets. Despite this earlier phenology, temperature-dependent pelagic larval durations were unchanged because the water column to which larvae were released earlier had also warmed. Larval transport simulations in the western Irish Sea (WIS) indicated that the phenology shift had minimal effects on larval retention and dispersal distance overall, because major variations were observed only at very early or late stages of the larval season, i.e. times when lower proportions of larvae were present. As the WIS ground exports small but consistent quantities of larvae to nearby populations, especially off Scotland, it may act as an important source of larvae, especially when retention of native larvae is low. Overall, larval transport tools may indicate grounds that are periodically vulnerable to recruitment failures and offer potentially valuable information in fishery management.

Keywords: Phenology, ocean warming, larvae, Norway lobster, *Nephrops norvegicus*, larval transport, retention, recruitment

3.2. Introduction

Major alterations in phenology, or the seasonal timing of biological events, have been documented in marine, limnological and terrestrial habitats worldwide (Walther et al. 2002; Root et al. 2003; Edwards and Richardson 2004). Global sea temperatures in the upper ocean have warmed by 0.11 °C decade^{-1} between 1971 - 2010 (Rhein et al. 2013), while in the Northeast Atlantic, surface temperatures have undergone an increasing trend of 0.1 - 0.5 °C decade^{-1} from 1983 to 2012 (Dye et al. 2013). Since the physiology of ectotherms is closely coupled to environmental temperature (Wear 1974), variations in sea temperature have been linked to changes in the timing of spawning, larval hatching and migrations of marine species including flatfish, crustaceans and squid in the North Atlantic (Sims et al. 2001; Richards 2012; Fincham et al. 2013).

Identifying altered seasonalities and understanding how variations in phenology affect abundance and recruitment is of critical importance to establish potential negative population effects, particularly to commercially harvested species. For example, in the Wadden Sea, increased winter temperatures influenced the recruitment of the bivalve *Macoma balthica* by lowering reproductive output, while earlier spawning led to a timing mismatch with the phytoplankton bloom and increased predation risk (Philippart et al. 2003). Interestingly, the reverse may also be true: decreasing temperatures were implicated in delayed spawning in Baltic cod in the mid-1990s, coinciding with lower than expected recruitment (Wieland et al. 2000). Despite several examples of phenology shifts in the marine environment (Poloczanska et al. 2013), less is known on how phenology changes can affect recruitment, even in commercially harvested species.

Ocean warming can lead to a contraction of embryo incubation periods and an earlier release of meroplankton larvae. Larval phenology changes can potentially affect mortality and settlement patterns of larvae. A timing mismatch with optimal food levels may result in increased likelihood of starvation (Cushing 1990). Due to seasonal oceanographic features, early- versus late-hatching larvae may be subjected to contrasting conditions that influence transport patterns. In spring-hatching larvae, temperature increases over the larval season so early hatchers encounter relatively cooler temperatures. Therefore, we might expect these to develop slower and take a longer time to settle, potentially increasing dispersal away from suitable habitat and reducing local retention. In contrast, we expect retention to be highest when larvae are

released late in the season, with higher temperatures leading to faster development and earlier settlement. So, does this mean that an earlier shift in larval phenology, e.g. earlier release of larvae into cooler waters, could prolong development and lead to lower retention? To examine this, we also must consider the relative change in temperature at the sea bottom compared to the surface, which determine benthic and pelagic warming impacts, respectively. Bottom temperature affects the timing of larval *release* in certain benthic species due to its influence on embryonic development, while surface temperature affects pelagic *duration* of surface-dwelling planktonic larvae. Hence, the rate at which surface and bottom temperature change relative to one another affects the processes that influence larval retention or loss.

Along with biological factors (hatching time, larval duration and behaviour), transport in the pelagic larval stages is dependent on physical factors such as ocean circulation patterns which will affect recruitment to the adult population (Ospina-Alvarez et al. 2018; Blanco et al. 2019). Considerable inter-annual variability can arise in oceanographic transport patterns (Espinasse et al. 2017). Therefore, we need to understand how important this inter-annual variation is for larval retention within grounds/habitat, or exports of larvae to neighbouring grounds. A spatial influence according to release location may also occur, if the ground where larvae are produced is large, larvae being released from one area may have a higher likelihood of retention than those from another area. Unfortunately, although the pelagic phase is crucial, both for survival of larvae and enabling exchange of larvae between distant populations, larval transport is difficult to observe *in-situ* due to the dispersal of vast numbers of miniscule larvae in very large water bodies. Larval transport models have been developed to address this difficulty and identify the processes that influence retention and connectivity (Metaxas and Saunders 2009).

Larval recruitment in certain crustacean populations is tied to the confines of suitable habitat, which make these ideal cases to examine how changes to larval phenology affect recruitment success via larval retention. *Nephrops norvegicus* is a small lobster and commercially important throughout its range in the Northeast Atlantic Ocean and Mediterranean Sea, with European landings of 44,000 tonnes valued at approximately 360 million EUR in 2016 (EUROSTAT, ec.europa.eu/eurostat/web/fisheries/data/database). The spatial distribution of benthic juvenile and adult *N. norvegicus* is patchy

due to their dependence on suitable muddy sediment to construct burrows. Adults spend much of their time within or close to their burrows, but the larval phase is pelagic. Larvae hatch into the water column after *first* experiencing a period of temperature-dependent embryo incubation during brooding by adult females (Dunthorn 1967; Farmer 1974). Spawning, i.e. extrusion of eggs to the female abdomen, takes place in late summer/early autumn and in the Irish Sea, embryo incubation is 7 - 9 months (Farmer 1974), whereas in warmer regions such as the Mediterranean it is approximately 6 months (Mori et al. 1998). Experiments by Farmer (1974) showed a 50% reduction in embryonic development duration as a result of a 10 °C increase in temperature. In a *second* temperature-dependent process, the planktonic larvae pass through three developmental stages with pelagic larval duration (PLD) lasting between 1 - 2 months at temperatures of 8.5 - 14 °C (Smith 1987; Thompson and Ayers 1989; Dickey-Collas et al. 2000) and larval transport is heavily influenced by local oceanographic conditions (O'Sullivan et al. 2015; Phelps et al. 2015). Larvae inhabit the upper 40 m of the water column and they perform a vertical migration over the diel cycle (McGeady et al. 2019). When larval development is complete, settlement on suitable muddy sediment is essential for survival and recruitment to the population. Subsequent development of the benthic juvenile is influenced by temperature, food availability, sediment type and population density (Bell et al. 2006).

The Irish Sea is a semi-enclosed water body between Ireland and Great Britain, where ocean circulation is mainly driven by tides; however, relatively weak tidal currents in the western Irish Sea (WIS) promote stratification during spring and summer (Simpson 1971). Mud patches in the WIS and eastern Irish Sea (EIS) provide habitat to *N. norvegicus* populations, which are assessed by the International Council for the Exploration of the Seas (ICES) as separate Functional Units (FUs; Ungfors et al. 2013). The WIS population of *N. norvegicus* supports a highly productive fishery with yields of 5000 - 10000 t annually and stock abundance has remained stable over the past 17 years (Lundy et al. 2019). It has high adult densities, although individuals are smaller in size relative to other grounds due to density-dependent growth suppression (Johnson et al. 2013; Merder et al. 2020). Most larvae are present from April - June in the Irish Sea (Nichols et al. 1987). A seasonal near-surface gyre in the WIS was thought to aid recruitment to the population by acting as a retention mechanism (Hill et al. 1996). However, the effectiveness of the gyre in retaining larvae has since been shown to be

significantly reduced because larvae perform a Diel Vertical Migration (DVM), limiting daily exposure to gyral flows (Phelps et al. 2015; McGeady et al. 2019). Due to the potentially large numbers of larvae produced in the WIS each year, the ground may act as an important, but variable (O'Sullivan et al. 2015), source of larval exports to other grounds, and exchange of larvae may be important to sustain the viability of individual patches/populations in the long term (Levins 1970).

In the present study we tested the hypothesis that ocean warming has led to a contraction of the *N. norvegicus* incubation period and resulted in earlier larval phenology (release of larvae) in the Irish Sea. We tested this hypothesis using two complementary approaches. The first used experimental data to create a predictive model of larval release timing and was fed with empirical temperature data. The second examined the timing of the *N. norvegicus* larval season empirically using historical zooplankton datasets. We also tested the hypothesis that a shift in larval phenology affects the transport patterns of pelagic larvae. This hypothesis was tested using a larval transport model to examine the effect of release date on larval retention, dispersal distance (including annual and spatial influences), exports and PLD. A final aim was to identify grounds which are recipients of larvae from the WIS, as these grounds may depend on larval exchange to maintain their populations.

3.3. Materials and Methods

Temperature-dependent larval release date estimation

Two empirical temperature datasets were acquired from the British Oceanographic Data Centre (bodc.ac.uk/data/bodc_database/, accessed 28/06/2019). The datasets were both part of the Isle of Man Long-term Environmental Time Series project, initiated by the University of Liverpool's Port Erin Marine Laboratory and taken over by the Isle of Man Government Laboratory in 2006. The first dataset (Port Erin surface temperature), was used to examine long-term surface temperature trends in the Irish Sea, data were obtained from 1904 - 2010 at the Port Erin Breakwater, Isle of Man (54.08522, -4.76805; Figure 1). From 1904 to 2006, a sample of water was collected from the sea surface twice daily, once in the morning and afternoon, and temperature was recorded using a thermometer. From 2006 - 2010, daily averages were calculated using logged

data taken two hours either side of high water. For the second dataset (Cypris Station bottom temperature), temperature data were available at 5 depths (0, 5, 10, 20, 37 m) from 1954 - 2010 at the Cypris Station (54.09167, -4.83333; Figure 1) approximately 5 km west of Port Erin. Data were collected on a weekly to monthly basis depending on boat availability, season and weather. Temperature data collected from 37 m (sea bottom) were used to examine long-term bottom temperature trends in the Irish Sea. The Cypris Station is situated approximately 6 km from the north eastern edge of the WIS *N. norvegicus* ground, making it a good approximation of bottom temperature on the ground (Figure 1).

To investigate temperature as a predictor of larval phenology, average temperature for the period 15th August, i.e. the approximate start of incubation (Farmer, 1974), until 31st March, i.e. the approximate date that marks the end of incubation/start of larval hatching (Nichols et al. 1987) was used to estimate larval release timing. Incubation duration was estimated by applying temperature data from the Port Erin surface temperature time series to regression parameters (Figure 2) from previous laboratory studies describing the relationship between temperature and embryo incubation (Dunthorn 1967; Farmer 1974). Daily surface temperature data from the Port Erin Breakwater sampling station were used to calculate incubation duration for 1905 - 2010, due to the lack of adequate temporal coverage in the Cypris Station bottom temperature dataset. However, inspection of Cypris Station bottom temperature data indicated that the water column is mostly mixed from September - March meaning little difference (<0.3 °C) between surface and bottom temperatures during the incubation period (Figure 3b,d). For 2011 - 2018, surface temperatures from the Hybrid Coordinate Ocean Model (HYCOM) model from a point source at the Port Erin Breakwater sampling site were used, due to a lack of empirical data and good agreement between HYCOM and Port Erin surface temperature was observed (Figure A1). Therefore, the annual date of temperature-dependent larval release was defined as the estimated embryo incubation duration in days (Figure 2) from August 15th, i.e. warmer incubation temperatures led to an earlier larval release date estimate.

Linear regression was used to examine if a trend existed in the annual timing of larval release, estimated by calculating the temperature-dependent incubation duration for each year using surface temperature at the Port Erin Breakwater sampling location, as

described above. Student's t-test for independent samples was used to test for differences in estimated temperature-dependent larval release dates between earlier (1982 - 1995) and later (2000 - 2010) time series.

Larval phenology

To examine the larval phenology of *N. norvegicus* in the Irish Sea with empirical observations, zooplankton datasets were obtained from the CEFAS data hub (https://www.cefas.co.uk/cefas-data-hub/, accessed 17/04/2017). Data on *N. norvegicus* larvae (Stage I, II and III) were available for 16 years between 1982 and 2010 (Table 1). Due to individual research cruises having distinct objectives, temporal coverage in sampled years did not always overlap. The temporal range for the entire dataset was Day of Year (DOY) 12 - 180 (i.e. January-June). Larval densities were extracted from 5,177 samples collected on 60 research cruises (Figure 1). Samples were considered part of the WIS or EIS, respectively, if collected west or east of -4.5 longitude. Samples were collected from several vessels using a variety of plankton samplers, mesh size was 250 - 270 µm except in 1993, when an 800 µm mesh was used (Table 1). Plankton samplers were fitted with a CTD and flowmeter to record temperature, salinity, depth and water volume filtered. Nets were deployed on a double oblique tow from the surface to within 2 m of the seabed. Hauling speeds were adjusted to ensure equal sampling of all depths. Upon recovery, nets were washed down and samples were preserved in a buffered 4% formaldehyde solution. Samples were transported to the laboratory where *N. norvegicus* larvae were sorted and staged. Larval densities were calculated as abundance m^{-2}, where the number of larvae in each sample was divided by the volume of water filtered and multiplied by the sampled depth.

To examine a potential shift in the timing of larval release, abundances of Stage I, II and III *N. norvegicus* larvae were compared between two *time series*, i.e. earlier (1982 - 1995) and later (2000 - 2010), chosen due to a natural break in sampled years. Within each time series three 20-day *time periods* were examined: DOY 85 - 104, 105 - 124 and 125 - 144. Time periods were chosen as they represented optimum temporal overlap between time series, were similar in duration and ensured that each contained data from at least half of the sampled years in each time series. Inverse distance weighted spatial interpolation was used to visualise the spatio-temporal distribution of larvae using ArcMap GIS 10.2. This approach uses measured values surrounding an unmeasured

location to predict a value, assuming that measured values closest to the predicted location have more influence than those further away. The timing of the seasonal peak of Stage I larval abundance over all three time periods, i.e. from DOY 85 - 144, was also estimated for each time series to quantify the difference in larval phenology. Timing of the seasonal peak (SP) was defined as $SP = \sum fi\ di\ / \sum fi$, where fi is the average larval abundance m^{-2} on each DOY (di) from DOY 85 - 144.

Mann-Whitney *U* tests were used to examine shifts in empirically observed larval phenology from Irish Sea zooplankton samples. Tests were used to compare abundance m^{-2} of *N. norvegicus* larvae between the earlier (1982 - 1995) and later (2000 - 2010) time series for time periods (DOY 85 - 104, 105 - 124, and 125 - 144) within the larval season.

Larval transport

To examine the influence of larval phenology on retention, dispersal distance, exports and PLD of larvae, including annual and spatial influences, a biophysical larval transport model was used. HYCOM (Chassignet et al., 2007) was used to simulate oceanographic conditions during the *N. norvegicus* larval season (when larvae were observed in empirical zooplankton datasets). HYCOM is a hybrid isopycnal coordinate model, i.e. isopycnal in the open stratified ocean, but terrain-following in shallow coastal areas, and has fixed depths in the mixed layer and/or unstratified seas. The model is data assimilative and receives data from satellite observations and *in-situ* temperature and salinity from expendable bathythermographs, Argo floats and moored buoys. HYCOM model output was available at a 3-hourly temporal resolution and $1/12^{th}$ degree spatial resolution between 40 °S and 40 °N and 1/24° poleward of these latitudes.

HYCOM output was coupled with particle-tracking software (Ichthyop v3.3; Lett et al. 2008) to simulate the transport of *N. norvegicus* larvae released from the WIS ground (Figure 1). Simulations were conducted for each of the years that HYCOM output was available, i.e. 25 years from 1994 - 2018. For each simulated year, 5,000 particles were released into the ocean domain every 5 days from DOY 46 - 166 (i.e. 25 release dates), resulting in a total of 3.125 million released particles (125,000 per year). Particles were released from three spatial sections on the ground, i.e. western (-6.20 to -5.58

longitude), centre (-5.58 to -5.26) and eastern (-5.26 to -4.76) zones, to examine spatial influences on larval transport. A DVM was incorporated to model larval behaviour in the water column, where particles made an ascent to 10 m at dusk, a midnight sink to 20 m followed by a subsequent ascent and another descent to 20 m at dawn, following previous empirical observations (McGeady et al. 2019). Simulations were forced using a Runge-Kutta 4^{th} order numerical scheme. Particle positions were calculated every 5 minutes and recorded every 3 hours.

The PLD was estimated using parameters from laboratory studies showing the temperature-dependent developmental rate of *N. norvegicus* pelagic larval stages I-III (Smith 1987; Thompson and Ayers 1989; Dickey-Collas et al. 2000) combined in Dickey-Collas et al. (2000). The temperature experienced by each particle was used to determine its PLD, and when the PLD had elapsed, the particle was considered ready to settle. Settlement positions were used to calculate larval retention (%) on the WIS ground, as well as exports to other nearby grounds. Particles settling outside of suitable habitat were considered 'lost'. In addition, the straight-line distance from initial release location to settlement position was calculated as dispersal distance (km).

To examine the influence of phenology on larval retention and dispersal distance, Generalised Linear Models (GLM) were used. Larval retention (%) and dispersal distance (km) for each release event (25 years x 25 release dates x 3 release zones = 1875 release events) were used as response variables in the respective models. Categorical predictor variables were: year, release day (grouped into categories: DOY 46 - 66, 71 - 91, 96 - 116, 121 - 141 & 146 - 166), release zone on the ground (west, centre & east) and their one-way interactions. Variance Inflation Factors (VIFs) were calculated to check for collinearity between predictors. It was not necessary to remove any of the predictors due to VIFs of <10 (Montgomery et al. 2012). Initially a GLM with larval retention expressed as a proportion as the response variable and a binomial error distribution was used; however, due to overdispersion a quasibinomial distribution was used. Dispersal distance as a response variable was log transformed to attain residual normality and used in a GLM with a Gaussian error distribution. A simple linear regression was also used to examine the effect of release day on PLD.

3.4. Results

Warming temperature trend

Surface temperature at Port Erin Breakwater displayed an increasing annual trend from 1904 - 2010. The maximum annual temperature (11.7 °C) was observed in 2007 and 9 of the 10 warmest years were from 1998 - 2010 (temperature anomalies relative to the 1904 - 2010 average are shown in Figure 3a). Annual temperature was above the 1904 - 2010 average for 14 consecutive years from 1997 - 2010 (Figure 3a). For the time series 2000 - 2010, average annual surface temperature was warmer by 0.8 °C compared to 1982 - 1995 (Figure 3b). June (1.1 °C), May (1.0 °C) and September (1.0 °C) had the largest increases and each month increased by a minimum of 0.6 °C except for December (0.3 °C; Figure 3b). Bottom temperature at the Cypris Station from 1954 to 2010 also showed a warming trend (Figure 3c). Due to gaps in sampling dates, the dataset was split into periods of 5 or 6 years to ensure adequate coverage of each month. A sharp increase occurred in the late 1980s/early 1990s and reached a peak in the early 2000s (Figure 3c). An annual bottom temperature increase of 0.9 °C was observed between the earlier (1982 - 1995) and later (2000 - 2010) time series, with the largest increases of >1.1 °C in the months May, August, September and October (Figure 3d).

Temperature-dependent larval release date estimation

The *estimated* date of larval release, calculated using temperature-dependent incubation rates (Figure 2) and the Port Erin surface temperature times series, showed an increasingly earlier trend over time between 1905 - 2018 (i.e. negative correlation $p < 0.001$, $R^2 = 0.23$) at a rate of 1.5 days decade^{-1} (Figure 4a). This trend was stronger from 1982 - 2010 ($p < 0.001$, $R^2 = 0.56$), when larval release timing showed an earlier trend of 10.1 days decade^{-1} (Figure 4a). Using the same temperature-dependent incubation relationship, a significant difference (Student's t-test, $t = 5.8$, $p < 0.001$) was observed between average larval release dates for 1982 - 1995 (DOY 119.8 ± 2.2, mean ± SE) and 2000 - 2010 (102.6 ± 1.8; Figure 4b), resulting in an estimated difference of 17.2 days. The 17.2 day earlier larval release date was associated with a 0.9 °C increase in temperature during the incubation period.

Larval phenology

In total, 85,654 *N. norvegicus* larvae were observed in 5,177 zooplankton samples collected in the Irish Sea. In the WIS, the earliest date that *N. norvegicus* larvae were observed was 31/01/2006 for Stage I, 21/02/2003 for Stage II and 30/03/2003 for Stage III. In the EIS, larvae first appeared on 26/01/2006 for Stage I, 20/02/2006 for Stage II and 27/03/2006 for Stage III. The temporal distribution of Stage I *N. norvegicus* larvae in the Irish Sea was inspected using an earlier (1982 - 1995) and later (2000 - 2010) time series. A well-distributed spatial coverage of sampling locations across the WIS and EIS ground was available for each time period (Figure 5).

It was evident that high densities appeared earlier in the larval season on both grounds in the 2000 - 2010 time series (Figure 5). This pattern of earlier peak densities in 2000 - 2010 was also apparent for Stage II (Figure A2) and III larvae (Figure A3). Stage I larvae in the WIS for DOY 85 - 104, were more abundant (Mann-Whitney *U* test, n_1 = 238, n_2 = 221, $p < 0.05$) in 2000 - 2010 (4.86 ± 0.70 abundance m^{-2} ± SE) compared to 1982 - 1995 (1.43 ± 0.35 abundance m^{-2}) indicating an earlier release of larvae (Figure 5). Meanwhile, larval abundance for DOY 125 - 144, was significantly higher (Mann-Whitney *U* test, n_1 = 472, n_2 = 120, $p < 0.001$) in the 1982 - 1995 time-series (5.81 ± 0.44) than in the 2000 - 2010 time series (2.14 ± 0.46), indicating that a high proportion of larvae had already progressed to the next stage of development in 2000 - 2010 (Figure 5).

An earlier timing of larval release was also apparent in the EIS as Stage I abundance was higher (Mann-Whitney *U* test, n_1 = 122, n_2 = 348, $p < 0.001$) from 2000 - 2010 (0.47 ± 0.09) than from 1982 - 1995 (0.05 ± 0.02) for DOY 85 - 104 (Figure 5). Larvae also progressed to the next stage earlier as lower densities were observed for DOY 124 - 145 (Mann-Whitney *U* test, n_1 = 132, n_2 = 208, $p < 0.001$) in the later 2000 - 2010 (0.09 ± 0.04) compared to the earlier 1982 - 1995 (0.79 ± 0.28) time series.

The seasonal peak of Stage I larval abundance from empirical observations was estimated as DOY 121.9 for 1982 - 1995 and DOY 102.8 for 2000 - 2010. Therefore, the seasonal peak of Stage I *N. norvegicus* larval abundance was 19.1 days earlier in the later time series. This empirical observation closely matched the difference in estimated

temperature-dependent larval release date between the two time series (17.2 days - see above).

Larval transport

Simulations were completed for 25 years in the WIS between 1994 and 2018 with virtual larvae released from three zones on 25 dates spaced 5 days apart from DOY 46 (15th February) to DOY 166 (15th June). Larval retention and dispersal distance was significantly influenced by release year, day, spatial zone and their one-way interactions ($p < 0.001$ in each case, Table 2). Average annual larval retention was 24.2% and fell below 20% only in 2002 (14.2%), 2014 (17.7%), 2016 (15.8%) and 2018 (17.7%; Figure 6a). Year explained 14.7% and 18.8% of deviance in retention and dispersal distance respectively, indicating that inter-annual variability is an important factor (Table 2). A sustained period of high retention (>27%) occurred from 2005 - 2009 and reached a maximum of 31.9% in 2006. However, a gradual decline was observed from 2009 - 2012, although high year-on-year variation was also apparent (2013 - 2018), showing a pattern of high retention followed by low retention until the end of the time series (Figure 6a).

The day of release ($p < 0.001$) explained 12.8% deviance in both retention and dispersal distance (Table 2). Retention was lowest (17.4%) when larvae were released early in the year between DOY 46 - 66 (15th February - 7th March) and increased substantially when released late in the year (32.0%) between DOY 146 - 166 (26th May - 15th June; Figure 6b). Although a trend was observed with gradually higher larval retention as the season progressed, little difference (<3.5%) was observed between DOY 71 - 141 (12th March - 21st May).

Spatial zone of release also affected retention and dispersal distance respectively by 5.4% and 8.9% ($p < 0.001$; Table 2), i.e. retention decreased, and dispersal distance increased when larvae were released from the east of the ground. Releases from the west had 28.5% retention, on average, but decreased to 23.4% in the centre zone and further reduced to 20.8% to the east (Figure 6c). The interaction between year and day of release explained the most deviance in retention and dispersal distance (27.3% and 32.1% respectively), indicating that inter-annual and intra-seasonal variation are very important factors in larval transport (Table 2; Figure 6d). In most years, retention

improved with a later release (Figure 6d), 15 of 25 years had the highest retention in the latest release period, DOY 146 - 166. By contrast, lowest retention was observed in the early season (DOY 46 - 66) for 13 of 25 simulated years.

The interaction between year and zone also had a significant influence on retention ($p < 0.001$) and dispersal distance ($p < 0.001$; Table 2). Larvae released from the western zone had the highest retention for 21/25 years and only had the lowest retention in 2001, 2010 and 2014; in these years, the eastern zone had highest retention. Release day and zone interaction explained only 1.4% deviance in retention and 0.4% in dispersal distance ($p < 0.001$; Table 2). The difference in retention between western and eastern releases was greatest for the earliest release dates (DOY 46 - 66, 8.7%) in comparison to the latest releases (DOY 146 - 166, 4.6%).

Temperature-dependent PLDs varied from 32 days at 13.6 °C to 78 days at 7.4 °C. Release day had a significant negative effect on PLD ($p < 0.001$, $R^2 = 0.87$; Figure A4) due to heating surface waters as the larval season progressed. Early releases (DOY 46 - 66) had an average duration of 69.9 days and PLDs reduced as larvae were released later in the season: DOY 71 - 91 (65.6 days), 96 - 116 (56.8 days), 121 - 141 (47.7 days) and 146 - 166 (39.4 days).

Exports from WIS

The WIS ground exported larvae to several nearby grounds to the north, east and south (Figure 7a). The Minch grounds received the highest average exports (2.0%) followed by the Clyde & Jura (0.8%), EIS (0.3%), Celtic Sea (0.2%) and Stanton grounds (0.1%; Figure 7). Exports were subject to large inter-annual variability with the Minch grounds receiving the highest exports in 1996, 2002 and 2018, yet receiving no exports in 2004 and 2007 (Figure 7b). An earlier release date was associated with higher exports, maximum exports to the EIS, Minch and Celtic Sea grounds occurred between DOY 46 - 91 (Figure 7c). Larvae released to the east or centre of the ground also had a higher likelihood of export to the Clyde & Jura, EIS, Minch and Stanton grounds, while those originating from the western zone were less likely to be exported (Figure 7d).

With an overall average of 3.4% of larvae exported and 24.2% retained, the majority of larvae failed to settle on suitable habitat and were ‘lost’ (72.4%). Due to high retention,

the proportion of 'lost' larvae was lowest late in the season, DOY 146 - 166 (66.9%) compared to early, DOY 46 - 66 (77.1%). This means that more larvae were lost early-on, when retention was lower and exports to other grounds were at their highest (Figure 7c).

3.5. Discussion

The results of the present study showed a marked shift in the larval phenology of *N. norvegicus* in the Irish Sea and linked this to temperature. Experimental data were used to create a predictive model of larval release timing using temperature data from Port Erin which agreed well with empirically observed shifts in larval phenology from historical datasets in the Irish Sea. Larval transport simulations indicated that larvae released very early in the season had lower retention compared to later releases; however, limited change in retention was apparent between larval phenology shift dates. Instead, large inter-annual variability in hydrography-forced larval transport was apparent, which can result in strong changes to retention of larvae within the ground, and can alter exports from the high-density WIS population to neighbouring grounds.

Temperature was considered a major contender as a causal factor in the larval phenology shift due to its importance in embryonic development (Dunthorn 1967; Farmer 1974). Our predictive model of larval release date based on temperature-dependent incubation rates predicted a 17.2 day earlier shift between 1982 - 1995 (DOY 119.8 ± 2.2) and 2000 - 2010 (DOY 102.6 ± 1.8) due to a 0.9 °C increase in temperature. This was very close to the empirical observation from historical larval datasets of a 19.1 day shift in the seasonal peak of Stage I larval abundance between 1982 - 1995 (DOY 121.9) and 2000 - 2010 (DOY 102.8), and provides support for the hypothesis that temperature is the causal mechanism. This phenology shift was observed in all three developmental stages and in both the WIS and EIS (Figure 5, A2, A3). The empirical larval phenology shift coincided with a bottom temperature increase of 0.9 °C at the Cypris Station between time series (1982 - 1995 and 2000 - 2010); with the largest temperature increases (>1.1 °C) occurring in August, September and October, i.e. at the early stages of embryo incubation (Figure 3d). Eiríksson (2014) observed an increased ratio of post-hatching: pre-hatching ovigerous *N. norvegicus*

females in May from the 1970 - 1990s to the 2000s, suggesting that the larval hatching season has also advanced in Icelandic waters. Earlier phenology due to temperature has similarly been recorded in other marine systems, for example, earlier timing of the biomass maximum of copepods in the North Pacific Ocean (Mackas et al. 1998) and the hatch timing of northern shrimp in the Northwest Atlantic Ocean (Richards 2012). However, far less is understood how ocean warming-driven phenology shifts affect recruitment dynamics.

Bottom temperature has increased decadally in the Irish Sea (Figure 3c-d) and brought larval release dates earlier (Figures 4, 5). This raises the question of whether temperature-dependent PLDs and transport patterns have also been altered? The surface temperature minimum occurs in February/March in the Irish Sea, after which time, temperature increases (Figure 3b). If pelagic larvae are released earlier (due to a contraction of the incubation period as a result of increased bottom temperatures) when surface temperatures are cooler, then PLDs may be extended as development is slowed at lower temperatures, potentially resulting in increased dispersal and lower larval retention. Despite this expectation, the Port Erin surface temperature time series showed that temperatures on the empirical larval phenology shift dates, i.e. DOY 121.9 (1982 - 1995) and DOY 102.8 (2000 - 2010) is relatively unchanged. Average surface temperature from Port Erin for the 1982 - 1995 time series was 8.49 °C at DOY 122 and 7.75 °C at DOY 103, for the 2000 - 2010 time series it was 9.63 °C at DOY 122 and 8.6 °C at DOY 103. Therefore, despite an earlier larval release, larvae would have experienced similar temperatures at the time of hatching, likely resulting in an unaltered larval duration. Regardless, in future, larvae may increasingly hatch when temperatures are at their lowest. The annual minima for surface and depth-averaged temperatures in the Irish Sea in February/March are projected to get later by 12 days from 1980 - 2100 (Olbert et al. 2012). Such a scenario could see increased overlap between a later-shifting annual temperature minima and an earlier-shifting larval season, with larvae increasingly hatching when surface temperatures are at their lowest, potentially prolonging development and increasing losses of larvae. The Irish Sea is forecasted to increase in surface and depth-averaged temperature by 1.89 °C and 1.79 °C respectively from the 1980s - 2090s, with higher increases projected for autumn and winter (embryo incubation) than for spring (larval season; Olbert et al. 2012).

As HYCOM model availability was restricted to 1994 - 2018, it was not possible to simulate larval transport for the time series 1982 - 1995 and directly compare it to 2000 - 2010, when the earlier larval phenology occurred. Instead, we simulated the effect of larval timing across all available years (1994 - 2018, Figure 6d) to examine a general effect of release date on larval transport. Differences in retention were greatest at opposite ends of the larval season and more subtle in the intervening periods. For example, an extremely late larval release (DOY 146 - 166) resulted in 14.6% higher retention, 51.6 km lower dispersal distance, and 30.4 day shorter PLD than an extremely early release (DOY 46 - 66; Figure 6b). Extreme early hatchers such as larvae observed on January 31st 2006 in empirical data, would have a lower likelihood of retention and higher dispersal potential than late-hatching larvae (Figure 6b). Thus, larvae released on the fringes of the larval season, be it the first or last hatchers, would be most affected by a phenology shift. Nevertheless, the significance of this is reduced since the relative abundance of larvae in 'fringe' periods is low. We can examine what the effect on the majority of larvae would be by applying the 19.1 day earlier shift, i.e. from DOY 121.9 to DOY 102.8, which results in limited changes to retention and dispersal distance from larval transport simulations in the WIS. Thus, this study found that the empirical shift in phenology did not result in reduced larval retention.

More significant for the future may be the fact that larval retention was subject to a high degree of inter-annual variability, particularly towards the end of the time series (Figure 6d). Although average retention (24.2%) in the WIS was generally high across the time series (Figure 6a), this is not the case on all grounds (O'Sullivan et al. 2015). The enclosed nature of the Irish Sea and relatively weak currents, particularly near the coast, proved conducive to retention. In the WIS, vast quantities of larvae produced from a large population coupled with high retention may contribute to the stable and high density adult stock observed in underwater television (UWTV) surveys (Lundy et al. 2019). In contrast, on isolated grounds with low densities and less potential for larval imports, inter-annual variability may have a significant effect on recruitment. For example, the relatively isolated Aran grounds off the west coast of Ireland has undergone stock fluctuations in recent years, with a decreasing density trend, and low modelled retention levels may render it vulnerable to periods of low recruitment (McGeady et al. 2019). Inter-annual variability has also been recognised as an important

contributor to the transport patterns and ultimately recruitment of ichthyoplankton larvae (Ospina-Alvarez et al. 2015; Kvile et al. 2018).

Retention was highest for releases from the west of the WIS ground and lowest to the east. Currents were weak in coastal areas to the west, resulting in short dispersal distances and enhanced retention. Releases to the east, particularly for earlier releases of larvae, were prone to advection through the North Channel by strong northward currents resulting in transport to grounds off the west of Scotland (Figure 7). For this reason, the spatial distribution of spawning females, which determines the 'zonation' of larval release densities on the ground, is another factor affecting larval transport patterns. Adult densities are not uniform across the ground and the 2019 UWTV survey indicated that highest burrow densities are to the east; however, spatial distribution is subject to inter-annual variation (Lundy et al. 2019). Additionally, a spatial gradient of 1.3 °C in bottom temperature was observed across the ground during the incubation period: lowest temperatures occurred in deeper channels to the centre, potentially resulting in prolonged incubation and later larval releases, while higher bottom temperatures near the coasts of Ireland and the Isle of Man, could lead to an earlier release. Overall, if most spawning females are near the coasts where temperatures are higher, the majority of larvae would be released earlier. This temperature gradient is projected to become stronger in the future as coastal areas warm faster than deeper channels of the Irish Sea (Olbert et al. 2012). In theory, fishing pressure could indirectly affect the timing of larval release by altering the distribution of females on the ground. For example, if fishing pressure was focused near the coast, resulting in diminished densities and proportionally higher densities to the centre, where incubation temperatures are lower, a shift in the timing of larval release from earlier to later, and spatially from coastal to central zones, could occur. In order to promote a long larval release that protects against poor retentive conditions in the short term, a harvesting strategy that promotes a spread of female *N. norvegicus* across the temperature gradient of the ground may be beneficial.

In terms of oceanography, the most favourable conditions for larval retention were low current velocities and high temperatures which led to shorter PLDs. In scenarios with high current velocities, larvae could potentially be transported great distances in a short length of time. Therefore, despite shorter PLDs associated with a later release,

unfavourable oceanography led to larvae being transported away from suitable habitat. No consistent seasonal differences were observed in current speeds as a high degree of inter-annual variability was evident and instances of poor retention were recorded both early (2017) and late (2012) in the season (Figure 6d). Circulation patterns in the Irish Sea are projected to change in the future, stronger southward currents and a strengthening of the WIS gyre as a result of sharpened stratification (Olbert et al. 2012) may result in increased southward transport of larvae.

Empirical observations of larvae beyond the boundaries of the WIS ground (Figure 5) demonstrated the clear potential for larvae to be transported to other grounds. Simulations showed a significant number of larval exports to large grounds off the west coast of Scotland, particularly the Minch grounds, even though this was not the most adjacent area. The EIS and Celtic Sea grounds also received small but consistent exports (Figure 7). Exports were highest early in the season, and larvae released from the east of the ground were more likely to be exported to northern grounds due to their proximity to the North Channel, where strong northward currents often persisted. Due to its high-density biomass and large spatial extent, the number of reproducing females on the WIS ground is vast. Therefore, larvae originating on the ground being exported elsewhere could be very important to the annual larval supply and recruitment levels of other grounds, particularly if retention is poor. The relatively high level of inter-ground connectivity may be the reason that *N. norvegicus* in the Atlantic Ocean exhibit low levels of genetic differentiation, reflecting this species capacity for gene-flow (Maltagliati et al. 1998; Stamatis et al. 2004). Some genetic differences have been detected between Atlantic and Mediterranean populations, however (Gallagher et al. 2019).

Although a first estimation, larval retention may be a good proxy for estimating recruitment in *N. norvegicus* and other species. Other ways of measuring recruitment are problematic: burrows of juveniles are not easily quantified in UWTV surveys due to tendencies to share burrows with adults (Tuck et al. 1994), length-frequency distributions on research surveys or in fishery catches tend to be rather uni-modal and hence difficult to separate into year-classes (Farmer 1973), and as of yet, there is no reliable ageing method (Sheridan et al. 2016). Since successful recruitment depends on larvae settling on suitable habitat, hydrography plays a particularly important role due to

this species potential for larval transport beyond the boundary of mud habitat which is critical for survival (Bell et al. 2006). In the absence of other data, estimating retention and receipt of larvae from other grounds by modelling larval transport could provide an index of recruitment. Indeed, a strong recruitment relationship was demonstrated in other systems, e.g. between modelled anchovy larvae reaching a nursery area and densities of age-0 individuals from acoustic surveys in the Mediterranean Sea (Ospina-Alvarez et al. 2015). Further improvements to the *N. norvegicus* larval retention index may include: applying a release schedule that accurately reflects the timing of peak larval release, using the spatial distribution of adults across the ground to determine the initial distribution of hatching larvae and estimating larval mortality before settlement. While potentially useful as an index, natural mortality due to parasites, predation or starvation etc. (Farmer 1975; Cushing 1990) could also be significant before juveniles recruit to the fishery. However, larval retention models could potentially be used as an early warning signal of low recruitment due to spells of poor retention and/or low larval imports. Early identification of poor recruitment could be accounted for in the management process of commercial species by reducing fishing mortality early-on, particularly in cases lacking alternative sources of recruitment data.

The observed phenology shift in the Irish Sea has relevance for *N. norvegicus* populations across its range which may have also been subjected to similar changes to phenology. Modelled larval retention may be useful as a proxy for recruitment in *N. norvegicus* and other species with a strong requirement for suitable habitat to survive. Such a retention/recruitment index could be highly beneficial in fisheries management and future work should examine whether modelled larval retention is linked to stock size estimates.

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3.7. Tables

Table 1. Summary of zooplankton datasets used to examine the distribution of *N. norvegicus* larvae in the Irish Sea.

Year	No. sampled days	Temporal range	Cruises	Samples	No. larvae	Gear	Mesh size (µm)
1982	31	98 - 155	3	337	14,552	Lowestoft high speed sampler (76 cm diameter)	270
1985	27	104 - 156	3	334	19,919	Lowestoft high speed sampler (76 cm diameter)	270
1987	8	133 - 143	1	79	2,530	Lowestoft high speed sampler (76 cm diameter)	270
1988	16	92 - 122	1	162	8,541	Lowestoft high speed sampler (76 cm diameter)	270
1989	13	105 - 117	1	89	1,612	High speed towed net (76 cm diameter)	250
1992	3	119 - 123	1	10	695	Lowestoft high speed sampler (76 cm diameter)	270
1993	14	127 - 149	1	107	4,888	Ring net (2 m diameter)	800
1994	3	118 - 122	1	14	163	High speed towed net (53 cm diameter)	250
1995	87	41 - 164	12	1,128	12,164	Gulf III plankton sampler (40 cm diameter)	270
2000	64	22 - 141	8	803	5,430	Gulf III plankton sampler (40 cm diameter)	270
2001	44	28 - 173	3	165	78	Gulf VII plankton sampler (20 cm diameter)	270
2002	35	49 - 176	5	254	177	Gulf VII plankton sampler (20 cm diameter)	270
2003	53	12 - 180	5	413	309	Gulf VII plankton sampler (20 cm diameter)	270
2006	27	26 - 110	5	258	4,463	Gulf VII plankton sampler (20 cm diameter)	270
2008	44	27 - 112	5	494	3,596	Gulf VII plankton sampler (20 cm diameter)	270
2010	41	19 - 110	5	530	6,537	Gulf VII plankton sampler (20 cm diameter)	270

Table 2. Analysis of deviance for Generalised Linear Model (GLM) examining the associations between the response variables: larval retention (%) and log dispersal distance (km) and the predictor variables: release year, day and zone from larval transport simulations on the western Irish Sea ground.

	SS	**df**	**MS**	***F*-value**	***p*-value**	**Deviance explained (%)**
Response: Retention (%)						
Year	46656	24	1944	32.5	<0.001	14.7
Release day	40671	4	10168	170.0	<0.001	12.8
Zone	17055	2	8528	142.6	<0.001	5.4
Release day x Year	86542	96	901	15.1	<0.001	27.3
Year x Zone	20227	48	421	7.0	<0.001	6.4
Release day x Zone	4278	8	535	8.9	<0.001	1.4
Residuals	101209	1692				
n = 1875						
Total deviance explained = 68.0%						
Response: Log dispersal distance (km)						
Year	63.5	24	2.6	54.6	<0.001	18.8
Release day	43.3	4	10.8	223.3	<0.001	12.8
Zone	30.1	2	15.1	311.1	<0.001	8.9
Release day x Year	108.5	96	1.1	23.3	<0.001	32.1
Year x Zone	9.3	48	0.2	4.0	<0.001	2.8
Release day x Zone	1.3	8	0.2	3.4	<0.001	0.4
Residuals	81.9	1692				
n = 1875						
Total deviance explained = 75.8%						

Abbreviations: SS - sum of squares; df - degrees of freedom; MS - mean sum of squares.

3.8. Figures

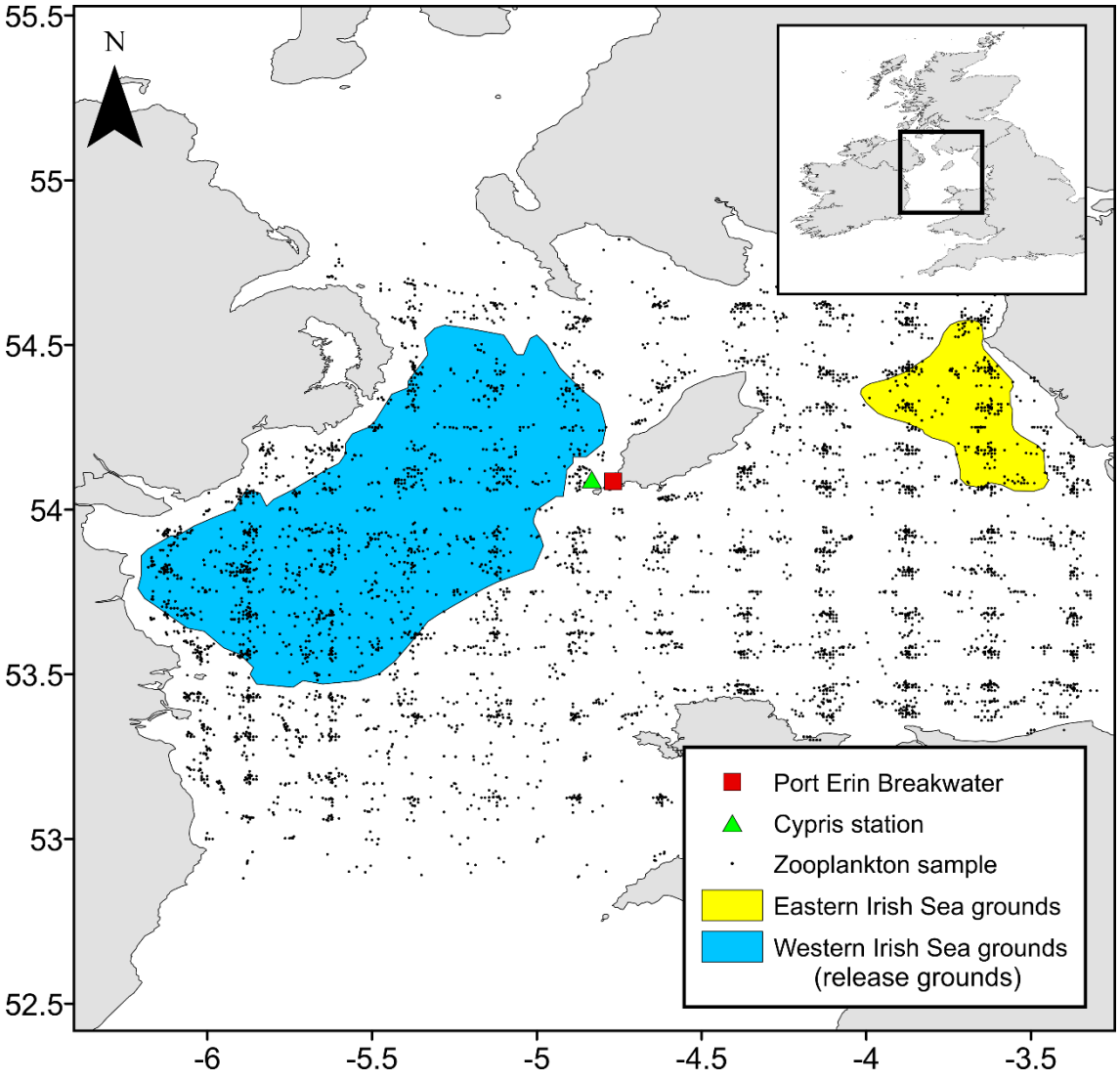

Figure 1. Map indicating the study area. Temperature time series at the sea surface were taken from the Port Erin Breakwater (Port Erin surface temperature, red square) and sea bottom were taken from the Cypris Station (Cypris Station bottom temperature, green triangle). Zooplankton samples are represented by black markers. Particles in larval transport simulations were released from the western Irish Sea *N. norvegicus* ground (blue). The eastern Irish Sea ground is also represented (yellow).

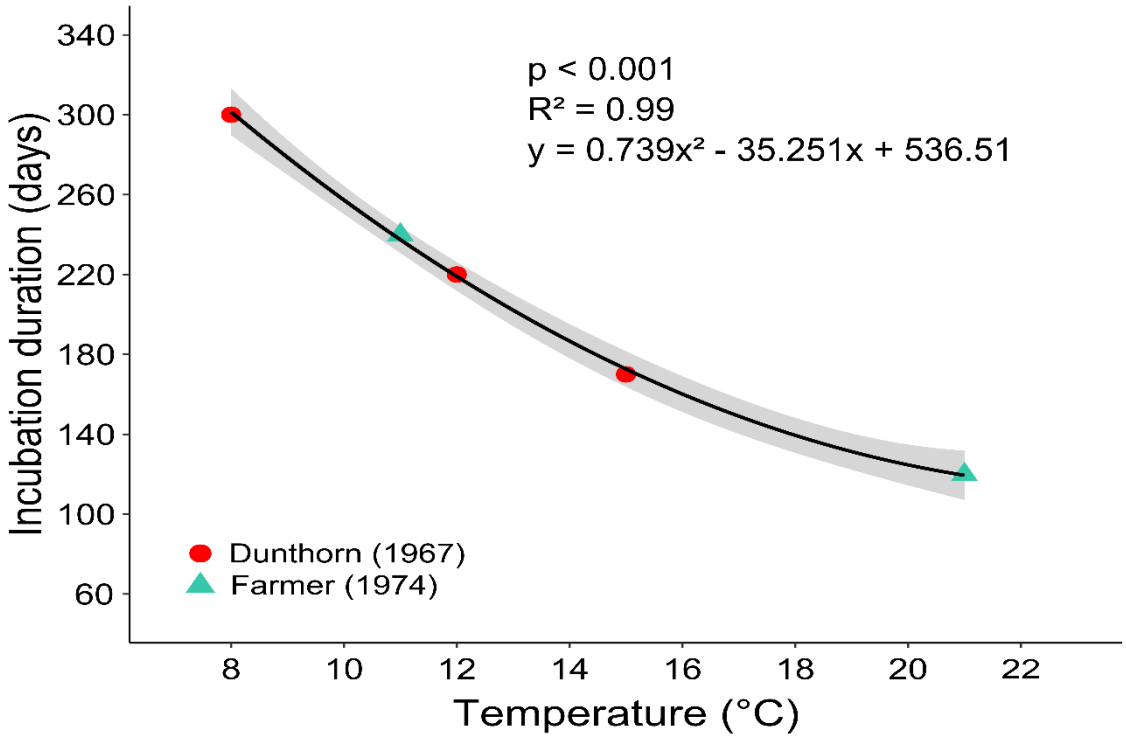

Figure 2. Association between temperature and embryo incubation duration from previous experimental studies, line fitted using polynomial regression.

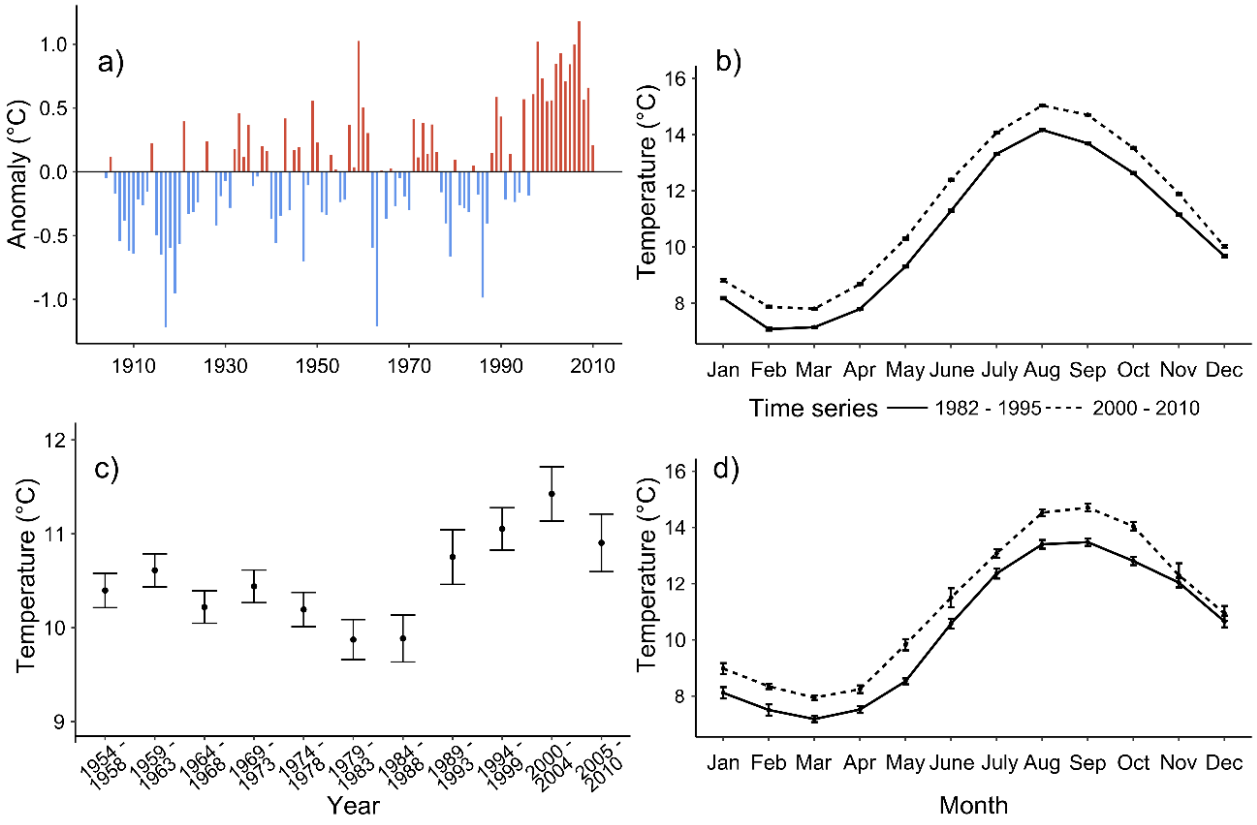

Figure 3. Sea surface a) annual temperature anomaly compared to 1904 - 2010 average and b) comparison of average monthly temperature between the time series 1982 - 1995 and 2000 - 2010 at the Port Erin Breakwater sampling site. Sea bottom (at 37 m) c) average multi-annual temperature and d) comparison of average monthly temperature between the time series 1982 - 1995 and 2000 - 2010 at the Cypris Station, located approximately 5 km west of Port Erin. Error bars represent standard error.

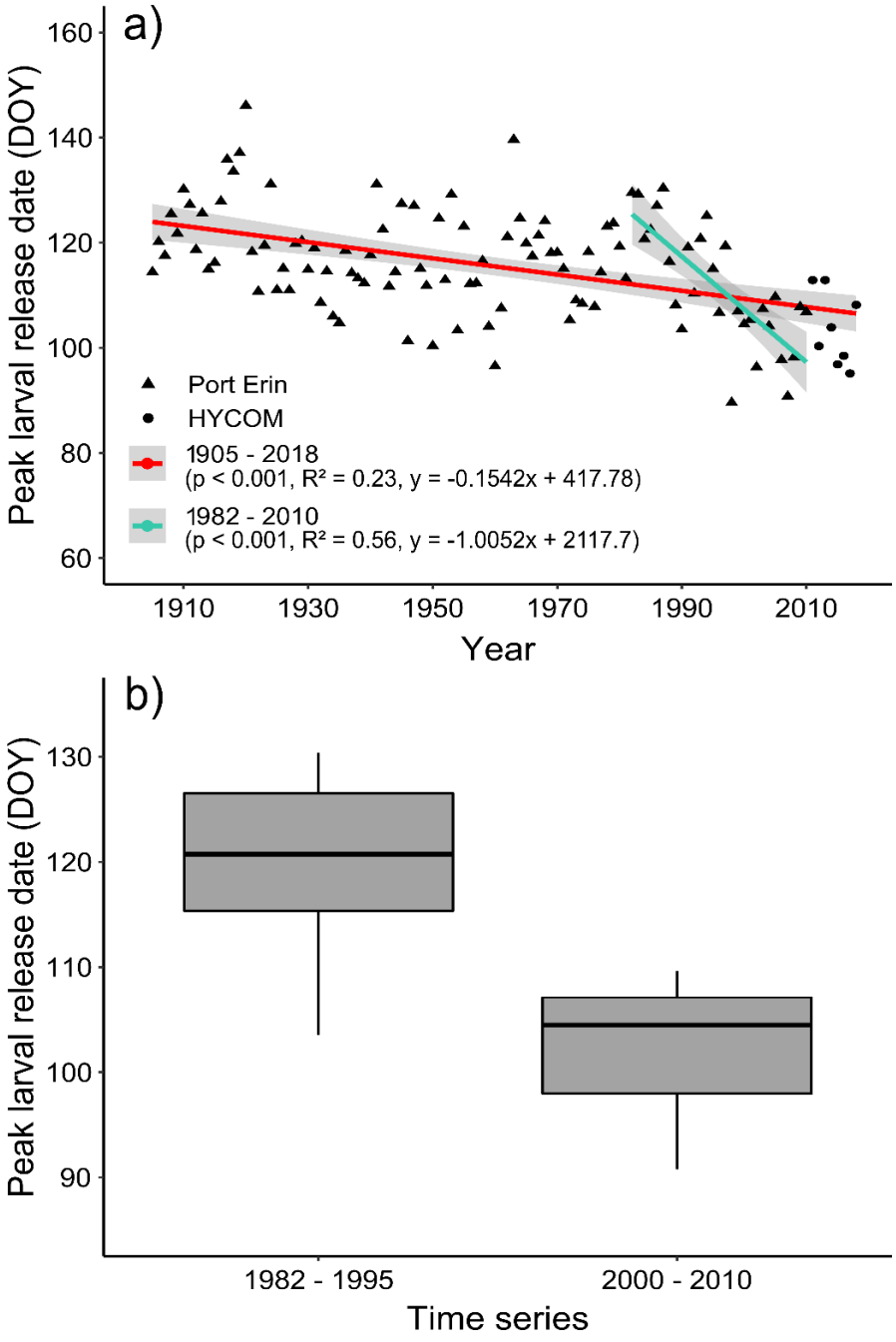

Figure 4. Association between a) date of larval release, expressed as Day of Year (DOY), on the western Irish Sea ground estimated using temperature-dependent incubation durations with surface temperature from Port Erin Breakwater (triangles) and HYCOM (circles). Lines indicate significant trend for 1905 - 2018 (red) and 1982 - 2010 (green) and shading specifies 95% confidence intervals. b) Boxplot with difference in estimated temperature-dependent larval release date between the time series 1982 - 1995 and 2000 - 2010. Central lines in boxplots represent the median, box extremities indicate 1st and 3rd quartiles and whiskers specify range.

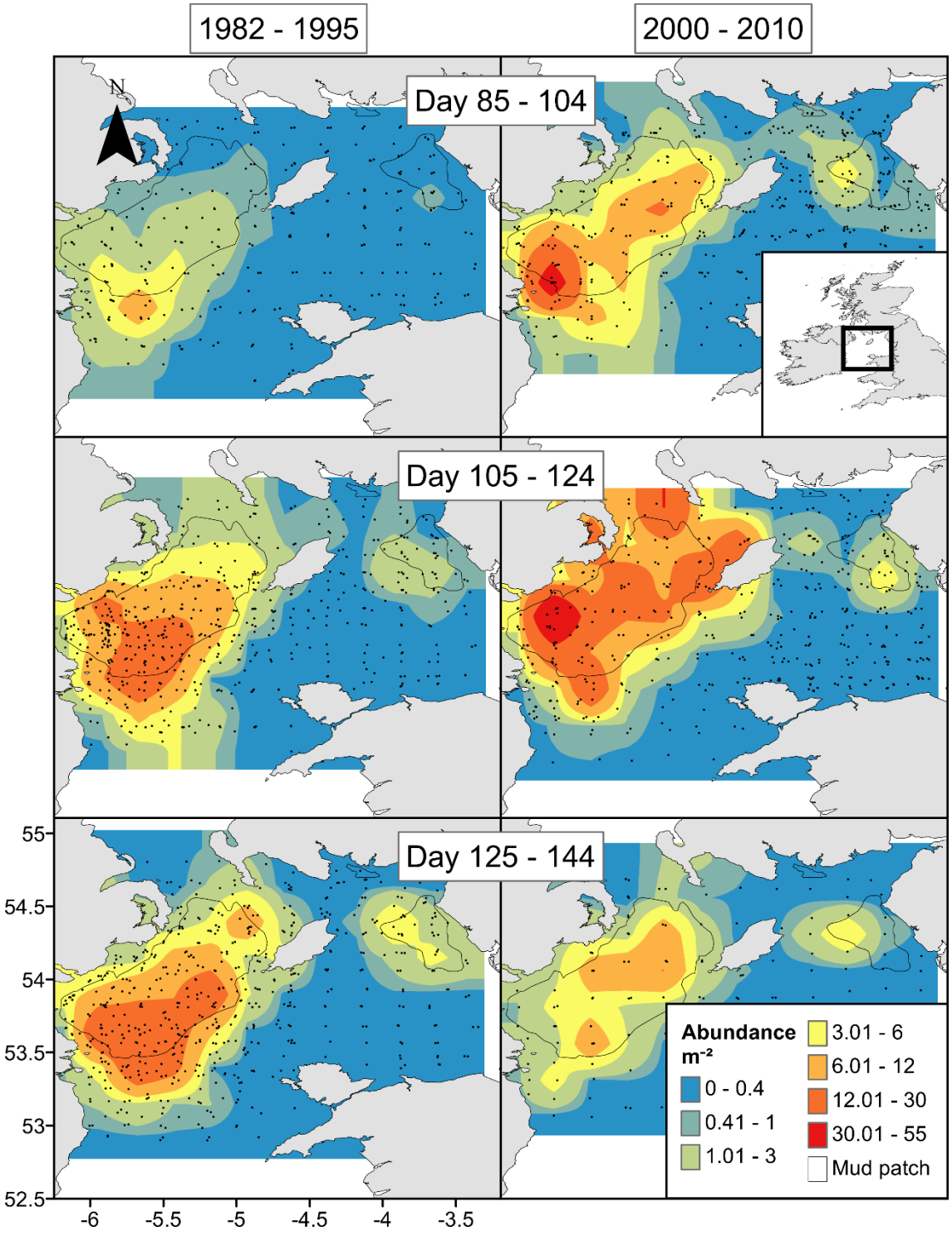

Figure 5. Comparison of Stage I *N. norvegicus* larval abundance m^{-2} in the Irish Sea during the time series 1982 - 1995 and 2000 - 2010 at distinct Day of Year (DOY) time periods. Black markers indicate the position of each sampling station and inverse distance weighted spatial interpolation is used. *Nephrops norvegicus* grounds for both western and eastern Irish Sea are indicated by the continuous black line.

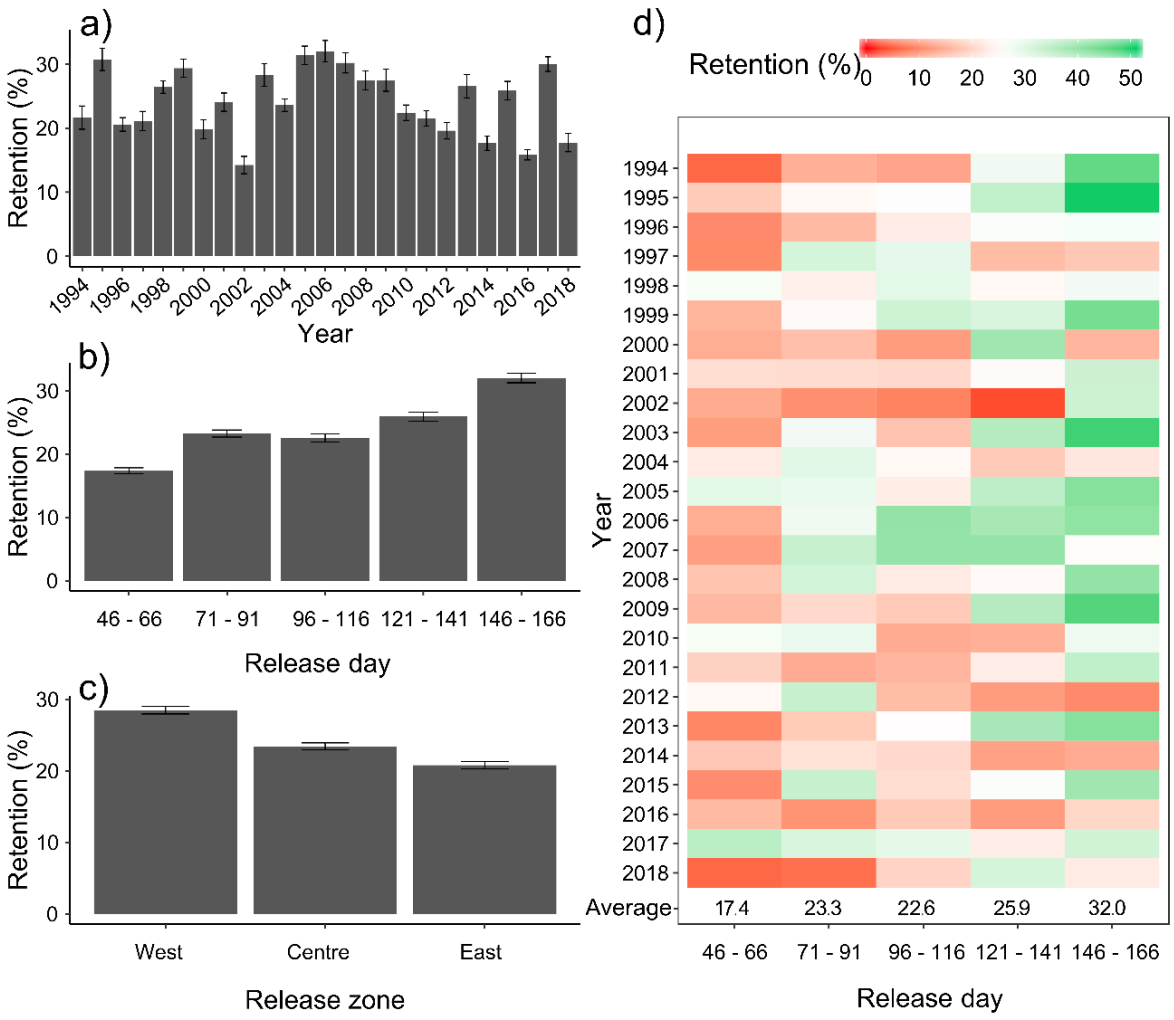

Figure 6. Relationship between average retention (%) on the western Irish Sea ground and a) year, b) release day, c) release zone and d) matrix showing interaction between year and day from larval transport simulation results. Error bars represent standard error.

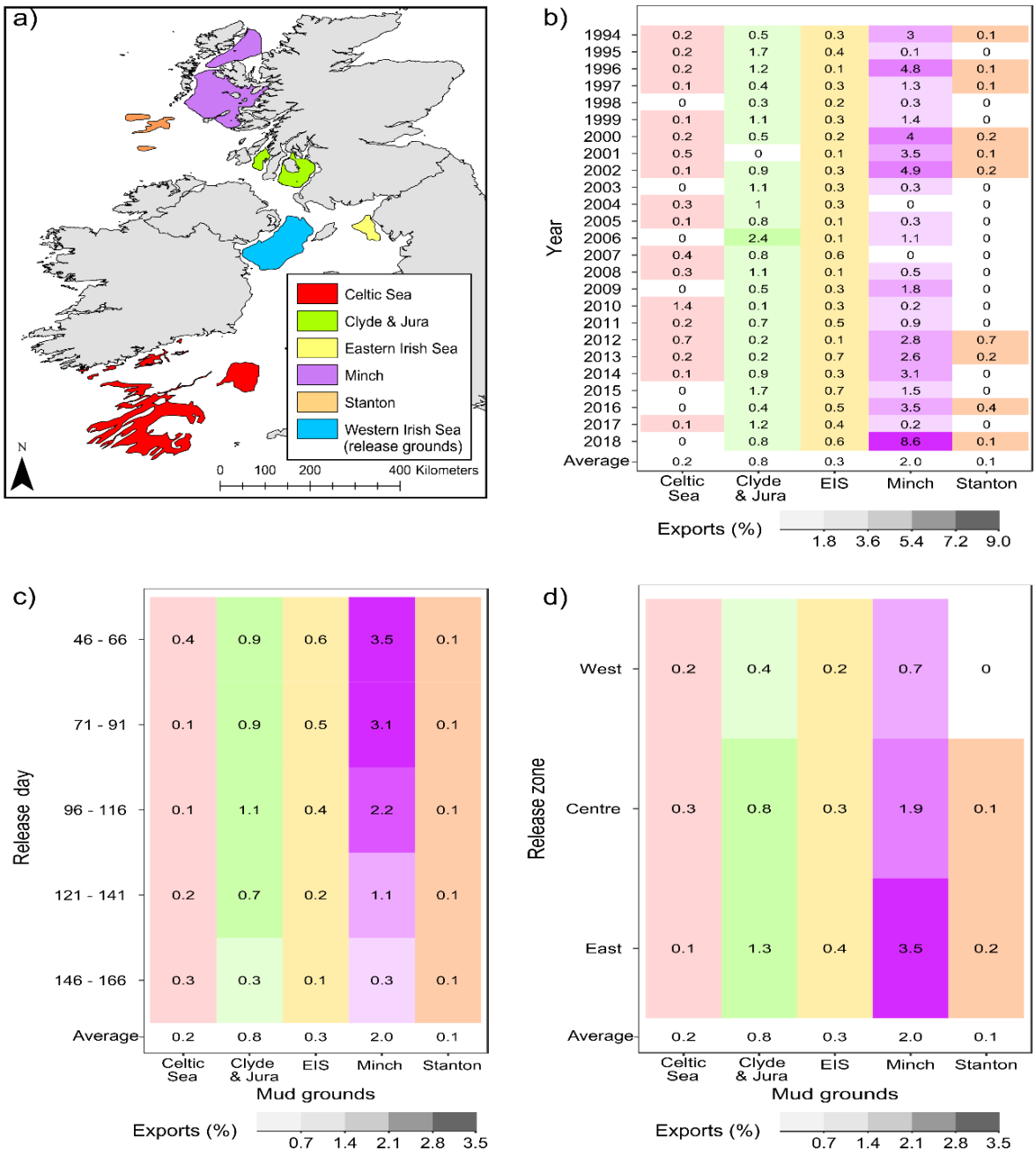

Figure 7. a) Map indicating release ground (western Irish Sea) and nearby *N. norvegicus* grounds and matrices representing the percentage of larval exports (%) to: Celtic Sea, Clyde & Jura, Eastern Irish Sea (EIS), Minch and Stanton grounds, broken down by b) year, c) release day and d) release zone.

3.9. Appendix

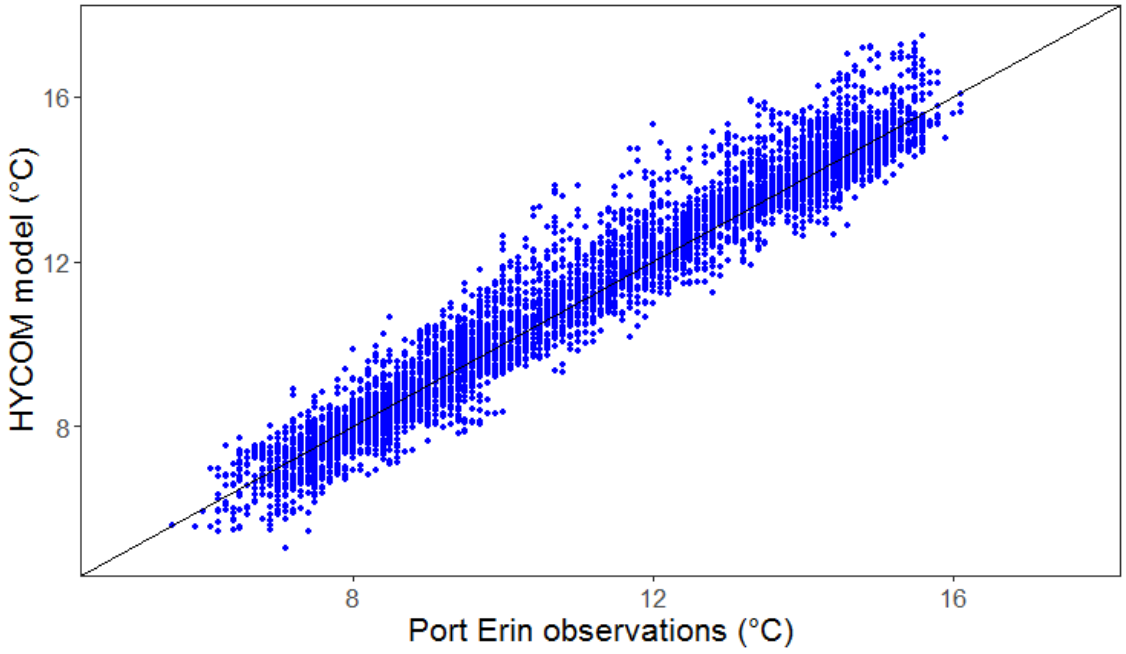

Figure A1. Scatter plot of HYCOM modelled vs empirical observations of sea surface temperature at the location of Port Erin Breakwater sampling station from 1994 - 2010. Line indicates significant correlation (Spearman's rank correlation = 0.97, $p < 0.001$).

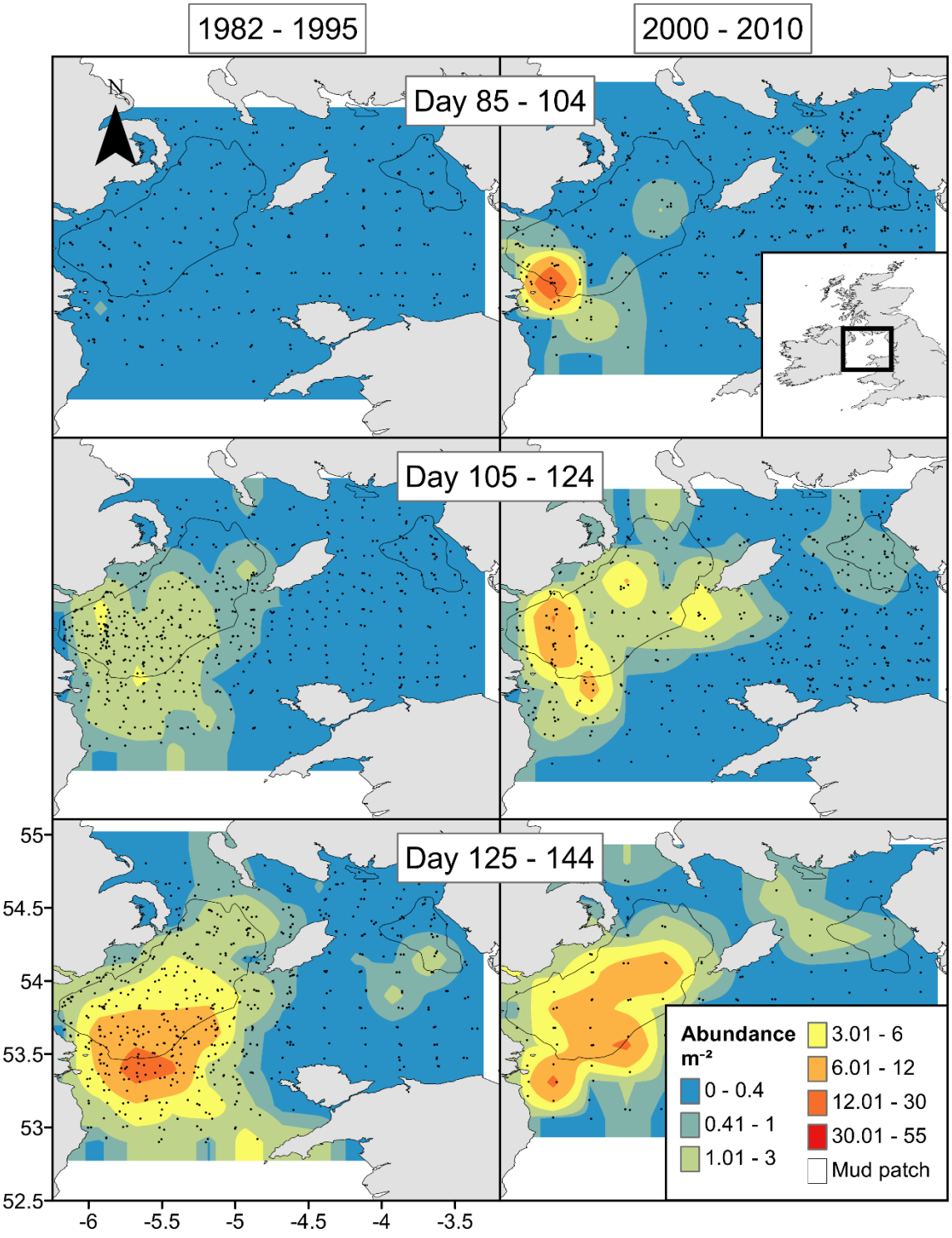

Figure A2. Comparison of Stage II *N. norvegicus* larval abundance m^{-2} in the Irish Sea during the time series 1982 - 1995 and 2000 - 2010 at distinct Day of Year (DOY) time periods. Black markers indicate the position of each station and inverse distance weighted spatial interpolation is used. *Nephrops norvegicus* grounds for both western and eastern Irish Sea are indicated by the continuous black line.

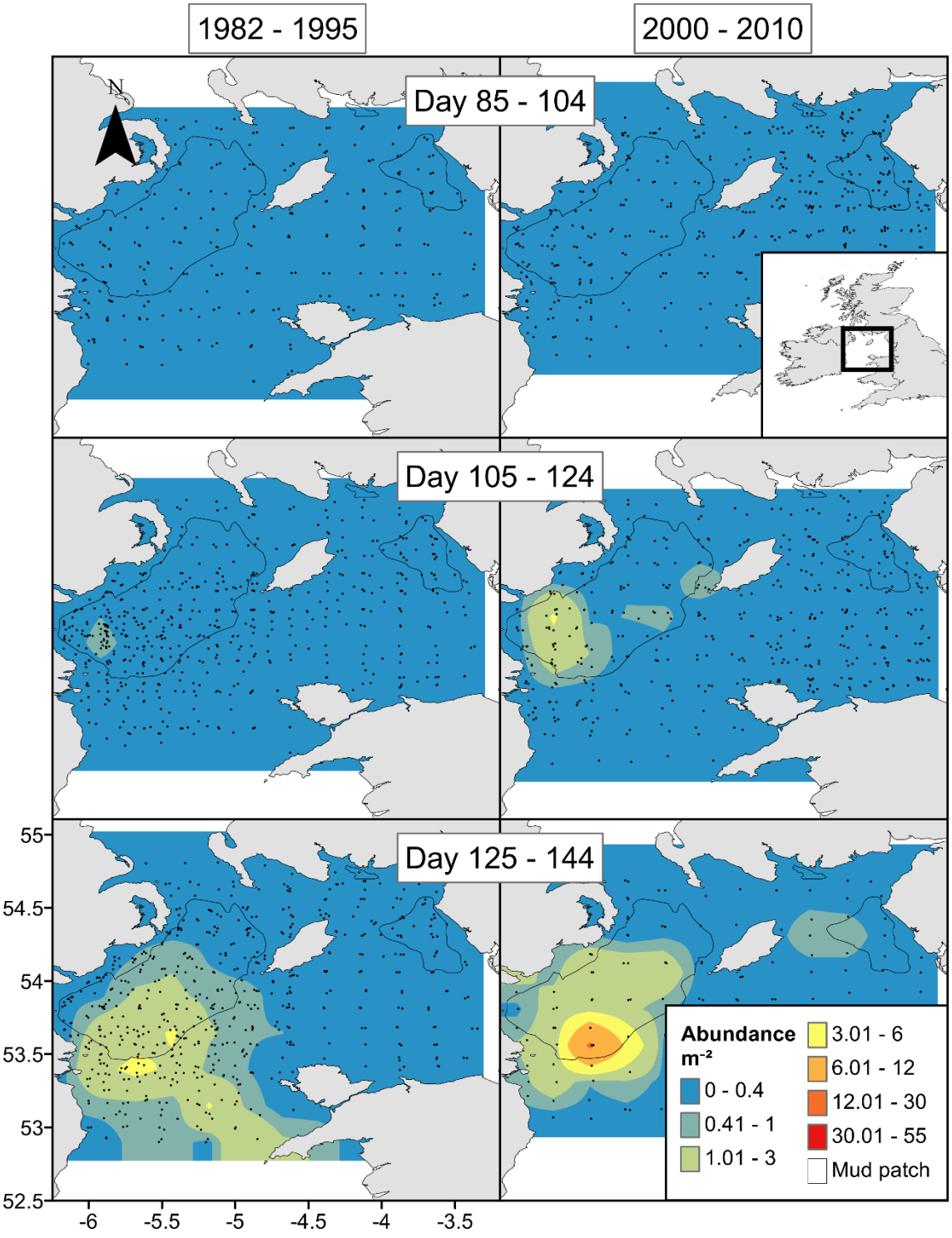

Figure A3. Comparison of Stage III *N. norvegicus* larval abundance m^{-2} in the Irish Sea during the time series 1982 - 1995 and 2000 - 2010 at distinct Day of Year (DOY) time periods. Black markers indicate the position of each station and inverse distance weighted spatial interpolation is used. *Nephrops norvegicus* grounds for both western and eastern Irish Sea are indicated by the continuous black line.

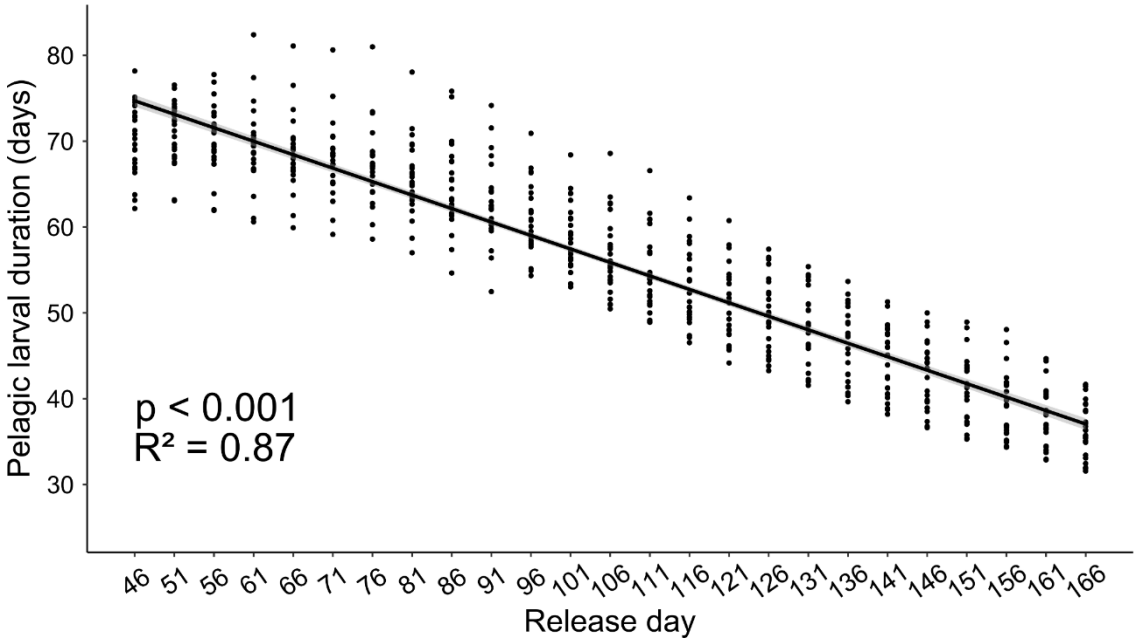

Figure A4. Association between Pelagic Larval Duration (PLD) and release day from larval transport simulations. Line indicates significant trend and shading specifies 95% confidence intervals.

Chapter 4

Larval Transport and Connectivity of the Norway Lobster (*Nephrops norvegicus*) Around Ireland

4.1. Abstract

Transport of meroplankton larvae in the ocean is a key process as it determines larval supply to areas of suitable habitat and enables connectivity between populations, particularly for sedentary 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. We also investigated if larval retention and dispersal distance estimates could be used to predict variations in population density. Grounds off Ireland had varying characteristics in relation to larval retention and imports which were influenced by the local hydrographic regime and spatial isolation from other grounds. On the Aran grounds to the west of Ireland, which has experienced stock fluctuations in the past, modelled larval retention (%) and dispersal distance (km) was linked to empirical burrow densities with a 3-year lag. Thus, models may provide important larval recruitment information early in the life cycle, particularly when recruitment is limited by low larval settlement as appeared to happen on the Aran grounds. Models can be used to supplement existing monitoring and management procedures for species of commercial or conservation importance.

Keywords: Norway lobster, *Nephrops norvegicus*, larvae, larval transport, retention, connectivity, recruitment

4.2. Introduction

In species with non-migratory or sessile adult stages, dispersal of meroplankton larvae in the ocean enables the colonisation of new areas and connectivity between distant populations. Both physical and biological factors affect larval dispersal. For ectotherms, the local temperature regime has a strong influence on development, warmer temperatures increase the growth rate of larvae, and therefore, reduce planktonic larval dispersal duration (O'Connor et al. 2007). Currents dictate the direction and distance of larval transport. However, larvae can influence their horizontal transport by regulating their vertical distribution in the presence of depth-varying currents (Queiroga and Blanton 2005). The timing of larval hatching also affects the conditions larvae are exposed to due to seasonal variations in oceanography (Fernand et al. 2006; Gilbert et al. 2010).

When survival is dependent on settlement of larvae on suitable habitat, hydrography may act as an important constraint on larval recruitment. Some populations may be vulnerable to low larval supply in certain years due to inter-annual variability in oceanography and limited larval imports if spatially isolated from other populations (Roughan et al. 2011; Ospina-Alvarez et al. 2015). Limited larval supply is important to recognise, particularly in commercially harvested species, as low larval settlement has been linked to poor recruitment, e.g. in flatfish in the Bering Sea and Atlantic cod in the Gulf of Maine (Wilderbuer et al. 2002; Churchill et al. 2011).

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 distribution of the benthic juvenile and adult stages is patchy 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 the burrow, only leaving in search of food and to mate (Sardà 1995). Ovigerous females carry the eggs during the temperature-dependent embryo incubation period, lasting from 7 - 9 months in the Irish Sea (Farmer 1974) or 6 months in the Mediterranean Sea (Mori et al. 1998). After hatching, the pelagic larvae swim up through the water column and inhabit the upper 40 m. Larvae pass through three developmental stages by moulting and their growth rate is temperature-dependent

(Dickey-Collas et al. 2000b). Pelagic larval durations (PLDs) can last 1 - 2 months at temperatures averaging 8.5 - 14 °C (Smith 1987; Thompson and Ayers 1989; Dickey-Collas et al. 2000b). 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 larval phase, the postlarvae descend to the benthos, where settlement on mud habitat is crucial to survival. After larval settlement, maturity is thought to be attained between 3 - 4 years of age, estimated using growth parameters and the presence of a fully grown male appendix masculina (Tuck et al. 2000; Bell et al. 2006).

Recruitment estimation is problematic due to the lack of a reliable ageing technique as hard structures are lost during moulting, therefore, no persistent anatomical features can be used to determine age (Hartnoll 2001). In addition, juveniles tend to remain in burrows and are rarely sampled (Cobb and Wahle 1994) and length-frequency distributions are difficult to separate into year classes (Farmer 1973), further complicating attempts to measure recruitment. Due to the requirement of larvae to settle on mud habitat, it is possible that a larval recruitment index may be provided by measuring larval transport to and from mud patches. In the absence of more direct methods, biophysical larval transport models could be used to estimate larval supply to certain populations and provide information on larval recruitment. For example, Ospina-Alvarez et al. (2015) reported a link between modelled anchovy larvae reaching a nursery area and densities of age-0 anchovies from an acoustic survey. In addition, the horizontal distribution of simulated larval sprat in the Baltic Sea displayed a similar distribution to that of empirically observed 0-group sprat (Hinrichsen et al. 2005). Such an index for *N. norvegicus* could be highly beneficial by acting as an early warning signal of poor recruitment due to low larval supply. This information would allow for pre-emptive fishery management actions to be taken to protect against overexploitation.

Several *N. norvegicus* grounds are situated off the coast of Ireland and are assessed as discrete Functional Units (FUs; Figure 1). Stock abundance is estimated using underwater television (UWTV), whereby, a camera mounted sledge is towed along the seabed and *N. norvegicus* burrows are counted. Off Ireland, the longest time series of UWTV burrow estimates are for the Aran (FU17) grounds, which has experienced fluctuations and a decline (2002 - 2019), and the western Irish Sea (WIS; FU15) ground, which has remained stable (2003 - 2019; ICES, 2020). The WIS ground is one

of the most productive *N. norvegicus* fisheries and is characterised by high adult densities with small average sizes (Johnson et al. 2013). The population experiences high larval retention and was thought to benefit from a seasonal gyre (Hill et al. 1996). However, the effectiveness of the gyre is somewhat diminished as larvae perform a Diel Vertical Migration (DVM) which reduces exposure to gyre currents optimal for retention (Phelps et al. 2015; McGeady et al. 2019). To the west of Ireland, the general decline in abundance on the Aran grounds may be attributed to periodically low larval retention levels (Figure A1; McGeady et al. 2019) coupled with its relative spatial isolation from other grounds, meaning few larval imports (O'Sullivan et al. 2015).

Further off the west coast, the Porcupine Bank (FU16) ground has low densities of large adults (Johnson et al. 2013). Past stock declines have led to seasonal fishery closures being implemented since 2010 (Aristegui et al. 2019b). Larval transport simulations for 2011 and 2012 suggest that this isolated population also receives few larval imports from elsewhere (O'Sullivan et al. 2015). By contrast, in the Celtic Sea, a network of closely-situated grounds are thought to act as a metapopulation with high levels of larval exchange (O'Sullivan et al. 2015). The above cases provide good examples of grounds with distinct characteristics in terms of population density, spatial isolation and larval retention, making it a useful regional test of the hypothesis of whether larval transport, specifically modelled larval retention and dispersal distances, can explain trends in *N. norvegicus* adult densities (estimated from burrow densities in annual UWTV surveys). If this is the case, it will help to identify scenarios in which larval transport models provide useful recruitment information.

The aims of this study were (1) to parameterise a biophysical larval transport model for *N. norvegicus* FUs off Ireland, (2) estimate larval retention, dispersal distance and exports between FUs and (3) examine if larval transport model output can be used to explain variations in population density using a time series of UWTV burrow density estimates.

4.3. Materials and Methods

Timing of larval season

To examine the timing of the *N. norvegicus* larval season for the Aran grounds, off the west coast of Ireland (Figure 2), light traps were deployed to collect larvae on selected dates during the larval season. Light traps were deployed between 14:00 - 19:00 and collected the next day between 09:00 - 12:00 on 7 sampling dates from March - June 2018 (10th March, 1st April, 12th April, 27th April, 17th May, 29th May and 12th June). 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, 5 - 6 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 5 light trap samples were recovered on 1st April, 12th April and 29th May and 4 light trap samples were recovered on 17th May. 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 for each sample were counted and sorted according to developmental stage I-III.

Underwater television

The UWTV survey has been conducted since 2002 to provide a fishery-independent estimate of stock size for *N. norvegicus* grounds around Ireland. Data from UWTV surveys were obtained from the Marine Institute for all available years. Survey data were available between 2002 - 2019 for Aran (Aristegui et al. 2019a), 2003 - 2019 for WIS (Lundy et al. 2019), 2006 - 2019 for Smalls (Doyle et al. 2019a), 2011 - 2019 for South Coast (Doyle et al. 2019b), 2012 - 2014, and 2016 - 2019 for Porcupine Bank (Aristegui et al. 2019b) and 2013 - 2019 for Labadie and Banana (White et al. 2019; Figure 1, A1). To conduct UWTV surveys, a camera-mounted sledge was deployed to the seabed and once stable, a 10 minute tow was recorded with vessel and sledge position recorded every two seconds. Two trained observers independently counted burrows from UWTV footage and if agreement was not reached a third counter was

used. Mean burrow density (burrow m^{-2}) was calculated as the total number of burrow systems divided by the observed survey area.

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 was used (HYCOM 3.1; 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). The model is data-assimilative and receives information from satellite observations and *in-situ* data from the ARGO observation program, expendable bathythermographs, moored buoys and other sources (www.hycom.org). Output from HYCOM was available at a 3-hourly temporal resolution and a 1/12° spatial resolution between 40 °S and 40 °N and 1/24° (~4 km) resolution poleward of these latitudes.

HYCOM output was coupled with a Lagrangian particle-tracking tool (Ichthyop v3.3; Lett et al. 2008) to simulate advection and dispersion 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 6 discrete FUs (Figure 1), namely WIS (FU15), Porcupine Bank (FU16), Aran (FU17), South Coast (FU19), Labadie & 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 (i.e. 11 release events). Release dates of virtual larvae for all FUs, except WIS, was every 5 days between 70 - 120 Day of Year (DOY; 11th March - 30th April) and was based on the observed temporal distribution of Stage I *N. norvegicus* larvae from light trap sampling (see Results). On the WIS ground, release days were every 5 days between 90 - 140 DOY (31st March - 20th May) to reflect later larval hatching (Dickey-Collas et al. 2000a; 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 separately from each of the 6 FUs each year, resulting in 660,000 particles released each year and 13.2 million in total over the 20 year study period. A total of 1,320 release events were simulated (11 days × 20 years × 6 FUs).

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 hatching location can have an influence on retention and dispersal distance of larvae (McGeady et al. 2020). The initial spatial distribution of particles (i.e. the horizontal distribution of larvae at hatching) for each FU in the model was based on the distribution of burrows from UWTV surveys in the same year. This ensured that larger proportions of particles were released from areas of a FU that had higher burrow densities. Ordinary kriging was used to spatially interpolate burrow densities at each UWTV station across the spatial extent of the FU (Figure A2-A7). A point grid, distanced 0.02° apart, was then overlain on the burrow density raster and densities were extracted at each grid point. For release events, the initial spatial distribution of particles on each FU was based on the extracted burrow densities at each grid point location while the total number of particles remained constant at 10,000 (i.e. burrow densities were not used to determine particle abundance but rather how particles were spatially distributed at the time of release). In years that no UWTV survey was conducted on a FU, the average spatial distribution of all available years was used (Figure A2-A7).

To compute trajectories of particles, Ichthyop used a Runge-Kutta 4^{th} order numerical scheme and a turbulent dissipation rate of 1×10^{-9} (Monin and Ozmidov 1981). Particle positions were updated every 5 minutes and information (latitude, longitude and temperature) was recorded every three hours. For each simulation, particles were programmed to perform a DVM to mimic larval vertical movements in the water column. Particles migrated between 10 - 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 post processing, observations in light trap sampling were used to apply a release schedule to each larval season. This involved using empirical observations to identify dates at the centre of the larval hatching season with highest densities of Stage I larvae and applying a release schedule that gave a greater weighting to these dates (i.e. release dates at the peak of larval hatching had a greater weighting when calculating estimated larval retention and dispersal distance than those on the fringes of the larval season). As such, release schedules for the Porcupine Bank, Aran, South Coast, Labadie & Banana

and Smalls grounds were centred on 95 DOY (see Results) and the WIS ground was centred on 115 DOY.

A temperature-dependent PLD for each particle was estimated using parameters from past laboratory studies describing the effect of temperature on the developmental rate of *N. norvegicus* larval stages I - III (Smith 1987; Thompson and Ayers 1989; Dickey-Collas et al. 2000b) following Dickey-Collas et al. (2000b; Table 1). The temperature experienced by particles was recorded every 3 hours and was used to determine its PLD (i.e. warmer temperatures resulted in shorter PLDs). When particles came to the end of their PLD, their position was used to determine 'settlement' location. The final positions of all particles at 'settlement' were used to calculate larval retention (%) on each FU (i.e. the proportion of locally produced larvae settling on its natal ground) and connectivity between FUs. Particles situated outside an area of suitable habitat (*N. norvegicus* mud ground) were considered 'lost'. The straight-line distance from initial release location to final settlement location was also calculated as dispersal distance (km).

Statistical analysis

An analysis of variance (ANOVA) was used to examine the effect of release day (intra-seasonal variability) on retention (%), dispersal distance (km) and PLD (days) for each FU. In instances where residual normality was not achieved, variables were log or square-root transformed. When transformations did not work, the non-parametric Kruskal-Wallis test was used.

To examine the association between larval retention and dispersal distance from model observations and burrow densities from empirical UWTV observations, Distributed Lag Models (DLMs) were used, a class of dynamic regression (Demirhan 2020). DLMs enable the use of lagged values of the predictor variable, beneficial when a delayed effect of the predictor on the response is expected (due to the lagged effect of larval settlement on 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 - 2019 and 2003 - 2019, respectively. The Aran grounds has experienced stock declines in the past, suggesting low larval recruitment. Whereas, the WIS ground has remained stable with high adult densities, suggesting high larval

recruitment. Therefore, the contrasting nature of the grounds may provide a good comparison of how larval recruitment influences burrow density. Annual UWTV burrow densities were used as response variables and separate models were built with modelled larval retention (%) and dispersal distance (km) as predictor variables for both the Aran and WIS grounds, respectively. The model with larval retention as a predictor variable did not include larval imports from other FUs, instead, the proportion of locally produced larvae retained on the FU was used as the response variable. Larval imports were not included because larval production from each FU could not be accurately weighted according to abundance due to the lack of UWTV temporal coverage for several FUs and absence of fecundity data. However, the Aran and WIS grounds are relatively isolated, meaning that local retention is likely the main contributor to larval settlement.

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 DLM is stationarity, i.e. mean and variance remain constant over time; therefore, first-order differencing (i.e. difference between consecutive years in the time series) was used for all variables. Response and predictor variables were tested for stationarity using the Dickey-Fuller test. Thus, response and predictor variables represented annual changes in values, e.g. Δ Burrow density (burrow m^{-2}) represents the change in density from the previous year and Δ Retention (%) is the change in retained larvae from the previous year etc.

Prior to running analyses, correlations between lagged predictor variables were examined by obtaining variance inflation factors (VIFs). When VIFs were less than 10, it was concluded that variables were not strongly correlated (Montgomery et al. 2012). The model simplification process followed a stepwise backward selection of variables. 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 non-normality, heteroscedasticity and autocorrelation. DLMs were implemented using the R package *dLagM* (Demirhan 2020) and all analyses were conducted using R version 4.0.1 (R Core Team 2020).

4.4. Results

Timing of larval season

On the Aran grounds, Stage I *N. norvegicus* larvae were first observed in low densities of 0.5 ± 0.2 ind. per trap (mean ± SE) on the first sampling date 69 DOY (10th March) and densities increased for the second (7.0 ± 1.5 ind. per trap) and third (6.7 ± 3.5 ind. per trap) sampling dates on 91 DOY (1st April) and 102 DOY (12th April). Densities then decreased (0.2 ± 0.1 ind. per trap) on 117 DOY (27th April) and were absent thereafter (Figure 3a). Stage II larvae first appeared (0.5 ± 0.2 ind. per trap) on 91 DOY (1st April) and reached a peak (2.5 ± 1.2 ind. per trap) on 102 DOY (12th April). Stage III larvae were low in abundance and appeared (0.2 ± 0.1 ind. per trap) on 117 DOY (27th April) and reached a peak (0.7 ± 0.1 ind. per trap) on 137 DOY (17th May). No larvae of any stage were observed for the final two sampling dates, 149 DOY (29th May) and 163 DOY (12th June; Figure 3b).

Larval transport

Release day had a significant effect on modelled larval retention on the Porcupine Bank (Kruskal-Wallis test, $\chi^2 = 21.9$, df = 10, $p < 0.05$) and Aran grounds (Kruskal-Wallis test, $\chi^2 = 26.5$, df = 10, $p < 0.01$), where retention was lowest for releases early in the season and highest for late releases (Figure 4a). Similarly, release day had a significant effect on dispersal distance on the Porcupine Bank (ANOVA, $F_{10, 209} = 3.86$, $p < 0.001$) and Aran grounds (ANOVA, $F_{10, 209} = 5.09$, $p < 0.001$). On both grounds, a decrease in dispersal distance was associated with late season releases (Figure 4b). PLD of virtual larvae was significantly affected by release day on all 6 FUs (ANOVA, $p < 0.001$) as PLD became shorter with a later release (Figure 4c). The reduction in PLD from first to last release day 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 days in the middle of the larval season (peak of larval hatching) had a greater weighting (see Materials and Methods; Figure 3), the WIS (23.9%) had the highest average retention across the study period (Figure 5), followed by Labadie & Banana (21.6%), Porcupine Bank (7.3%) and the Smalls (6.9%). Retention was low on the Aran (2.6%) and South Coast (3%) grounds. Highest retention

recorded was 42.2% in 2007 on the WIS and lowest was <0.1% in 2018 on the Aran grounds. Annual retention was less than 2% for 12 years on the Aran grounds (Figure 5d), 8 years on the South Coast grounds (Figure 5c) and 3 years on the Smalls ground (Figure 5a, please note y-axis change). On the South Coast and Aran grounds, there was a decreasing trend in retention over the time series (Figure 5c-d), average retention in the first half of the study period, 2000 - 2009, was ~twice as high (South Coast: 3.9%, Aran: 3.4%) as in the second half, 2010 - 2019 (South Coast: 2.1%, Aran: 1.7%).

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

The Celtic Sea FUs (South Coast, Labadie & Banana and Smalls), were the most important FUs in terms of larval exports (Figure 7). The Smalls on average received 1.7% of larvae originating from the South Coast grounds. It also received imports from Labadie & Banana (0.4%) and small infrequent imports from the WIS ground (Figure 7a). In 2002, the Smalls relied almost exclusively on the South Coast grounds for larvae, as retention of native larvae was very low (0.2%). Labadie & Banana had imports from the South Coast (4.7%) and Smalls (2.2%). However, larval imports to these grounds were at a low level since 2015 (Figure 7b, please note y-axis change). South Coast relied mostly on Smalls (1.4%) and Labadie & Banana (0.9%) as sources of imported larvae, but also had small irregular imports from Porcupine Bank and the WIS in the middle of the time series (Figure 7c). Overall, South Coast was the most important source of larval exports as it supplied 8.0% of its larvae to other FUs and was the only FU to export more larvae than it retained (3.0%). Moving outside of the Celtic

Sea area, most of the imports settling on the Aran grounds originated on the South Coast (1.2%; Figure 7d). It also had the highest proportion of lost (failed to settle on suitable habitat) larvae (97.4%) due to a combination of low retention and few exported larvae. Porcupine Bank had infrequent imports from South Coast (0.4%), Aran (0.1%) and Smalls (<0.1%) and predominantly relied on retention of locally produced larvae (Figure 7e). The WIS received few imports from the Smalls (0.1%) and despite its low levels of exports to other Irish FUs, it had the lowest proportion of lost larvae (76.0%), due to high retention (Figure 7f, please note y-axis change in this plot). In general, grounds outside the Celtic Sea, i.e. Aran, Porcupine Bank and WIS were reliant on local production of larvae because imports were low. Except for the WIS, the South Coast exported larvae to all FUs and provided an increasing proportion of larvae to the Aran grounds in recent years.

Optimal DLMs explaining variations in UWTV burrow densities on the Aran grounds were found using AIC (Table 2). On the Aran grounds, Δ Retention (%; i.e. annual changes in retention from one year to the next) had a significant positive association (Figure 8a) with Δ Burrow density with a 3-year lag (burrow m^{-2}). A 1% increase in Δ Retention corresponded to a 0.02 burrow m^{-2} increase in Δ Burrow density three years later (DLM, $R^2 = 0.40$, $p < 0.01$). With a 3-year lag, fluctuations in larval retention and burrow density appeared to match each other, particularly from 2000 to 2008 when densities declined on the Aran grounds (Figure 8b). Δ Dispersal distance (km) also had a significant association with Δ Burrow density with a 3-year lag on the Aran grounds (Figure 8c). A 10 km increase in Δ Dispersal distance corresponded to a 0.03 burrow m^{-2} decrease in Δ Burrow density (DLM, $R^2 = 0.51$, $p < 0.01$). 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. By contrast, on the WIS ground, no significant associations were observed between response and predictor variables.

4.5. Discussion

This study is the first to create a long-term time series of *N. norvegicus* larval transport estimates for multiple FUs and record a link between modelled larval transport and empirical burrow densities (with a 3-year lag) for a population which has experienced declines in density. Biophysical larval transport models may provide a useful larval recruitment index, particularly for populations such as the Aran grounds, where recruitment appears to be limited by low larval supply. It can also be used to identify grounds (e.g. South Coast) that are an important source of larvae and alleviate the effects of poor local retention. Finally, it was possible to examine trends in simulated larval retention and dispersal distance over time and hint at potential mechanisms for those trends. For example, to show that the most recent decade on the Aran and South Coast grounds had lower retention (Figure 5) and higher dispersal distances (Figure 6) due to increased current velocities (Figure A8).

To improve model accuracy with regards to temporal distribution of larvae, a larval release schedule was applied using observations in light trap sampling. Previously, little was known of the temporal distribution of *N. norvegicus* larvae to the west of Ireland. On the small coastal Galway Bay ground, de Bhaldraithe (1976) recorded the majority of larval hatching from March to April. For the larger Aran grounds off Ireland's west coast, McGeady et al. (2019) conducted virtually simultaneous sampling on the Aran and WIS grounds in 2018, noting higher densities of Stage II larvae suggestive of earlier larval timing on the Aran grounds. In the present study, highest densities of Stage I larvae in light traps were recorded on 1st and 12th April 2018, indicating peak hatching on these dates. For later larval stages, densities were very low and were absent after 17th May 2018 (Figure 3). Due to high larval mortality, only a fraction of Stage I larvae survive to Stage III (Nichols et al. 1987). Furthermore, observed low levels of retention on the Aran grounds in 2018 (Figure 5d) indicated that most larvae were transported away from the grounds in that year, depleting densities of late-stage larvae, which would have otherwise been expected in light traps.

Release day had a significant effect on larval transport patterns for the Aran and Porcupine Bank grounds with earlier releases linked to lower retention rates and higher dispersal distances (Figure 4). On the Aran grounds, earlier releases were transported further north along the Irish coast due to longer PLDs and strong northward currents.

Similarly, on the Porcupine Bank ground, early releases had a higher likelihood of dispersal away from the ground due to strong currents early in the season, although PLD variation between early and late releases was low at this FU. Temperature is an important determinant of PLD in *N. norvegicus*, as it is with many ectotherms (Dickey-Collas et al. 2000b; O'Connor et al. 2007). For this reason, on all FUs, PLDs were reduced with a later release as water temperature increased over the larval season (Figure 4).

Temperature is also an important influence on embryo incubation, the period that ovigerous females carry eggs prior to larval release. Farmer (1974) demonstrated that a 10 °C increase in temperature halved the incubation duration. Average HYCOM bottom temperature spatial gradients across FUs during the incubation period (approximately September - March), were 0.4 °C for Porcupine Bank, 0.8 °C for the Smalls, 1.3 °C for Aran, 1.3 °C for the WIS, 1.5 °C for Labadie & Banana and 2.1 °C for South Coast grounds. The relatively uniform bottom temperature profile on the Porcupine Bank ground could mean that developing embryos across the ground experience similar temperatures, resulting in a relatively condensed larval hatching period. In contrast, strong temperature gradients across the multiple spaced-out South Coast grounds and large Labadie & Banana grounds indicate more asynchronous hatching and an extended larval release period. A prolonged larval hatching season may benefit the population by buffering against short term periods of unfavourable oceanography for retention, poor food availability, and/or high predation risk (Mertz and Myers 1994).

The network of closely situated grounds in the Celtic Sea had high levels of larval exchange. For the 2011/2012 larval seasons, O'Sullivan et al. (2015) similarly documented high inter-ground connectivity in Celtic Sea *N. norvegicus* grounds and noted that South Coast grounds had the highest rates of larval exchange. Throughout the time series, the South Coast grounds had high larval exports and was the only FU to export more than it retained. This FU is unique in consisting of 9 small coastal mud areas rather than one large continuous mud area (Figure 1). Due to the patchy nature of the South Coast grounds, it is distributed across a large spatial extent, with a distance of 210 km from its western to its eastern edge (Figure 1). But, in terms of mud habitat area, it is relatively small (only larger than the Aran grounds). In contrast, Labadie & Banana had the largest area (10,191 km²) and had high retention throughout the time

series, with relatively few exports. For most of the time series, the Labadie & Banana grounds had imports from other Celtic Sea grounds; however, since 2015 larval imports were at a very low level (Figure 7). The increasingly northward transport of South Coast larvae was the main contributor to decreasing exports to the Labadie & Banana grounds. The Smalls and South Coast grounds were the most interconnected in terms of larval exchange. On average, the Smalls exported 1.4% to the South Coast and received 1.7%. For the Smalls, the advantage of being closely situated to other grounds was evident in 2002 when it had very low retention (0.2%), but received 10.8% of larvae from South Coast grounds to compensate. This is a stark example of the occasional inter-reliance of FUs for larval exchange, which is significant for their management. It is also ecologically significant, as a marine example where persistence of local populations (via annual larval supply) is facilitated by larval connectivity within the larger metapopulation (Cowen and Sponaugle 2009).

Dispersal distance was highest on the Porcupine Bank ground (134.1 km) and remained relatively consistent throughout the time series (Figure 6e). This FU was also the furthest offshore, meaning larvae were transported large distances before being impeded by coastline. Fast shelf edge currents close to the Porcupine Bank ground (Figure A8) contributed to high dispersal potential. Considering its large extent (7,174 km^2), retention was relatively low (7.3%) compared to other large grounds such as the WIS (23.9%) and Labadie & Banana (21.6%) with respective areas of 5,826 km^2 and 10,191 km^2. High current velocities were observed along the shelf edge and larvae often became entrained in circular gyres off the ground to the south and southeast (Figure A8). Retention estimates for Porcupine Bank were significantly less than the 12% (2011) and 30.2% (2012) observed by O'Sullivan et al. (2015). Several model parameterisation distinctions likely account for disparities between the two studies, including vertical behaviour, hatching distribution, release dates and ocean model. In addition to low retention, the Porcupine Bank ground was relatively isolated from other FUs, receiving infrequent exports from the South Coast and Aran grounds (Figure 7e). Porcupine Bank has large adult *N. norvegicus* at low densities and has undergone stock declines in the past, although better recruitment levels recently have improved the outlook for the stock (Johnson et al. 2013; Aristegui et al. 2019b). Low adult densities likely limit the amount of larvae produced relative to higher density grounds. However, fecundity is correlated with body size, meaning large females would produce more

larvae (Briggs et al. 2002). For the Porcupine Bank ground, poor and changeable retention levels (relative to similar large grounds) and spatial isolation are further compounded by lower larval production. These factors presumably render it vulnerable to periods of low recruitment which may have contributed to past stock declines (Ungfors et al. 2013).

The WIS had the highest average retention of all FUs (23.9%) and in 2007 recorded the highest annual retention (42.2%) over the time series. The enclosed nature of the Irish Sea, along with relatively weak currents proved conducive to high retention (Figure 5f). *Nephrops norvegicus* occur at high densities in this FU and adults grow to small sizes relative to other grounds, which has been linked to density-dependent suppression of growth (Merder et al. 2020). However, there may also be recruitment effects, i.e. where abundant recruits reduce the average size (Johnson et al. 2013). UWTV abundance estimates indicate that the population has been in a stable healthy state throughout the time series (2003 - 2019; Figure A1) and has always well-exceeded the Maximum Sustainable Yield (MSY) biomass trigger (the biomass at which management advice should be implemented to prevent further decline) set by the International Council for the Exploration of the Seas (ICES) of 3 billion burrows (Lundy et al. 2019).

High larval retention on the WIS ground, also observed in previous studies (O'Sullivan et al. 2015; Phelps et al. 2015), likely contributes to high adult densities and resulting competition for space and resources (Johnson et al. 2013). Hill and White (1990) suggested that high densities mean more larvae settle than can be accommodated and that larval settlement exceeds carrying capacity. This would imply that *N. norvegicus* are subject to high post-settlement mortality on the WIS ground. Increased juvenile mortality due to predation and cannibalism would be expected in such high-density scenarios (Bell et al. 2006). Therefore, larval recruitment is likely a poor indicator of adult density fluctuations, perhaps explaining why no relationship between modelled larval transport and burrow density was observed. Instead, burrow density fluctuations may be more heavily influenced by factors that occur after larval settlement, such as fishing pressure and predation, although, cod, the main predator of *N. norvegicus* in the Irish Sea have been at low abundances since the 1980s (Kelly et al. 2006; Johnson et al. 2013). In terms of connectivity, the ground received few imports and exported little to other Irish FUs in the present study. However, 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 FUs in the current study, the WIS has been shown to be a source of larvae to important Scottish and EIS grounds (McGeady et al. 2020).

The Aran grounds had <2% retention for 12 out of 20 years and had the lowest retention (2.6%) overall (Figure 5d). Larvae were consistently transported north by the Irish coastal current (Fernand et al. 2006) and large numbers settled in Donegal Bay and off North Mayo (Figure A8). 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 annual retention (Figure 5, A8). Again, larval retention estimates were significantly lower than in 2011 (15.8%) and 2012 (14.4%), as estimated by O'Sullivan et al. (2015). Our 2018 retention estimate for 16th March (0%) was similar to that of McGeady et al. (2019) for 15th March 2018 (0.2%) despite the present study using the HYCOM ocean model as opposed to the Regional Ocean Modelling System model (McGeady et al. 2019), with a vertical migration implemented in both cases. UWTV surveys have been conducted on the Aran grounds since 2002, providing the longest time series of burrow estimates in Irish waters (Figure A1). At the beginning of the time series (2002 - 2005), burrow densities were considered moderate to high (0.8 - 1.1 burrow m^{-2}). From 2004 - 2012 densities fluctuated widely with a general decline before stabilising at a lower level (0.3 - 0.4 burrows m^{-2}) from 2012 until the present date (Figure A1). Since 2012, abundance estimates for the Aran grounds have been below the MSY biomass trigger of 540 million burrows in all but two years, signifying potential recruitment issues.

On the Aran grounds, larval retention and dispersal distance from larval transport models were linked to empirical changes in burrow density with a 3-year lag (Figure 8). At the end of the larval phase, postlarvae descend to the benthos and often excavate their own tunnel within existing burrow complexes (Tuck et al. 1994). In the first year of life, growth is very fast and moulting can occur once a month, in the second and third year, time between moults gradually increases to 3 - 4 moults per year (Bell et al. 2006). After sexual maturity, growth is further reduced, particularly for females (Haynes et al. 2016), and size at maturity varies within and between populations; although age at

maturity is more consistent, usually occurring between 3 - 4 years for males and females (Tuck et al. 2000; Bell et al. 2006). In females, onset of maturity is linked to population density, with females in high density grounds reaching maturity at smaller sizes (C. A. Santana, unpublished data). On the Aran grounds, length frequency distributions from beam trawl surveys (2006 - 2018) show peak abundances between 20 - 31 mm Carapace Length (CL) for males and females (Doyle et al. 2018). Applying the age-length relationships of Sardà (1995), compiled from several studies, to the above lengths would make the majority of males on the Aran grounds between 2 - 4 years of age and females 2 - 5 years. This would indicate that 3-year old *N. norvegicus* make up a significant proportion of the population. Moreover, any fluctuation in year class abundance could have a significant effect on burrow density. Due to the importance of larvae settling on mud habitat, larval settlement rates may act as a constraint on recruitment, particularly for stocks such as the Aran grounds, which are small, relatively isolated and suffer from low and inconsistent larval supply. The findings of the current study suggest that persistent low levels of larval retention on the Aran grounds has given rise to poor recruitment and combined with commercial exploitation has contributed to a reduction in adult densities.

Despite the demonstrated link between larval transport and burrow density on the Aran grounds, several other processes can influence adult densities 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 'supply-side' component, juveniles will not exist to survive sources of mortality later in benthic life (Gaines and Roughgarden 1985). Future work should be conducted to improve the model by including a feeding and predation component, collecting further data on larval release timing for data-deficient grounds, calculating accurate larval settlement levels by estimating production on each ground and validation of modelled oceanography and larval distributions (Swearer et al. 2019).

Larval transport models may be utilised as a valuable tool in assisting fishery managers to identify instances of low larval recruitment early in the management cycle, long before its impacts manifest in the adult population (Hinrichsen et al. 2011). Models may also be helpful to identify whether poor larval settlement was a contributing factor in other areas where historic fluctuations in *N. norvegicus* abundance have been observed

(Fariña and González Herraiz 2003; ICES 2020). Although the current study focused on *N. norvegicus*, and in certain respects it was a model species due its relatively sedentary adult stage and close ties with mud habitat, the use of larval transport indices as a proxy for recruitment can be applied to many species with defined habitat and a pelagic larval phase. A wealth of larval transport studies have been produced in recent years (Swearer et al. 2019); though, very few have linked larval transport to recruitment or population size. Biophysical larval transport models offer a method of estimating larval retention and connectivity, which are extremely difficult to observe *in-situ* due to the inherent difficulties in tracking miniscule larvae in large water bodies. Such larval recruitment predictions can supplement existing monitoring and management procedures and may assist in reducing overexploitation during periods of low productivity or to enhance conservation measures, particularly in the face of climate change and the knock-on effects to oceanography (Harley et al. 2006).

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4.7. Tables

Table 1. Regression parameters for ln (larval stage duration) vs temperature relationship from Dickey-Collas et al. (2000b), Thompson and Ayers (1989) and Smith (1987).

Stage	Slope	Intercept	Source
I	-0.161	4.265	Dickey-Collas et al. (2000b)
II	-0.175	4.646	Dickey-Collas et al. (2000b)
III	-0.133	4.188	Smith (1987)

Table 2. Distributed lag model selection process based on backwards selection of variables that minimised Akaike's information criterion (AIC). Model 4 (bold) was selected as the optimal model for both Δ Retention and Δ Dispersal distance based on AIC. Lags refer to 1-, 2-, 3- and 4-years.

	Structure	AIC
Predictor: Δ Retention		
1	Δ Burrow density ~ Δ Retention Lag 1 + Δ Retention Lag 2 + Δ Retention Lag 3 + Δ Retention Lag 4	-7.2
2	Δ Burrow density ~ Δ Retention Lag 1 + Δ Retention Lag 3 + Δ Retention Lag 4	-9.1
3	Δ Burrow density ~ Δ Retention Lag 3 + Δ Retention Lag 4	-10.8
4	**Δ Burrow density ~ Δ Retention Lag 3**	**-14.3**
R^2 = 0.40		
Predictor: Δ Dispersal distance		
1	Δ Burrow density ~ Δ Distance Lag 1 + Δ Distance Lag 2 + Δ Distance Lag 3 + Δ Distance Lag 4	-12.4
2	Δ Burrow density ~ Δ Distance Lag 1 + Δ Distance Lag 2 + Δ Distance Lag 3	-15.4
3	Δ Burrow density ~ Δ Distance Lag 2 + Δ Distance Lag 3	-16.2
4	**Δ Burrow density ~ Δ Distance Lag 3**	**-17.6**
R^2 = 0.51		

4.8. Figures

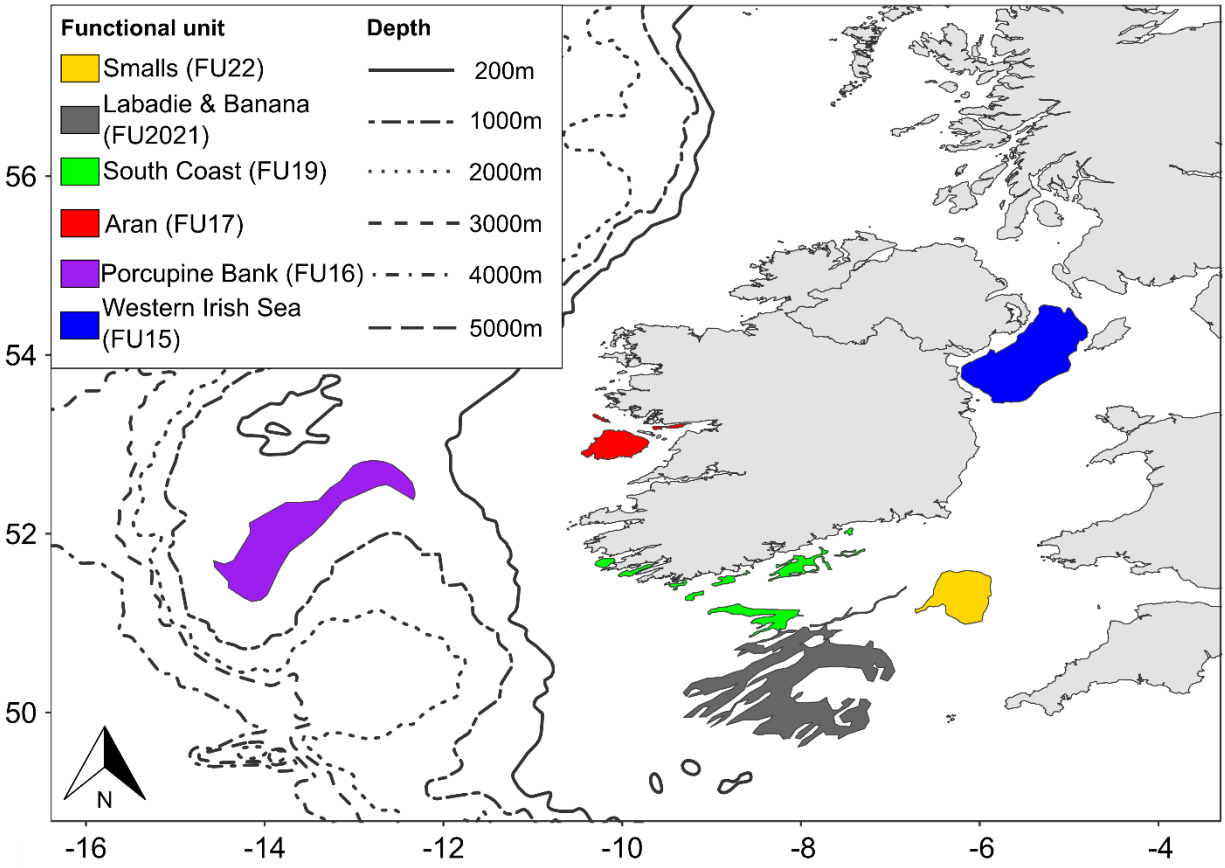

Figure 1. Map of *N. norvegicus* Functional Units (FUs) around Ireland used in larval transport simulations. Particle releases were conducted separately from each of the 6 FUs. Bathymetry is represented by contour lines.

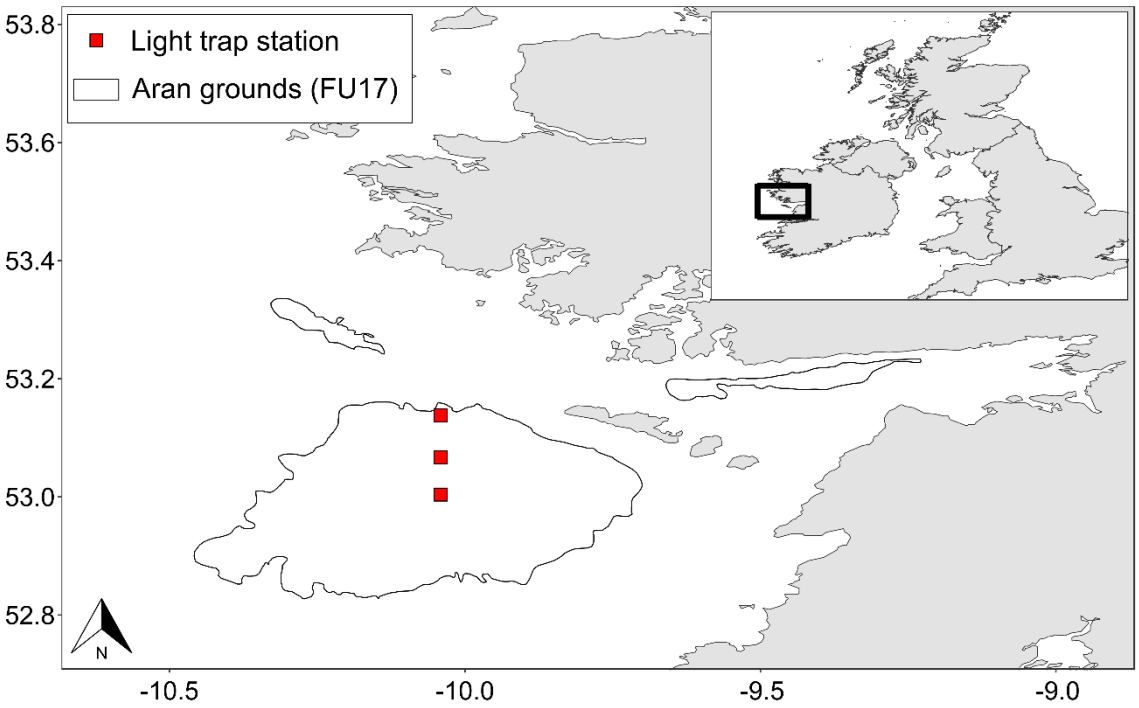

Figure 2. Locations of light trap stations on the Aran (FU17) grounds (red squares). At each station, two light traps were deployed and collected the next day on 7 sampling dates from 10th March to 12th June 2018.

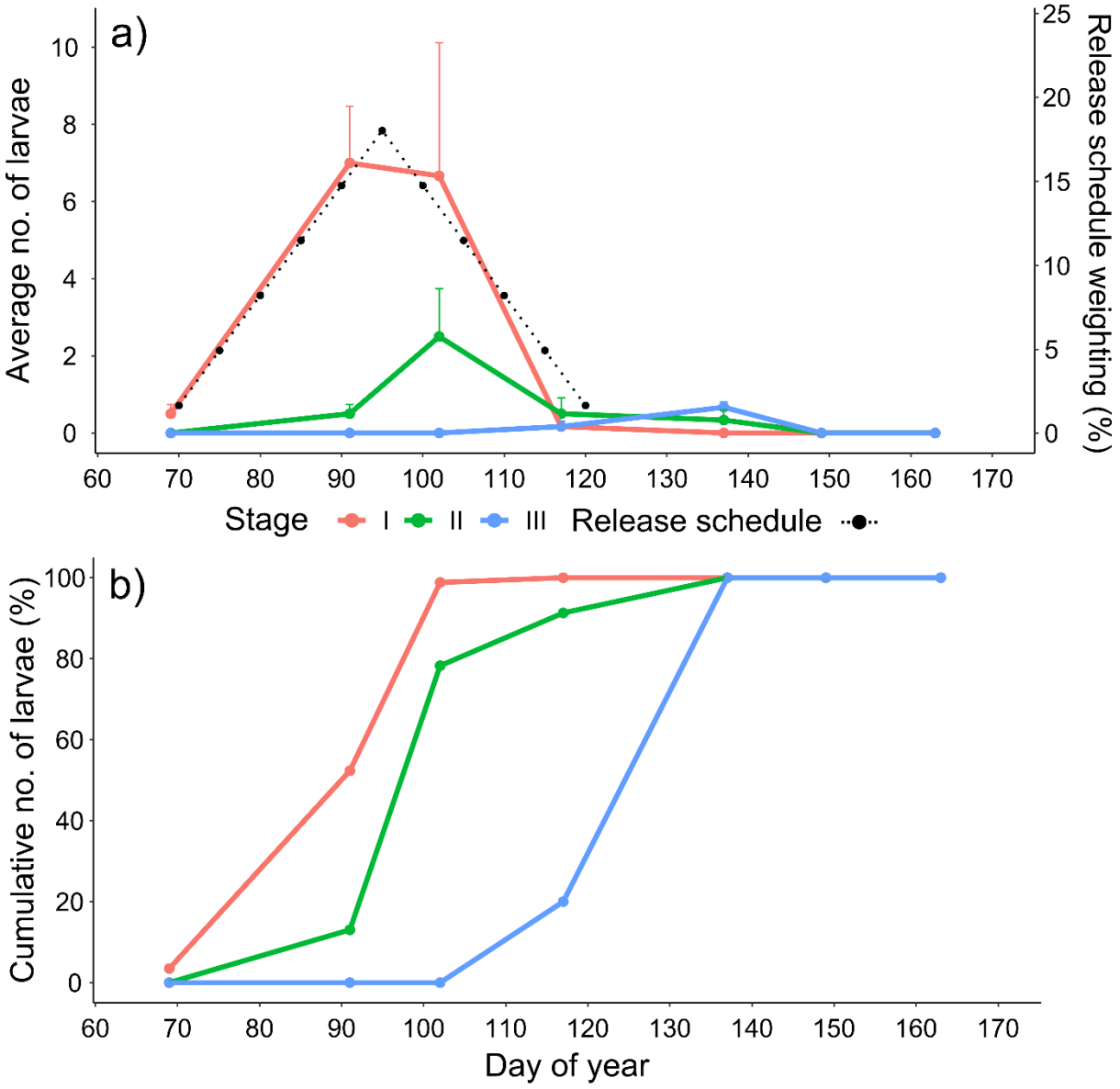

Figure 3. a) Average number of *N. norvegicus* larvae per light trap at Stage I (red), II (green) and III (blue) observed on the Aran (FU17) grounds. Standard error is represented by error bars. Temporal distribution of Stage I larvae was used to create a particle release schedule centred on the dates of highest densities for larval transport simulations (black points and dotted line). b) Cumulative proportion of larvae across the sampling period.

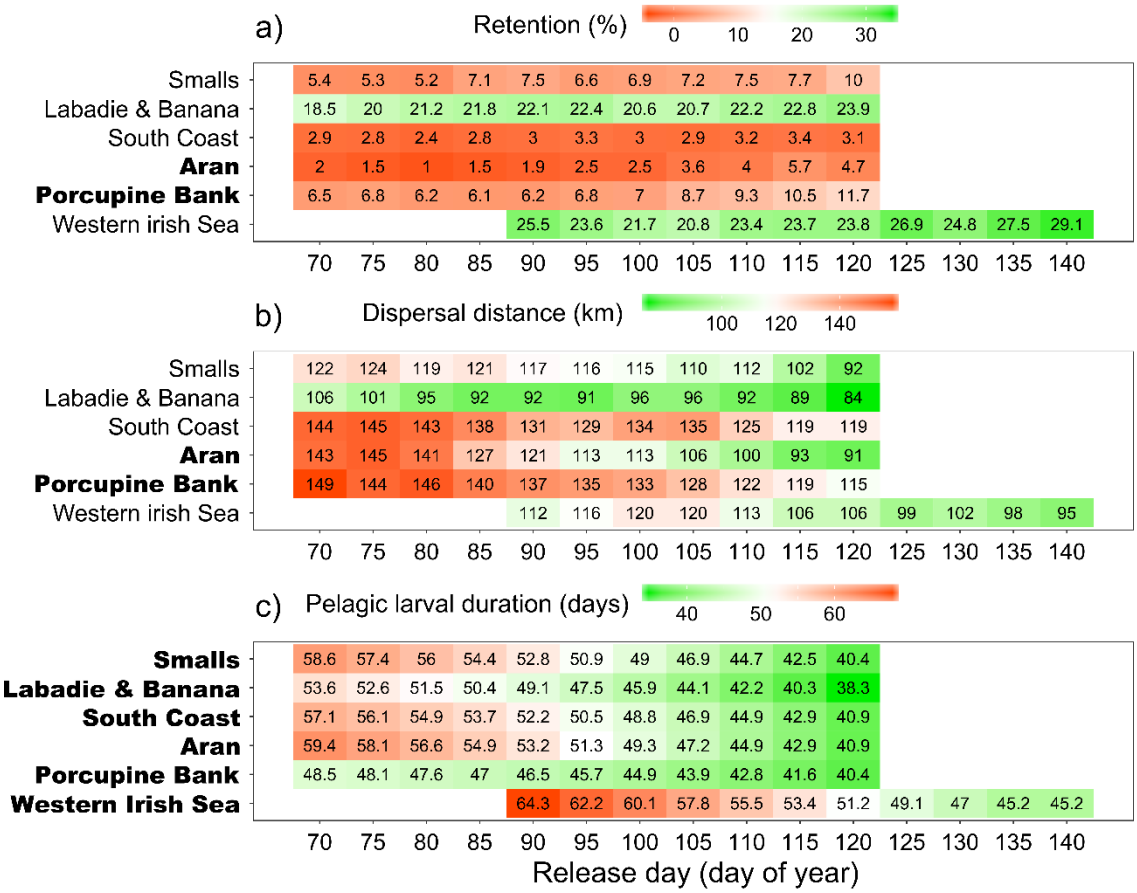

Figure 4. The effect of release day (DOY) on average simulated a) Larval retention (%), b) Dispersal distance (km) and c) Pelagic larval duration (days) for each Functional Unit (FU) from 2000 - 2019. FU names in bold represent a significant relationship between release day and the respective variable. The offset in release days in the western Irish Sea is due to a later larval season (see Materials and Methods).

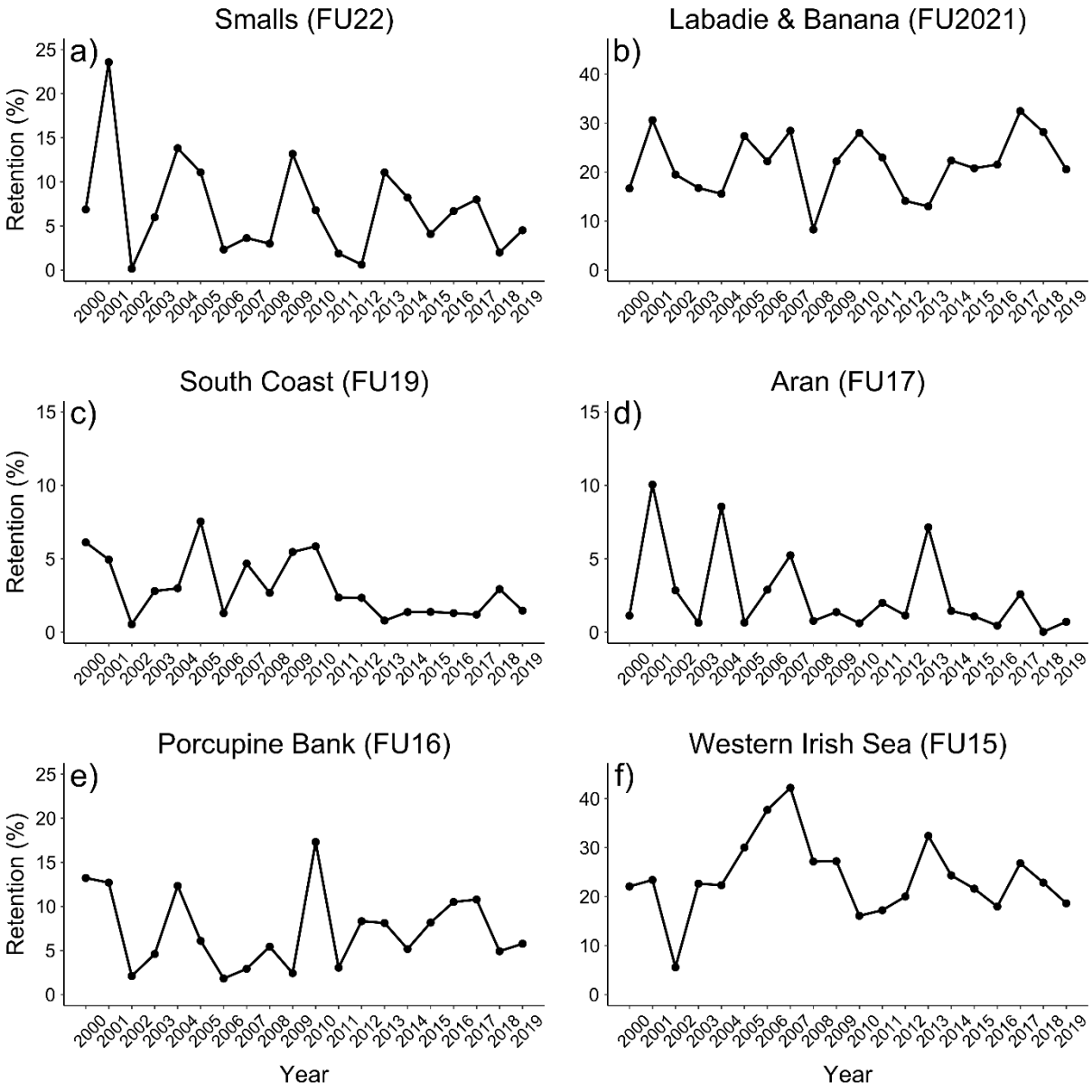

Figure 5. Time series of simulated annual larval retention (%) using release schedule (see Figure 3a) for Functional Units (FUs) a) - f) around the Irish coast. Note y-axis changes between FUs.

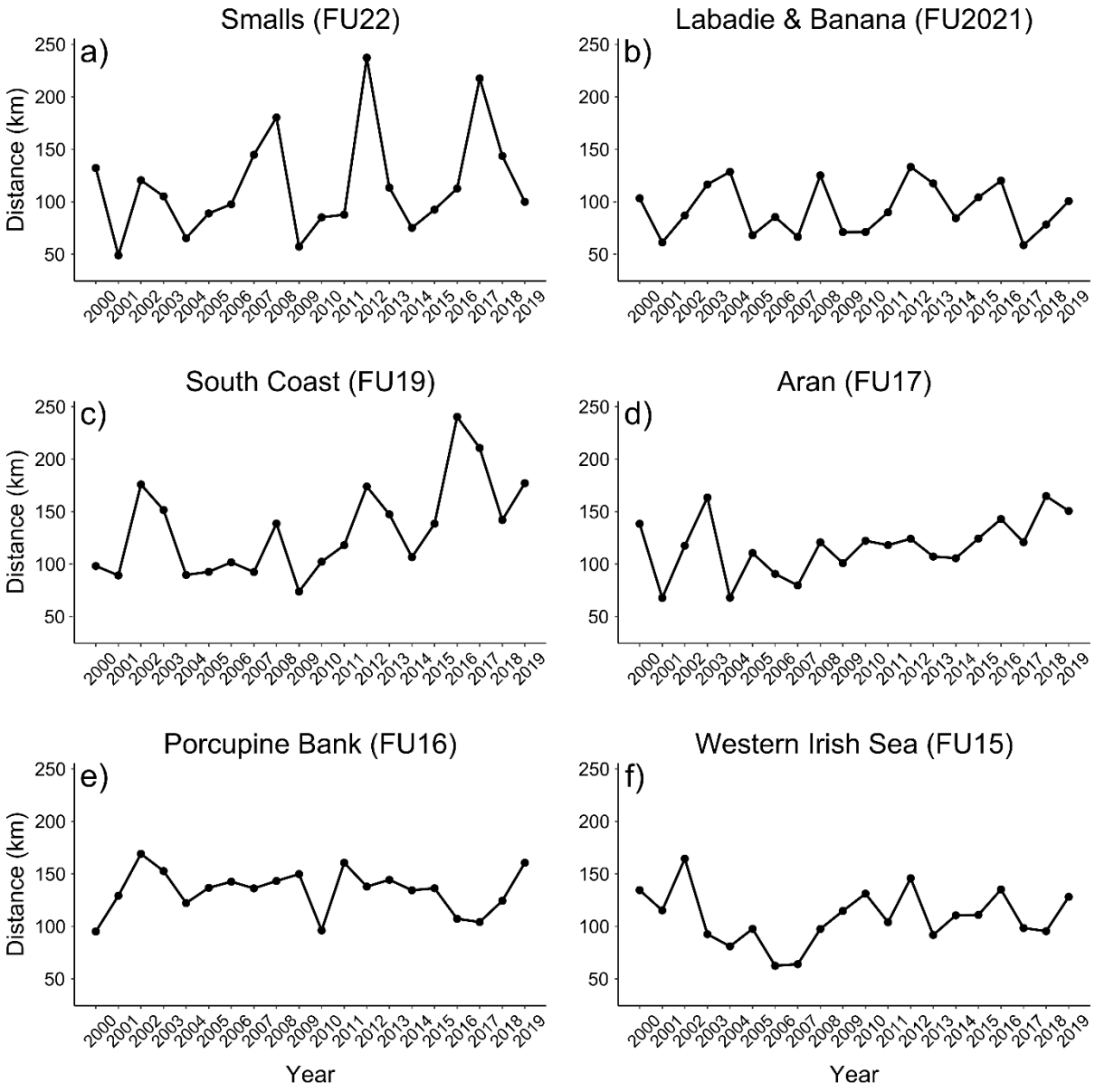

Figure 6. Time series of simulated annual larval dispersal distance (km) using release schedule (see Figure 3a) for Functional Units (FUs) a) - f) around the Irish coast.

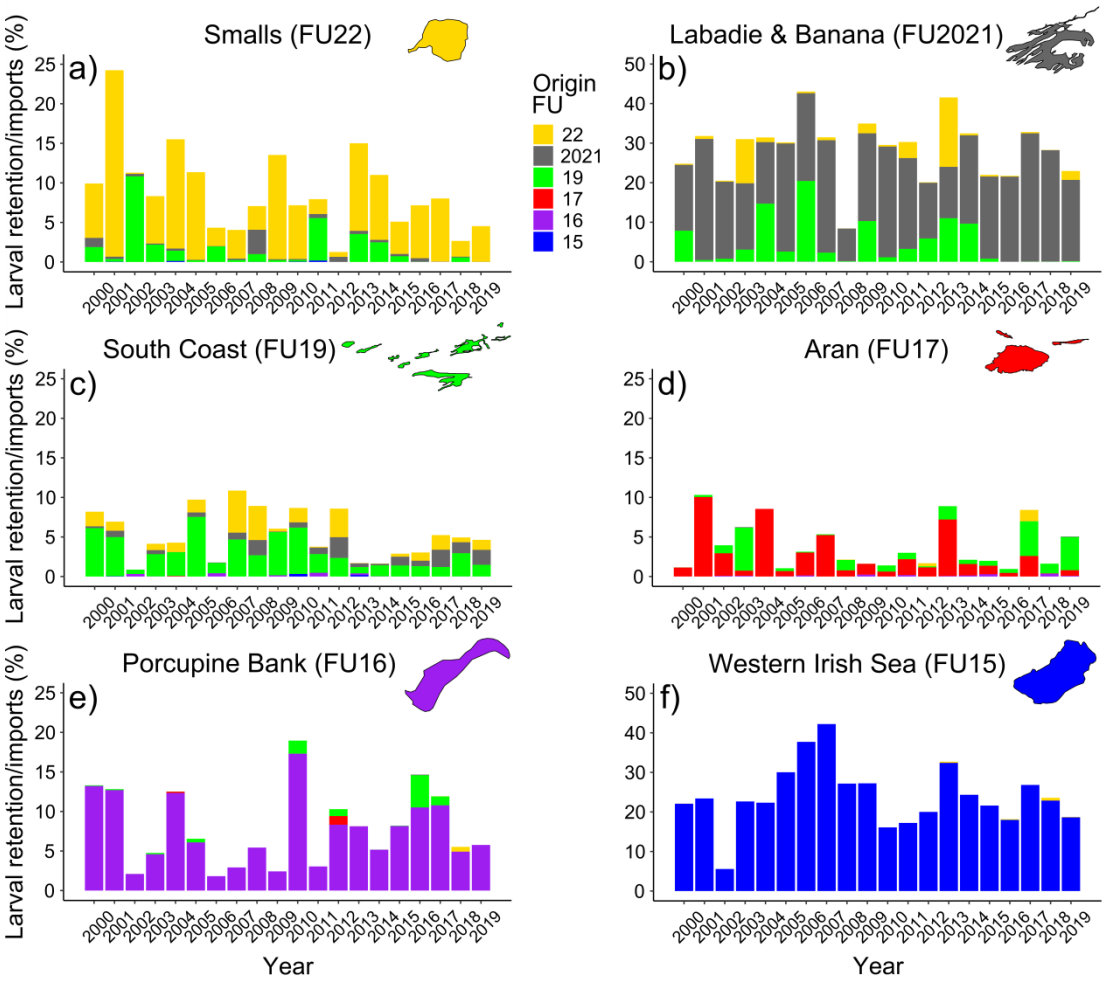

Figure 7. Simulated proportion of settled larvae on Irish *N. norvegicus* Functional Units (FUs) through retention and imports from other FUs (see legend indicating 'origin FU') from larval transport models from 2000 to 2019. Please note that the y-axis varies on plots b) and f).

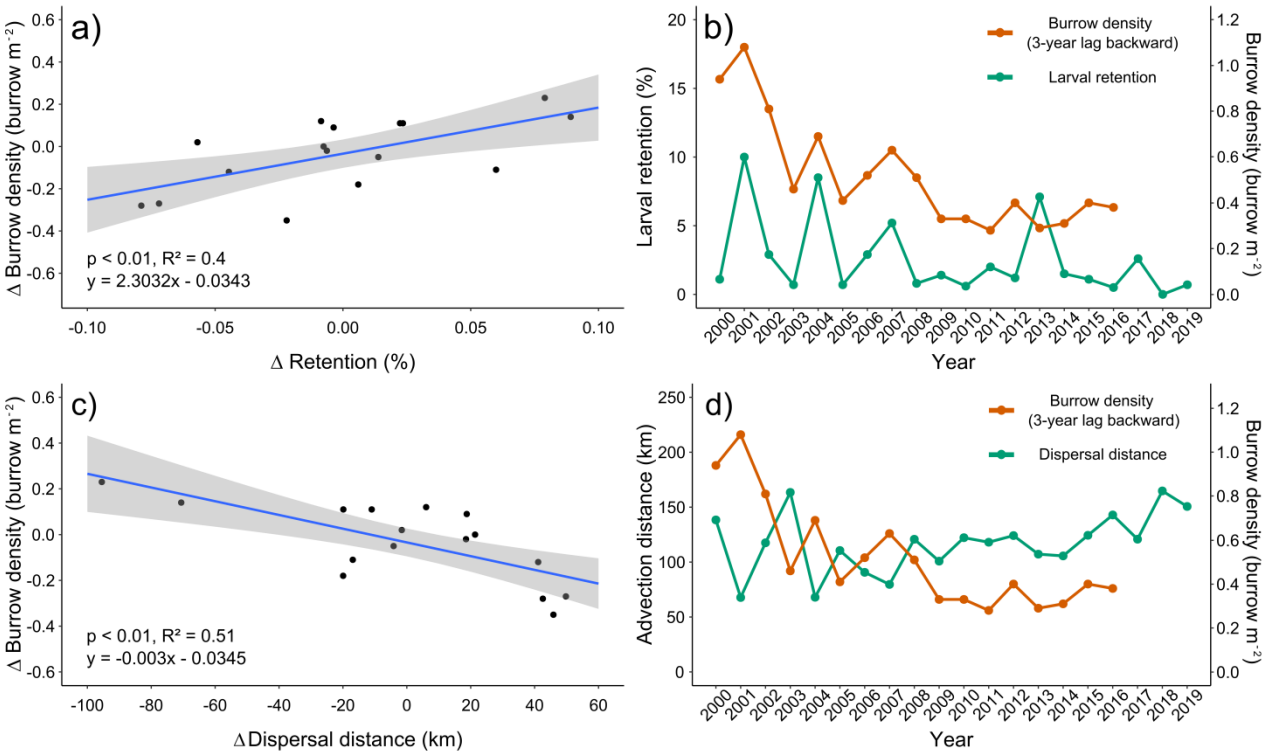

Figure 8. Association on the Aran grounds between Δ Burrow density (annual changes to density) and a) Δ Retention (annual changes to Retention) and c) Δ Dispersal distance (annual changes to Dispersal distance) with a 3-year lag. Comparison of modelled b) Larval retention (%) and d) Dispersal distance (km) with 3-year (backwards) lagged burrow densities. Trend lines indicate significant relationships from distributed lag models (see Results) and shading represents 95% confidence intervals.

4.9. Appendix

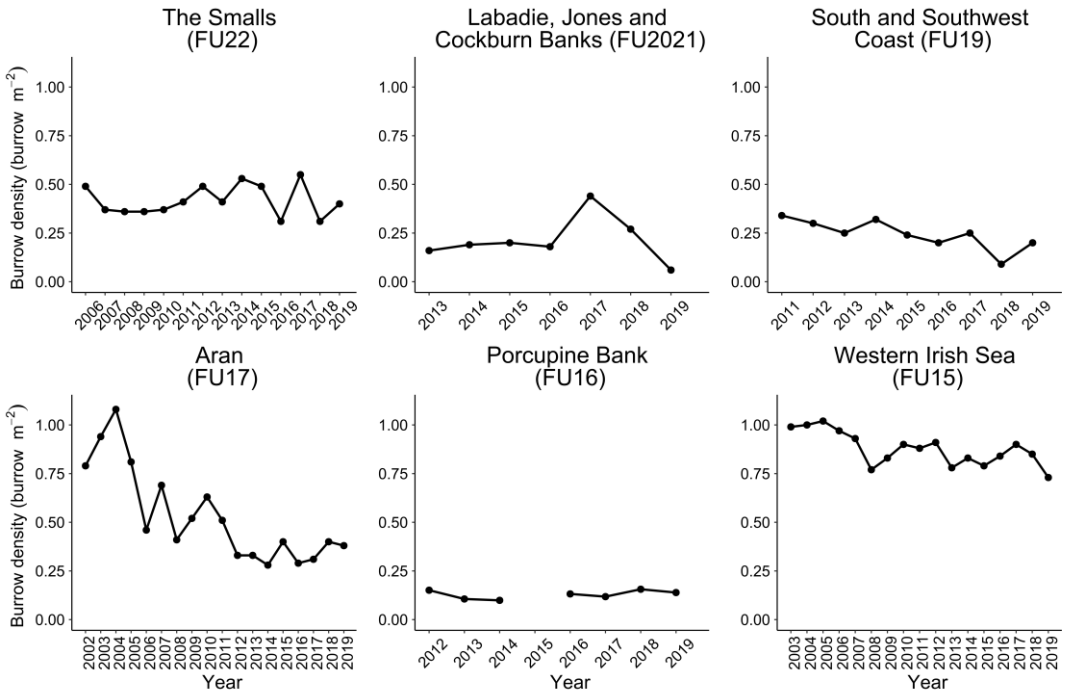

Figure A1. Time series of burrow density estimates (burrow m^{-2}) obtained from underwater television surveys on Irish Functional Units (FU).

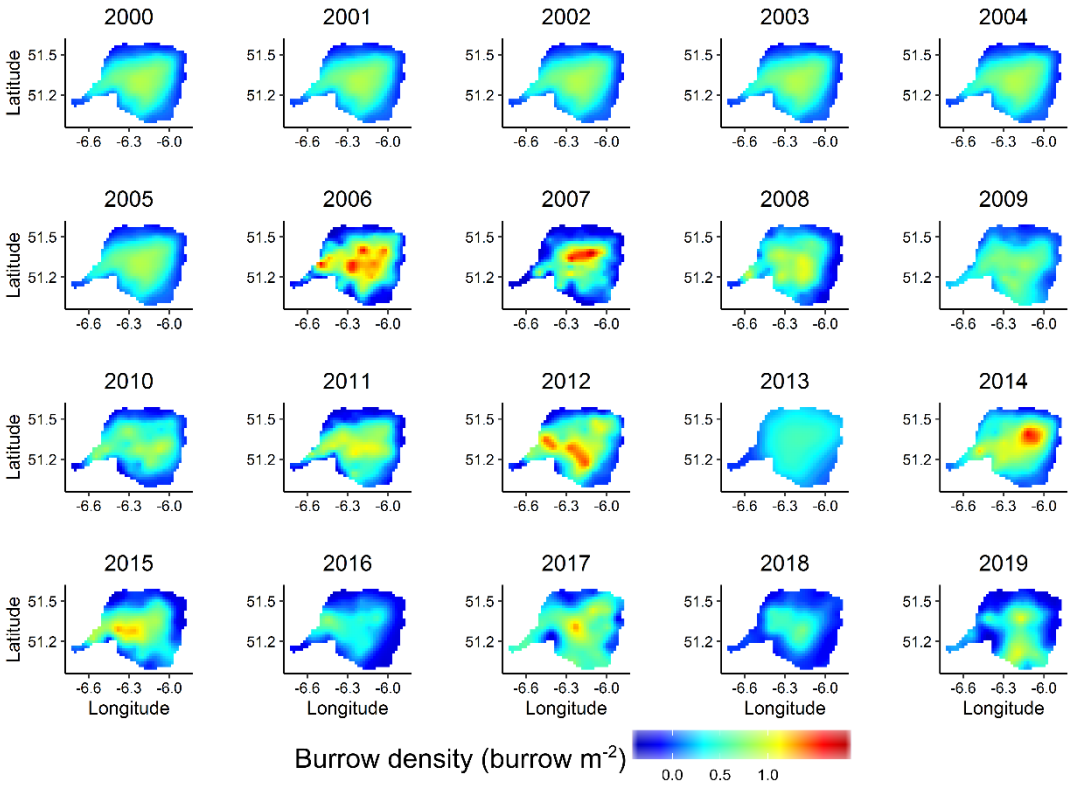

Figure A2. Spatial distribution of *N. norvegicus* burrow densities from underwater TV survey on the Smalls (FU22) ground. Initial horizontal distribution of particles was based on spatial distribution of burrows, whereby higher proportions of particles were released from areas of the ground with higher burrow densities. Please note number of particles remained constant (10,000) for each release. For years that burrow distribution data were unavailable, an average distribution of available years was used (2000 - 2005).

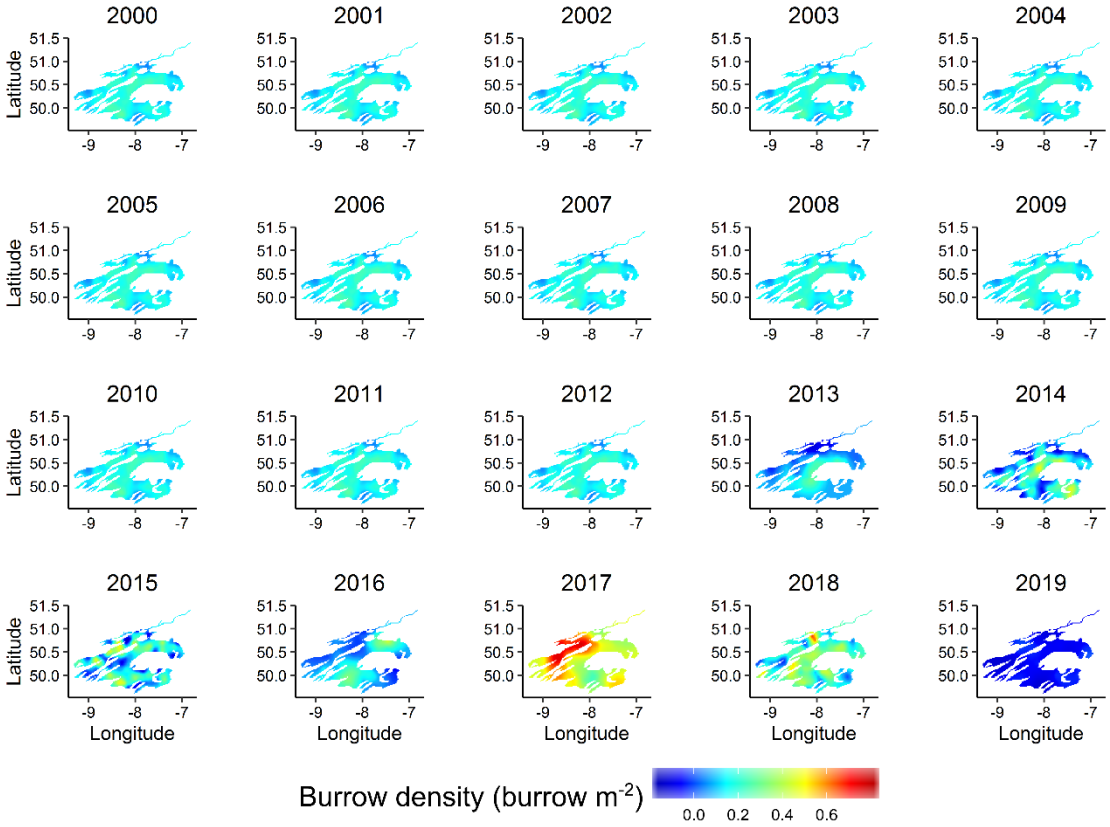

Figure A3. Spatial distribution of *N. norvegicus* burrow densities from underwater TV survey on the Labadie and Banana (FU2021) grounds. Initial horizontal distribution of particles was based on spatial distribution of burrows, whereby higher proportions of particles were released from areas of the grounds with higher burrow densities. Please note number of particles remained constant (10,000). For years that burrow distribution data were unavailable, an average distribution of available years was used (2000 - 2012).

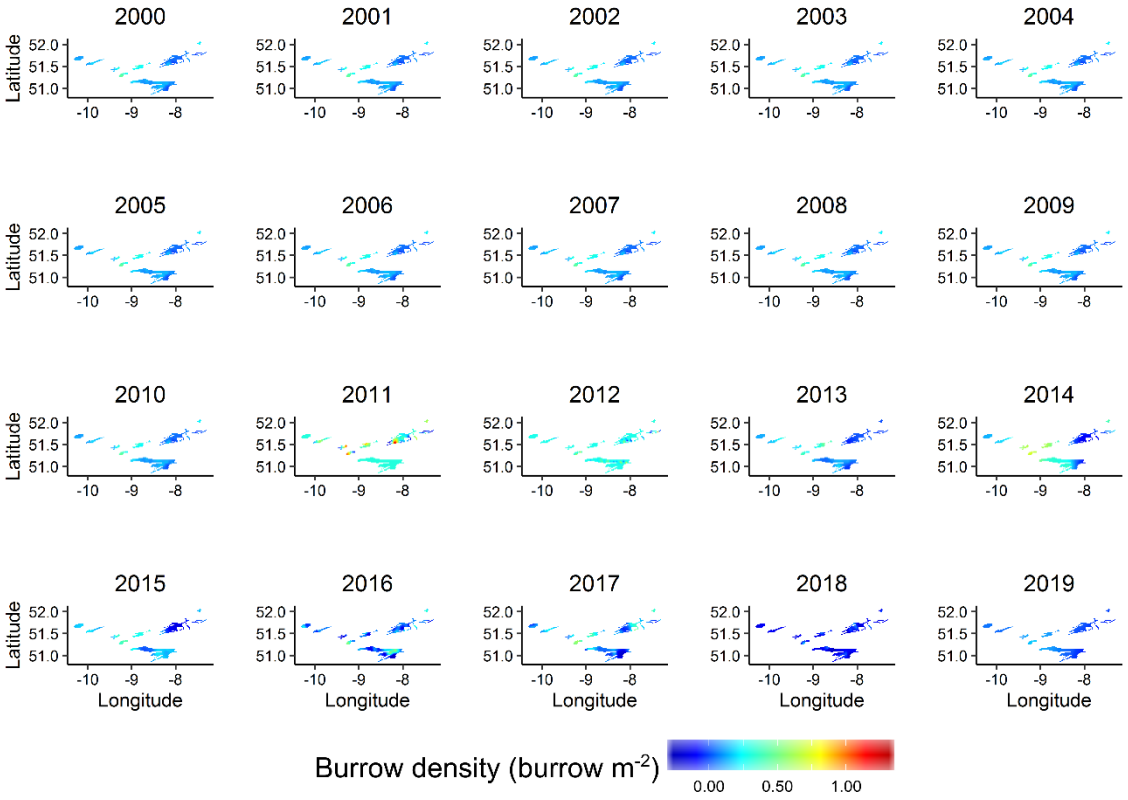

Figure A4. Spatial distribution of *N. norvegicus* burrow densities from underwater TV survey on the South Coast (FU19) grounds. Initial horizontal distribution of particles was based on spatial distribution of burrows, whereby higher proportions of particles were released from areas of the grounds with higher burrow densities. Please note number of particles remained constant (10,000). For years that burrow distribution data were unavailable, an average distribution of available years was used (2000 - 2010).

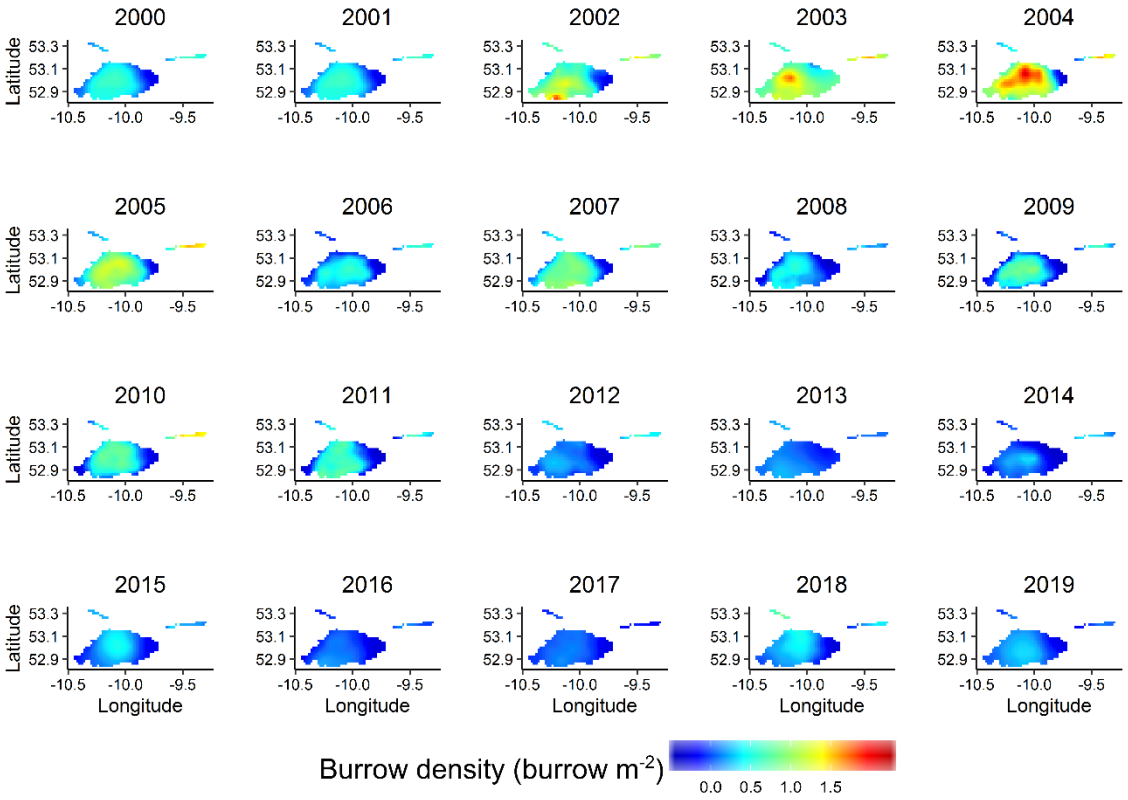

Figure A5. Spatial distribution of *N. norvegicus* burrow densities from underwater TV survey on the Aran (FU17) grounds. Initial horizontal distribution of particles was based on spatial distribution of burrows, whereby higher proportions of particles were released from areas of the grounds with higher burrow densities. Please note number of particles remained constant (10,000). For years that burrow distribution data were unavailable, an average distribution of available years was used (2000 and 2001).

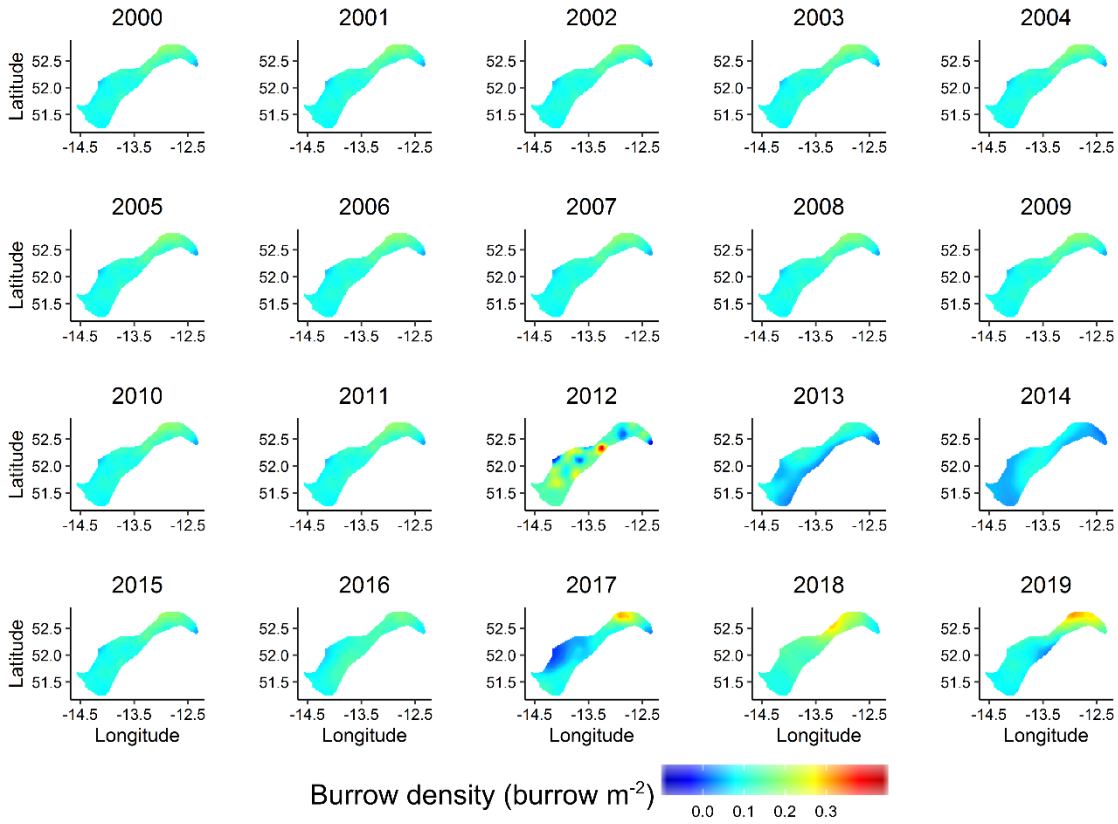

Figure A6. Spatial distribution of *N. norvegicus* burrow densities from underwater TV survey on the Porcupine (FU16) ground. Initial horizontal distribution of particles was based on spatial distribution of burrows, whereby higher proportions of particles were released from areas of the ground with higher burrow densities. Please note number of particles remained constant (10,000). For years that burrow distribution data were unavailable, an average distribution of available years was used (2000 - 2011 and 2015).

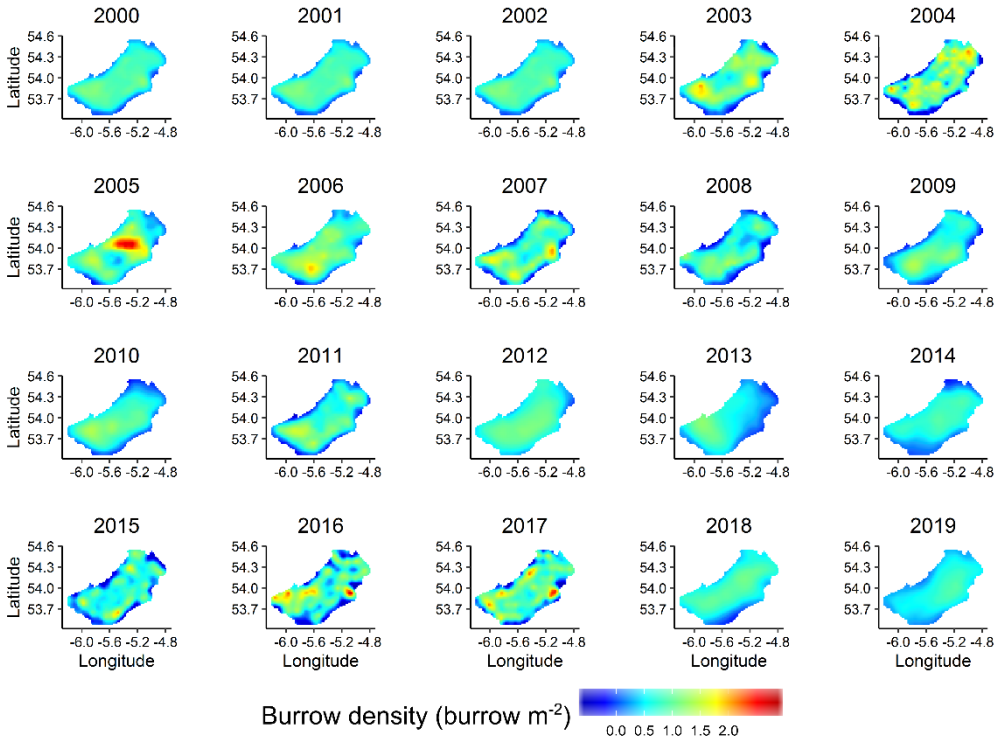

Figure A7. Spatial distribution of *N. norvegicus* burrow densities from underwater TV survey on the western Irish Sea (FU15) ground. Initial horizontal distribution of particles was based on spatial distribution of burrows, whereby higher proportions of particles were released from areas of the ground with higher burrow densities. Please note number of particles remained constant (10,000). For years that burrow distribution data were unavailable, an average distribution of available years was used (2000 - 2002).

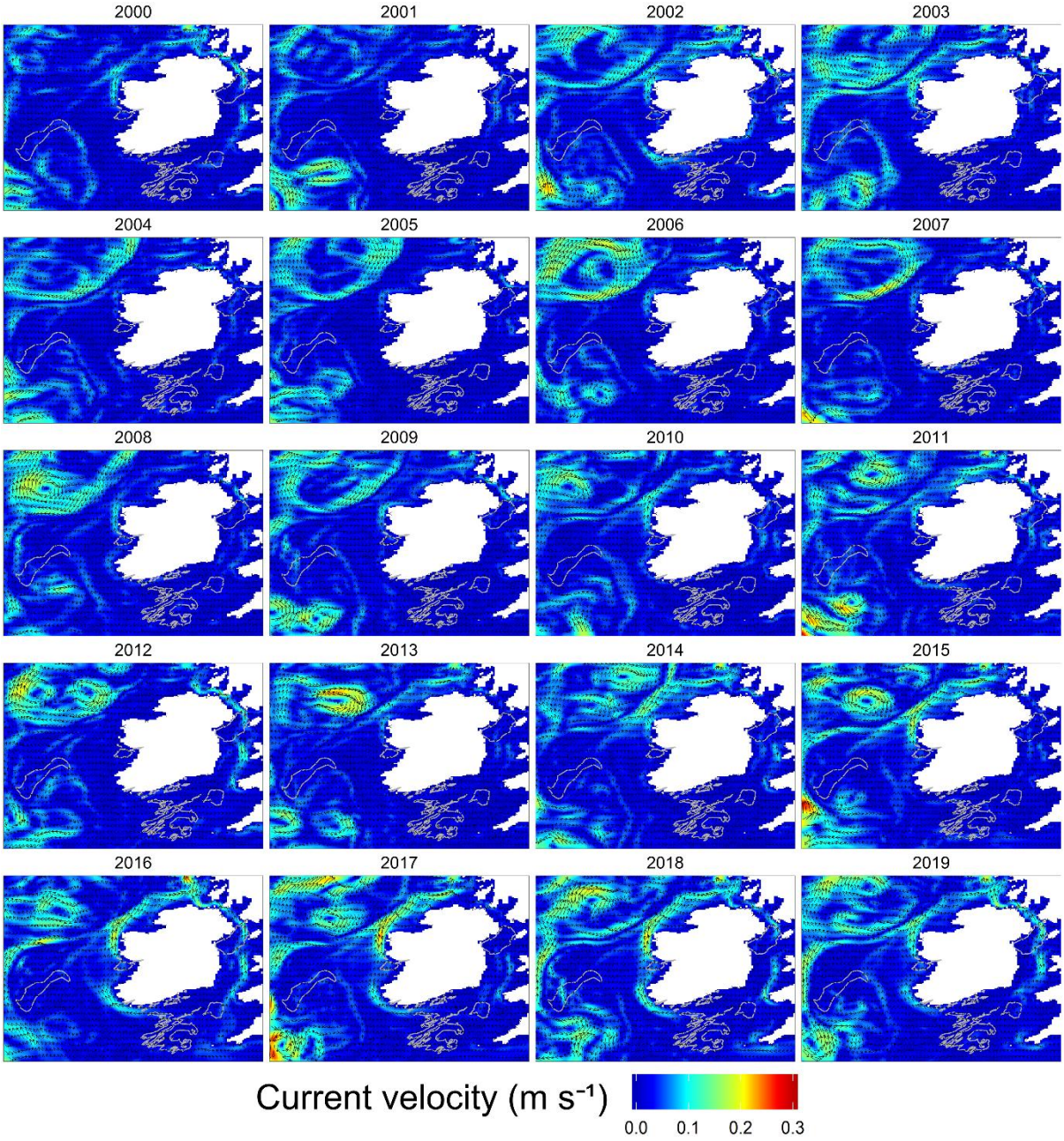

Figure A8. Average April - June current directions and velocities between 10 m and 20 m depth from HYCOM output (2000-2019) indicating the hydrographic regime off the coast of Ireland during the *N. norvegicus* larval season. Arrow orientation indicates current direction. Arrow length and tile colour represents current velocity. Grey line indicates *N. norvegicus* functional units.

Chapter 5

General Discussion

5.1. Discussion

The overall objective of the study was to test whether *Nephrops norvegicus* larval transport (retention and dispersal distance) can influence adult population density fluctuations. For species like *N. norvegicus* with narrow habitat requirements and a sedentary adult stage, the pelagic larval phase enables colonisation of new areas and connectivity between populations separated by uninhabitable substrate. Due to the importance of postlarvae settling on mud habitat for survival, larval supply may constrain recruitment in populations with limited and/or variable larval retention and imports. A biophysical larval transport model was implemented to test the aforementioned objective. Due to the importance of biological characteristics in larval transport (e.g. spawner distribution, hatching time, larval development and vertical behaviour), it was important to accurately parameterise this component of the model prior to performing simulations.

In Chapter 2, key findings relating to the vertical distribution and Diel Vertical Migration (DVM) of *N. norvegicus* larvae were presented. Simulations were conducted to test the importance of DVMs in larval transport and indicated that in areas where circular gyres occur, like the in western Irish Sea (WIS), DVMs can decrease retention. In Chapter 3, historical zooplankton datasets in the Irish Sea were used to examine larval phenology from the 1980s to the 2000s. An earlier phenology shift was identified and attributed to ocean warming due to the role of temperature in determining embryo incubation duration. Modelling indicated that the observed phenology shift had a limited effect on larval transport, although larval retention and dispersal distance was subject to intra-seasonal, inter-annual and spatial variability. Larval duration was also relatively unaltered as surface temperatures had similarly undergone warming over the same time period. Finally, in Chapter 4, a 20-year time series of larval retention, dispersal distance and connectivity estimates were produced for 6 Functional Units (FUs) in Irish territorial waters. The larval transport time series enabled the classification of FUs according to their capacity to retain, import and export larvae. A number of larval transport trends were detected over the time series and could be important for predicting the future outlook of particular stocks. The key findings of Chapter 4 was the link between modelled larval retention/dispersal distance and empirical burrow densities (with a 3-year lag) on the Aran grounds. Therefore, the

results presented in Chapter 4 support the primary hypothesis that larval transport can influence population density fluctuations in *N. norvegicus*.

In Chapter 2, the main objectives were to describe the vertical distribution of *N. norvegicus* larvae, identify biotic and abiotic factors that influence vertical distribution and examine whether larvae perform a DVM. *Nephrops norvegicus* larvae primarily inhabit the upper 40 m of the water column (Hillis 1974; Lindley et al. 1994), though, few studies in the past have examined vertical distribution and DVMs in great detail. The vertical positioning of planktonic organisms can have a determining role in transport patterns due to depth-varying currents and also their likelihood of predator and prey encounters (Huntley and Brooks 1982; Bollens and Frost 1989; Queiroga and Blanton 2005). The vertical distribution of *N. norvegicus* larvae was influenced by temperature, zooplankton biomass and less so from potential energy anomaly. Development is temperature-dependent, therefore, larvae showing a preference for warmer layers of the water column are reducing larval duration (Thompson and Ayers 1989; Dickey-Collas et al. 2000b) and potentially the probability of transport away from suitable habitat (Shanks 2009). However, exposure to warmer temperatures also increases metabolic activity and consequently, food demand (Clarke and Fraser 2004; Jones 2009). A response to zooplankton biomass levels was also observed, larvae were shallower when biomass levels were low and deeper when high. This behaviour suggests that when food availability is low, to avoid starvation larvae occupy shallower depths where biomass was generally more abundant, though risk of mortality by visual-based predators is also elevated. Mortality rates are high for meroplankton larvae (Rumrill 1990), therefore, exhibiting behavioural plasticity that balances feeding and predation risk may enhance survival probability. The specific mechanism mediating the response may be a starvation-induced increase in positive photoaxis which would attract larvae closer to the sea surface during the day, similar to that observed in *Rhithropanopeus harrisii* larvae (Cronin and Forward 1980).

Across the earth's oceans DVMs are common in zooplankton, and Nocturnal DVMs are thought to primarily be used for predator avoidance by occupying surface waters at night when risk of visual predation is lowest (Hays 2003). *Nephrops norvegicus* larvae completed an ascent at dusk and a descent at dawn, indicating their migration was in response to rapidly changing light levels (Forward 1988). Potential explanations for the

'midnight sink' are more complex and range from satiation to avoiding predators that also vertically migrate (Simard et al. 1985; Tarling et al. 2002). As zooplankton sampling was conducted during the early stages of the larval season in the WIS, the DVM behaviour could only be observed in Stage I larvae due to a relative lack of Stage II and III larvae in samples. Differences in vertical distribution between larval stages have been recorded in other species such as the American lobster, where Stage I and IV occupy shallow water while Stage II and III prefer deeper areas (Stanley et al. 2016). Late season larval sampling is required to examine if Stage II and/or III larvae show contrasting DVM behaviours to Stage I, though consistent differences in depth distribution between stages were not evident in previous studies (Hillis 1974; Smith 1987; Lindley et al. 1994).

According to larval transport modelling, the twilight DVM performed by *N. norvegicus* larvae in the WIS reduced retention and increased dispersal distance in comparison to remaining fixed at 20 m depth. The discovery of a seasonal, cyclonic, near-surface gyre forming in spring in the WIS was thought to enhance retention of *N. norvegicus* larvae and promote high adult densities for the WIS *N. norvegicus* population (Hill et al. 1994, 1996). However, the findings of Chapter 2 support that of Phelps et al. (2015), that is, DVMs reduce larval retention when gyres are present as larvae move away from retention-enhancing gyral currents for part of the diel cycle. Furthermore, peak larval hatching in the WIS occurs in April and early May when the gyre is only beginning to establish, and the gyre does not reach its peak until July when most larvae have settled (Olbert et al. 2011). The gyre is quite consistent in its formation timing, although larval hatching has shifted earlier in previous years (see Chapter 3), further reducing temporal overlap between larvae and the gyre (Hill et al. 1996; Olbert et al. 2011). Despite the perceived negative effect of DVM on larval retention, due to the enclosed nature of the WIS and relatively weak currents, the WIS ground maintained the highest retention levels in Irish waters (see Chapter 4).

Several studies to date have modelled larval transport in *N. norvegicus* (Marta-Almeida et al. 2008; O'Sullivan et al. 2015; Phelps et al. 2015). When the extent of a DVM is unknown, both passive and active vertical behaviours are often simulated to account for uncertainty, and as a result, contrasting larval transport patterns are frequently demonstrated (Marta-Almeida et al. 2008; Phelps et al. 2015). Variation in transport

patterns due to vertical positioning underlines the importance of correct model parameterisation of vertical behaviour, supported by empirical data (Metaxas and Saunders 2009).

In Chapter 3, a larval phenology shift in the Irish Sea was identified and attributed to increasing sea temperatures. Ocean warming has led to changes in abundance, distribution and phenology of many marine species (Poloczanska et al. 2016). In response to increasing temperatures, mobile species can alter their geographical distribution, often in poleward directions, to occupy suitable thermal conditions (Beaugrand et al. 2009; Bruge et al. 2016). For less mobile species, such as *N. norvegicus*, that are fixed to patches of suitable habitat and lack migratory behaviour, adults must remain in place and adjust to warmer conditions. However, *N. norvegicus* can withstand a wide range of thermal conditions which is reflected in their distribution from Iceland to the Mediterranean (Bell et al. 2006; Johnson et al. 2013). Species with fixed distributions are however, prone to changes in phenology which can manifest in several forms, for example, timing of spawning, larval hatching or breeding. Many marine species have exhibited phenology changes and a common pattern is earlier for spring phenology events and later for autumn events (Edwards and Richardson 2004; Brown et al. 2016). Later autumn phenology events are thought to occur when cooler conditions are preferred, such as in the northern limpet which exhibits later spawning and higher likelihood of reproductive failure in warmer conditions (Moore et al. 2011). Irish *N. norvegicus* populations have a spring phenology and an earlier shift was identified in the WIS. Ocean warming was identified as the most likely causal mechanism due to the importance of temperature in determining embryo incubation duration. A model of larval release timing using Irish Sea temperature data from Port Erin provided similar larval phenology estimates to those using empirical zooplankton time series. The findings provide evidence that ocean warming has caused a contraction of the embryo incubation period which led to earlier larval phenology in *N. norvegicus*.

After larval hatching, females moult and mate while in the soft post-moult condition. Spawning (i.e. egg extrusion) phenology is an important consideration when estimating larval release date. That is, if an earlier larval phenology leads to females moulting, mating and spawning earlier, then larval phenology would be even earlier again the following year. However, the timing of spawning in *N. norvegicus* appears to be

relatively synchronous between populations with an annual reproductive cycle, mainly occurring in August/September (Bell et al. 2006). Despite larval phenology occurring as early as December in the Mediterranean, females appear to delay spawning until autumn (Orsi Relini and Relini 1989). Though temperature is the main determinant of larval phenology, it does not appear to have much of an influence on spawning phenology. Instead, alternative factors induce spawning such that it is relatively synchronous between populations. However, research is needed to identify the major factors that induce spawning in *N. norvegicus* populations.

Larval phenology, as well as inter-annual and spatial variability, can be an important influence on larval transport. On the Aran, Porcupine Bank and WIS grounds, release day had a significant effect on larval retention and dispersal distance (see Chapters 3 & 4). Earlier releases were associated with longer Pelagic Larval Durations (PLDs; due to cooler temperatures), lower retention and higher dispersal distances. However, the observed phenology shift on the WIS ground appeared to have a limited effect on larval transport. Larval phenology has shifted earlier at a rate that surface temperature increase has kept pace with, therefore, earlier hatching larvae experience similar temperatures to that of later hatching larvae several decades ago. The WIS ground benefits from good larval retention throughout the larval season with only extremely early and late hatchers having large differences in retention and dispersal distance, primarily due to contrasting PLDs. Despite a limited effect in the WIS, phenology shifts may have more pronounced implications for larval transport elsewhere such as in coastal regions of the Bay of Biscay, where drift patterns of anchovy early life stages shift from northward to southward in May (Huret et al. 2010).

In Chapter 4, a time series of larval transport estimates demonstrated the capacity for larval retention and connectivity of 6 Irish *N. norvegicus* FUs. Larger grounds such as WIS and Labadie & Banana had high and consistent retention from year to year. Although the Porcupine Bank ground was also large in size, it had considerably lower retention and higher dispersal distances. For smaller grounds, such as the Aran, Smalls and South Coast grounds, retention and dispersal distance fluctuated more often between years. In the case of the Aran and South Coast grounds, a general decline in retention over the time series was evident. For Celtic Sea FUs, larval imports from nearby grounds often mitigated against poor retention. However, imports were limited

on the Aran, Porcupine Bank and WIS grounds due to their relative spatial isolation, though low imports were less of a concern for the latter due to high retention.

As *N. norvegicus* postlarvae must settle on suitable mud habitat to survive, larval supply is a crucial process that enables recruitment. Modelling indicated that annual larval settlement rates were low and highly variable on certain FUs. Information such as this can be essential in monitoring and management of exploited species as it may reveal limiting constraints on recruitment. Recruitment is difficult to measure due to problems associated with ageing, juvenile sampling and year class separation using length data (Farmer 1973; Cobb and Wahle 1994). The primary stock assessment method for *N. norvegicus* involves the use of underwater television (UWTV) to count adult burrows and estimate absolute abundance (Leocádio et al. 2018). Periods of low recruitment are usually not identified until they manifest in the adult population. Ideally they would be spotted much earlier so measures could be implemented to protect the population. Several *N. norvegicus* FUs have displayed fluctuations in annual burrow density estimates which suggests inter-annual recruitment variability (ICES 2020). The observed link between modelled larval retention/dispersal distance and empirical burrow densities indicate that low larval supply has contributed to past density declines on the Aran grounds and its inability to recover. These findings demonstrate the importance of larval settlement to recruitment and the potential benefits of applying larval transport information to the assessment procedures of *N. norvegicus* as an early warning signal of low recruitment. Information may also be useful for similar benthic species with specific habitat requirements and a planktonic life phase.

Larval supply is more likely to constrain recruitment in scenarios where populations exhibit low and changeable larval retention and spatial isolation limits imports of larvae, such as was demonstrated on the Aran grounds. For the Aran grounds and similar populations, larval transport information can provide a valuable index that enables the identification of low larval supply leading to poor recruitment. However, in high density populations such as the WIS ground where larval settlement rates likely exceed carrying capacity (Hill and White 1990), alternative factors post-settlement may have a greater influence on recruitment. Nonetheless, biophysical models offer valuable information on a key life cycle stage for *N. norvegicus* regardless of population and can be

employed to identify instances of poor settlement and long-term trends in larval transport patterns throughout its distribution.

5.2. Future Work

Biophysical larval transport modelling efforts may be improved by adding a component that reflects feeding conditions. Starved *N. norvegicus* larvae exhibit slower development and starvation for more than one day leads to significantly increased mortality (Smith 1987). Therefore, despite favourable hydrodynamic conditions for larval settlement, unfavourable feeding conditions could lead to high rates of starvation mortality. In Chapter 2, it was evident that zooplankton biomass levels in April were higher off the west coast of Ireland compared to the Irish Sea. Therefore, April hatching larvae on the Aran and WIS grounds would have been subject to contrasting feeding conditions, potentially affecting development and mortality. Low zooplankton biomass along with increased spring temperatures were implicated in a recruitment decline in North Sea cod (Nicolas et al. 2014). In addition, *N. norvegicus* larval phenology is shifting earlier in response to ocean warming (see Chapter 3). Despite many species exhibiting phenology shifts, response to environmental change varies across trophic levels, making mismatch more likely (Edwards and Richardson 2004; Poloczanska et al. 2013). Copepod abundance in several areas of the North Atlantic have declined in recent decades perhaps indicating spatial shifts in zooplankton groups, which ultimately may affect prey availability for *N. norvegicus* larvae (Pitois and Fox 2006). Implementing a model feeding component requires knowledge of optimal prey concentrations for survival. Several experimental studies have demonstrated the effect of diet and starvation on growth and mortality of *N. norvegicus* larvae and their findings could be utilised to add a feeding element to the model (Smith 1987; Rotllant et al. 2001; Pochelon et al. 2009).

A predation component may also be beneficial, *N. norvegicus* larvae are likely to be predated by ctenophores, jellyfish and plankton eating fish (Farmer 1975). In the Irish Sea, jellyfish abundance has increased from 1994 - 2009 due to increasing surface temperatures (Lynam et al. 2011). Large numbers of *N. norvegicus* larvae have been observed in the tentacles of *Cyanea* spp. indicating they are an important predator and

future predation mortality rates may become more intense with increasing jellyfish abundance (Bastian et al. 2014). Predator and prey information could potentially be provided by the low and mid-trophic component of the Spatial Ecosystem and Population Dynamic Model (SEAPODYM) produced by Collecte Localisation Satellite (CLS) with 2D fields of zooplankton concentrations and 6 groups of micronekton (Lehodey et al. 2008, 2010). Output is available from 1998 to present at a weekly temporal resolution and 0.25° spatial resolution. The model is forced by temperature, currents, primary production, euphotic depth and dissolved oxygen levels. Zooplankton concentration in the model represents small organisms ranging in size from 200 µm - 2 cm and would be suitable to mimic feeding conditions. Whereas, 6 micronekton variable groups are defined based on vertical distribution and migratory behaviour. These represent organisms in the size range 2 - 20 cm and could be used to mimic predation risk. An approach that incorporates hydrodynamic conditions as well as mortality rates would be valuable to help identify the most important processes affecting larval recruitment and also the effect of phenology on larval mortality could be fully examined.

To correctly parameterise model larval release timing, sampling was conducted for the Aran grounds and historical zooplankton data as well as findings of previous studies were used for the WIS ground (Nichols et al. 1987; Dickey-Collas et al. 2000a). It was demonstrated in Chapter 3 & 4 that release timing has a significant effect on larval retention and dispersal distance for several grounds. Therefore, dedicated larval sampling should be conducted on the Porcupine Bank and Celtic Sea grounds to ensure larval release timing is accurately represented in model simulations. Alternatively, Continuous Plankton Recorder (CPR) data could be used to this end. Furthermore, CPR data could also be utilised to examine long term trends in larval phenology and abundance for populations outside of the Irish Sea (see Hays et al. 2005).

Scaling a ground's larval production based on its abundance, or more precisely its spawning stock biomass, would give a more accurate contribution of larval imports to overall settlement levels. For example, 1% of exports is considerably more larvae if its origin was the high abundance WIS (4400 million) ground compared to the South Coast (430 million) grounds (Doyle et al. 2019; Lundy et al. 2019). A further consideration for estimating larval production is that fecundity is correlated with female size, so more

larvae are hatched from females in populations such as the Porcupine Bank ground which has low densities of large adults (Bell et al. 2006; Johnson et al. 2013). Nonetheless, UWTV surveys are now conducted on each Irish *N. norvegicus* FU annually, meaning that abundance estimates are readily available each year. Therefore, future larval transport modelling efforts can weight larval production based on population abundance and incorporate this information into connectivity estimates.

Another potential model improvement that requires dedicated research is whether postlarvae at settlement stage can respond to sensory cues to find and orientate themselves towards suitable habitat (Swearer et al. 2019). Reef fish and crustacean larvae display behaviour that suggests orientation towards auditory and olfactory cues that assist with settlement on reef habitat (Montgomery et al. 2006; Gerlach et al. 2007). It is also interesting to note that in experimental settings, *N. norvegicus* postlarvae show a preference for burrows which were excavated and previously occupied by adults as opposed to artificial hand constructed burrows, suggesting a response to a chemical stimulus produced by adults (Powell and Eriksson 2013).

In Chapter 3 & 4, Hybrid Coordinate Ocean Model (HYCOM) output was used to represent oceanographic conditions in larval transport simulations. HYCOM is a global model that is widely used in larval transport studies and has a 3-hourly temporal resolution and a 1/12° (~9 km) spatial resolution between 40 °S and 40 °N and 1/24° (~4 km) resolution poleward of these latitudes (Chassignet et al. 2007; Kendall et al. 2016; Blanco et al. 2019; Swearer et al. 2019). Model output was available from 1994 to present for HYCOM, making it suitable to examine long-term trends in larval transport dynamics. A Northeast Atlantic ROMS model for Irish territorial waters has been developed by the Marine Institute and has been operational since 2008 (Dabrowski et al. 2016). It is highly resolved with a 3- and 1-hour temporal resolution, 1.1 - 1.6 km horizontal resolution in coastal areas and 40 vertical levels. The Northeast Atlantic ROMS model was suitable for use in Chapter 2 as the objective of larval transport modelling was to compare DVM behaviours in 2018. It is important to choose a model that will adequately fulfil the requirements of research objectives, e.g. resolution, time frame and domain size.

Due to its high spatial and temporal resolution and extensive validation in the area of interest, the Northeast Atlantic ROMS model may be better suited for future *N.*

norvegicus larval transport studies in Irish waters (Nagy et al. 2020), particularly if larval transport information is to be adopted into its assessment protocols. Two higher resolution (200 - 250 m) models are nested within the Northeast Atlantic model and encapsulate or are in close proximity to the Aran (Connemara model) and South Coast (Bantry Bay model) *N. norvegicus* grounds. In addition, the Scottish operational west coast Finite Volume Community Ocean Model (FVCOM) is also nested within the Northeast Atlantic ROMS model (Aleynik et al 2016). Of course it would also be interesting to compare larval transport results using ROMS and HYCOM models. Hufnagl et al. (2017) compared 11 North Sea models (not including Northeast Atlantic ROMS or HYCOM) to examine variability between models and although inter-annual trends in larval transport were similar, variations in absolute values were reported. Ocean model validation is also important to compare estimated current velocities with observed values. In 2018, an Acoustic Doppler Current Profiler (ADCP) was deployed on the Aran grounds to collect empirical current velocity data throughout the water column. However, only on recovery it was discovered that the ADCP did not settle on the seabed correctly and ultimately failed to collect usable data.

Future work should attempt to test and validate larval transport estimates with empirical observations. It is extremely difficult to directly track planktonic larvae *in-situ* due to their minute size, long larval durations and vast dispersal area, possibly explaining why few studies have taken on this challenge (Swearer et al. 2019). Larval sampling could be conducted in areas away from the natal ground that have been recognised from model observations as dispersal hotspots. For example, large proportions of larvae from the Aran grounds were transported north into Donegal Bay. Larval sampling which tests for the presence of *N. norvegicus* larvae along the northwest and west coast of Ireland could be an effective method of validating model transport predictions. In areas where several grounds are closely situated, mixing of larvae from several grounds could make it difficult to distinguish where larvae originated. Therefore, validation efforts with the use of larval sampling would likely be more effective for relatively isolated populations. Genetic parentage data may also be used to validate dispersal pathways observed in simulations (Bode et al. 2019).

Another potential method of validation is the use of small underwater robots which record near real-time data (latitude, longitude and depth) as they are transported by

currents and can be programmed to perform vertical migrations that mimic larval behaviour in the water column (Jaffe et al. 2017). However, transport distances are currently limited as robots can only detect pings from surface floats at a range of 5 - 6 km (Jaffe et al. 2017), though efforts to enable larger transport times and distances could make this an attractive method of observing and validating larval transport against model estimates in the future. All in all, validation efforts can establish credibility and promote confidence in model observations, particularly if they are to inform fishery management decision-making.

Numerous *N. norvegicus* populations are distributed across the Northeast Atlantic and Mediterranean and several have undergone stock fluctuations (ICES 2020). Biophysical larval transport models offer an opportunity to examine whether stock fluctuations are due to larval settlement constraints on recruitment. Up to 2019, only two Irish FUs have UWTV burrow density time series lasting more than 15 years (Aran and WIS grounds). Whereas, several Scottish and English grounds (Farn Deeps FU6, Fladen FU7, Firth of Forth FU8, Moray Firth FU9, North Minch FU11, South Minch FU12, Clyde FU13) have UWTV time series well in excess of 15 years (ICES 2020). Grounds such as the Farn Deeps, Fladen, Firth of Forth and Clyde have also displayed fluctuations and trends over their time series (ICES 2020). It would be useful to construct a time series of modelled larval transport estimates for these grounds and examine whether a link with population density exists. Such an exercise could be used to examine if the findings in Chapter 4 are similarly observed in other areas, specifically whether larval retention and dispersal distance influence population density. Also, to get a true picture of *N. norvegicus* population connectivity, a large scale larval transport study that releases virtual larvae from each of the large habitat areas across its distribution would provide valuable insights into larval exchange and enable identification of isolated habitat patches and metapopulations within the wider species context.

Biophysical models may also be successfully applied to examine larval transport patterns of other species with planktonic larval phases, particularly those of commercial or conservation importance. From a fishery management point of view, larval transport information can supplement assessment procedures by providing insights into larval supply and exchange between populations. Each of the 10 most captured fishery species worldwide in 2018 (anchoveta, Alaska pollock, skipjack tuna, Atlantic herring, blue

whiting, European pilchard, Pacific chub mackerel, yellowfin tuna and Atlantic cod) have planktonic egg and/or larval phases (FAO 2020). The United States most important fishery species, the American lobster (*Homarus americanus*) is similar to *N. norvegicu*s with ovigerous females carrying eggs on the underside of the abdomen during incubation after which planktonic larvae hatch to begin the pelagic phase of the lifecycle (Factor 1995).

Conservation efforts can also benefit from larval transport information by quantifying larval retention within or exchange between existing or proposed Marine Protected Areas (MPAs; Kaplan et al. 2009; Fox et al. 2016). It may also assist efforts to conserve meroplankton species classified as endangered/critically endangered by the International Union for Conservation of Nature (IUCN), e.g. fan mussel (*Pinna nobilis*), seventy-four seabream (*Polysteganus undulosus*) and Atlantic halibut (*Hippoglossus hippoglossus*). Another application could be to identify potential dispersal pathways and to track the spread of marine invasive species (David et al. 2015; Stuer-Lauridsen et al. 2018). In addition, models may complement genetic studies to examine gene flow and identify genetically isolated populations (Segura-García et al. 2019; Valencia et al. 2020). Biophysical modelling has great potential as a tool in larval ecology research; however, to ensure confidence in model output, model parameters such as larval timing, developmental rates and behaviour must be supported by empirical information.

Future climate change may impact larval development, survival and transport through changes to temperature, circulation patterns, salinity, oxygen, pH, predators and prey (Graham and Harrod 2009; Bashevkin et al. 2020). Biophysical models enable users to examine how larvae are impacted by these changes. However, ocean models providing future climate change scenarios are first required to project future effects. In the Mediterranean, an emissions driven model for 1970 - 2099 was used to demonstrate a 10% decrease in dispersal distance, 5% decrease in retention and 5% increase in connectivity between MPAs (Andrello et al. 2015). Moreover, eastern rock lobster larval dispersal off southeastern Australia was compared between the 1990s and 2060s, and despite ocean warming being favourable towards larval survival, this effect was counteracted by fewer larvae reaching coastal habitat due to intensification of currents (Cetina-Heredia et al. 2015). Olbert et al. (2012) presented a regional model for 1980 - 2099 that suggested local climate changes in the Irish Sea contrast from those projected

on a global scale. Projections included surface temperature increases of 1.9 °C, stronger warming in shallow areas, later shift of the annual temperature minima and maxima by approximately two weeks, strengthening of the WIS gyre and stronger southward currents, each of which have implications for *N. norvegicus* larval phenology, development and transport for the commercially important WIS population (Olbert et al. 2012). The use of ocean models that project future scenarios can, therefore, provide value by assisting efforts to forecast the effects of climate change on larval dynamics.

5.3. References

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