Understanding the recent range expansion of the hermit crab, *Clibanarius erythropus*, to the British Isles through larval dispersal models and phylogeographic analysis

Submitted by *Christophe William Patterson* to the University of Exeter as a thesis for the degree of *Masters by Research in Biological Sciences*, *September 2020*.

I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

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Abstract

As climate change progresses, the ranges of many species will begin to shift. Which species will have their ranges shifted and where, will have major consequences for conservation, habitat management, agriculture, and human health. This thesis furthers our understanding of the processes that limit and facilitate range expansion by investigating the appearance of the hermit crab *Clibanarius erythropus* to the southwest United Kingdom (UK). Evidence suggests that *C. erythropus* arrived in the southwest UK via the species' pelagic larvae drifting on ocean currents. The Mer d'Iroise, the historical limit of *C. erythropus'* range, is a biological transition zone where the warm-water species found in the Bay of Biscay transition to the colder-water species of Northern Europe. Consequently, *C. erythropus* may be one of the first of many species whose range will expand to the southwest UK in the future. In chapter one, we study the phylogeographic structure of *C. erythropus* across its historic and newly established range. *C. erythropus* is a rare example of panmixia in the European seascape, indicating that populations of *C. erythropus* are interconnected and that the species has overcome most barriers to gene flow seen in other intertidal species. Panmixia suggests that the range of *C. erythropus* can readily shift with environmental change. In chapter two, we investigate the oceanographic processes that facilitated the transportation of *C. erythropus* to the UK. Using a hydrodynamic model, we simulate the dispersal of *C. erythropus* larvae in the English Channel over a number of years. Simulations suggest the larvae of *C. erythropus* arrived in 2014, originated from North Brittany, experienced a mean temperature of around 16 °C, and took longer than 20 days to be transported across the

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Author's declaration

All research conducted as part of this Masters by Research was carried out by myself, Christophe Patterson, under the guidance of Dr Regan Early and Dr Chris Lowe. Additional input was given by Dr Chris Laing.

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General Introduction

The spatial extent of a species, or a species' range, is governed by physical barriers to dispersal or the climatic tolerances of the species (MacArthur, 1974). Due to the industrial-scale combustion of fossil fuels, habitat destruction, and cement production, the levels of carbon dioxide (CO_2) and other greenhouse gases in the atmosphere have risen considerably since the 19th century (Gregg *et al.*, 2008). The earth's climate has begun to change with marked shifts in temperature and seasonal weather patterns (O'Neill *et al.*, 2017). In regions where the climate shifts, species may find themselves inhabiting areas that they are no longer physically or behaviourally adapted to survive and become locally extinct. (Thomas *et al.*, 2004). Other regions that were previously inhospitable may become more climatically suitable and the ranges of many species will expand to novel areas that they were previously absent from (Parmesan *et al.*, 1999). In short, the ranges of species are beginning to shift (Parmesan *et al.*, 1999; Parmesan & Yohe, 2003; Hickling *et al.*, 2006; Alsos *et al.*, 2007; Hawkins *et al.*, 2008b).

Even when novel climatically suitable habitat is created, a species may still go extinct if its dispersal to new areas is prevented or if the shift in a species' range is slower than the speed at which the climate shifts. The expected number of extinctions due to anthropogenic climate change is hotly contested, but is likely to play a major role in the distribution and level of biodiversity seen beyond the 21st century (Pereira *et al.*, 2010; Thomas, 2010; Bellard *et al.*, 2012; Bates *et al.*, 2014). Predicting which species will undergo range-shifts, and where, has implications for conservation (Marini *et al.*, 2009), habitat management (Gimona *et al.*, 2015), agriculture (Peters *et al.*, 2014), and human health (Tonnang *et al.*, 2010; Kulkarni *et al.*, 2016).

This thesis aims to increase our understanding of the processes that limit and facilitate range expansions by investigating the appearance of the hermit crab, *Clibanarius erythropus*, to the southwest of the British Isles. *C. erythropus* has historically inhabited the Mediterranean Sea and the Atlantic coasts of Spain, Portugal, and southwest France. In the 1950s the range of *C. erythropus* expanded northwards along the coast of France around Brittany (Carlisle & Tregenza, 1961). In the winter of 1959/60, the range of *C. erythropus* crossed the English Channel and appeared in the southwest United Kingdom (UK) (Carlisle & Tregenza, 1961). However, the species did not persist in the southwest UK, disappearing in the 1980s (Southward & Southward, 1988), but then reappeared 30 years later in 2016 (Patterson *et al.*, 2020).

Determining the factors that facilitated the arrival of *C. erythropus* is vital, because *C. erythropus* is one of the first of many warm-water species whose ranges could shift beyond Brittany to the southwest UK with climate change. The Mer d'Iroise, the sea neighbouring the peninsula of Brittany, is described as a biological transition zone where the warm-water species found in the Bay of Biscay transition to the colder-water species of Northern Europe (Ingle & Clark, 2008; Dauvin, 2009; Grall *et al.*, 2015; Gallon *et al.*, 2017; Deli *et al.*, 2019). See Mieszkowska & Sugden (2016) for an in-depth review. If climate change permits warm-water species to extend their ranges further north, the marine and intertidal habitats of the southwest UK and the wider English Channel may see a substantial shift in community composition and structure in the coming decades (Helmuth *et al.*, 2006; Mieszkowska *et al.*, 2006; Hawkins *et al.*, 2008a; Mieszkowska & Sugden, 2016). Studying the range expansion of *C. erythropus* will provide key insights into how the ecological communities of the Western English Channel will change in the coming decades.

The intertidal zone of the UK, and southwest in particular, has been extensively studied and monitored over the last 70 years. As such, the appearance *C. erythropus* has undergone substantial study. After the first record of *C. erythropus* in the UK by Carlisle & Tregenza (1961), Southward and Southward (1977) conducted surveys of *C. erythropus'* distribution and ecology in the UK and Northern France. Surveys from 1960 to 1967 show the species was found from the north coast of Cornwall to the south coast of Devon. Unfortunately, many locations were heavily affected by the 1967 Torrey Canyon oil spill and the subsequent application of toxic cleaning chemicals. Searches conducted during the disaster confirmed multiple dead *C. erythropus*. At two sites, Marazion, which was impacted by the oil spill, and Wembury, which avoided the oil spill, *C. erythropus* continued to be found after the disaster. At both Marazion and Wembury, searches were conducted until 1987 and recorded a declining population until the species was last sighted in 1985. Due to budget constraints these searches were stopped in 1987 and Southward and Southward (1988) declared the species no longer present in the UK. Surveys of Wembury resumed in 1997 and Marazion in 2008 (Hawkins *et al.*, 2017), meaning if *C. erythropus* returned to the UK records of the species should have occurred at either of these sites.

No further records of *C. erythropus* occurred in the UK until March of 2016, when an individual was found at Castle Beach, Falmouth, in Cornwall (Patterson *et al.*, 2020). Subsequently, within a month, sightings of the species were recorded along the north and south coast, including during the now resumed yearly surveys of Wembury and Marizion (Hawkins *et al.*, 2017). Due to *C. erythropus'* highly distinctive features and the active marine recording community in the UK, populations of *C. erythropus* are unlikely to have gone unnoticed for long. It seems *C. erythropus* disappeared from the UK in the 1980s and did not return to detectable levels, if at all, for 30 years. The *C. erythropus* seen in 2016 likely arrived in the UK only a few years prior to 2016.

The Torrey Canyon oil spill has often been cited as the reason *C. erythropus* disappeared from the southwest UK. However, the oil spill does not explain why the species was absent from the UK historically, nor why populations continued to decline and reach undetectable levels after the effects of the disaster had dissipated (Hawkins *et al.*, 2008a). A further suggestion for why *C. erythropus* disappeared, is that the preferred gastropod shell of the species, the Dogwhelk *Nucella lapillus,* was heavily impacted by tributyltin (TBT) pollution and declined throughout the 1970s and 1980s (Hawkins *et al.*, 2008a). However, *C. erythropus* readily inhabits other species of gastropod shell and the lack of Dogwhelks is unlikely to have prevented the return of *C. erythropus* beyond the 1990s, after TBT was banned and populations of *N. lapillus* recovered (Birchenough *et al.*, 2002). In both 1950s and 2010s, *C. erythropus* appeared instantaneously at multiple sites not associated with intensive human activities (Carlisle & Tregenza, 1961; Southward & Southward, 1977; Patterson *et al.*, 2020). The appearance of *C. erythropus* in regions of the UK not associated with intensive shipping activity, suggests that translocation of the species larvae in ballast water is unlikely. Predation can also limit the range of a species (Jankowski *et al.*, 2013) but, in the case of *C. erythropus*, we are unaware of any evidence that links the decline of a predatory species with either the recent or the historical reappearance of *C. erythropus* in the southwest UK.

The remaining proposed reasons for why *C. erythropus* has been historically limited to Brittany and did not return to the UK until 2016, are related to the climate and oceanic currents of the English Channel. Firstly, the populations of *C. erythropus* found in the UK are the highest latitude records of the species and, as such, the sea temperature in the southwest UK may prevent reproduction and be lethal to the species' pelagic larvae. Hawkins *et al.*, (2017) draws attention to the rise in water temperature around the southwest UK in the 1950s as a potential reason for *C. erythropus* initial appearance in 1959/60. The colder water temperatures seen in the southwest UK throughout the 1960s, 70s and 80s, may then have prevented any further influxes of *C. erythropus* larvae and prevented the reproduction of the adult *C. erythropus* that survived the Torrey Canyon oil spill. The sea temperature of Brittany, the closest known populations of *C. erythropus* to the UK, may be too cool for reproduction. This would result in few larvae emanating from Brittany, and thus low propagule pressure on the UK. Alternatively, the oceanic currents in the Western English Channel may only rarely carry *C. erythropus'* larvae from Brittany to the UK, even though water temperatures are adequate for reproduction in Brittany and recruitment in the UK. The decline of the UK populations during the 1980s suggests that *C. erythropus* was unable to successfully reproduce in the UK during this time.

Which factor prevented *C. erythropus* from returning to the UK until the mid-2010s; the climates of Brittany and the southwest UK or the oceanic currents in the English Channel? If oceanic currents prevented *C. erythropus* from returning to the UK even though the sea temperature had returned to hospitable levels, it suggests the English Channel is a major barrier to the dispersal of intertidal species. The English Channel may prevent the ranges of species shifting in response to climate change. In this thesis, I attempt to determine the role climate and oceanic currents played in the range expansion of *C. erythropus* by two methods. Firstly, I investigate the phylogeographic structure of *C. erythropus* in its historic and recently expanded range. Secondly, I model the dispersal of *C. erythropus* larvae in the English Channel in the years prior to the species' arrival in 2016.

Studying the spatial distribution of genetic diversity can provide important insights into the historical and contemporary distribution and connectivity of a species' populations (Maggs *et al.*, 2008). The Last Glacial Period drastically changed the distribution of intertidal habitat in Europe and phylogeographic studies often show how species' ranges responded, for instance retreating into isolated glacial refugia. Understanding how *C. erythropus* shifted its range historically and how connected populations of the species are, could shed light on why *C. erythropus* was one of the first warm-water species to expand into the southwest UK. Low heterogeneity across populations of *C. erythropus* could indicate that populations of *C. erythropus* are interconnected and that the species has overcome most barriers to gene flow that prevented the intermixing of populations of other intertidal species. In chapter one, I investigate the phylogeographic structure of *C. erythropus* using the DNA marker mitochondrial cytochrome oxidase subunit gene (mtCOI). Globally, hermit crabs (Paguroidea) trend towards panmixia but no study has investigated the phylogeographic structure of a European hermit crab across multiple oceanographic regions. Furthermore, studying the genetic distribution of *C. erythropus* in the UK and Brittany could provide evidence for the geographical origin of the *C. erythropus* larvae that reached the UK. Knowing where the larvae of *C. erythropus* originated is important as it will give insight into which species could arrive in the southwest UK in the future.

Chapter two attempts to understand the oceanographic processes that facilitated the transportation of *C. erythropus* to the UK. Studies of larval dispersal in the English Channel have shown no connectivity between Brittany and the southwest UK

(Lefebvre *et al.*, 2003; Nicolle *et al.*, 2017). This suggests the English Channel is a major barrier to dispersal and will limit species' ranges from adequately responding to anthropogenic climate change even if the southwest UK becomes more climatically suitable. However, these prior studies are based on less detailed oceanic models and may not depict the specific biology of *C. erythropus* larvae. In chapter two, I conduct larval dispersal models, to simulate the trajectory of virtual larvae released from Brittany in the years prior to the 2016 appearance of *C. erythropus*. I use these simulations to investigate **1)** whether the larvae of *C. erythropus* can be transported across the English Channel via ocean currents, **2)** when and how often this can occur, **3)** whether the 2016 arrival of *C. erythropus* was caused by a rare (occurring only once in the 5 years simulated) combination of ocean currents, and **4)** where any larvae of *C. erythropus* that reached the southwest UK could have originated from.

Understanding the role that stochasticity of oceanic currents played in the arrival of *C. erythropus* will help predict how often the ranges of other species will expand to the southwest UK as the climate changes. Monitoring the geographic origin of *C. erythropus'* pelagic larvae could show which other species have a high likelihood of future transportation to the UK. The duration of transportation and the temperature experienced by larvae during transportation to the UK will further help predict which species will be able to overcome the barrier of the English Channel in the future.

Chapter 1: The hermit crab *Clibanarius erythropus* shows little phylogeographic structure across the European seascape.

Abstract

Phylogeographic structure is driven by the historic and contemporary connectivity of a species' populations, which gives us key insights into the processes that determine species distributions. The intertidal hermit crab, *Clibanarius erythropus,* has recently undergone a range expansion into the UK. Prior to this study, nothing was known about the phylogeographic structure of *C. erythropus,* and little about other European hermit crabs (Paguroidea). Using mitochondrial cytochrome oxidase subunit gene (mtCOI), from samples collected across Europe, we find that the species has near complete panmixia across and between the regions studied. As such, *C. erythropus* is a rare example of panmixia in the European seascape, where most intertidal species show some level of heterogeneity. Worldwide, species of hermit crab trend towards panmixia and this study is the first to demonstrate a similar pattern in the phylogeographic structure of a hermit crab across Europe. Panmixia indicates that populations of *C. erythropus* are interconnected and that the species has overcome barriers to gene flow that other intertidal species could not. This suggests that the range of *C. erythropus*, and perhaps other hermit crab species, will be able to readily shift in response to environmental change.

Introduction

The spatial distribution of genetic diversity, or phylogeographic structure, arises from the historic and contemporary connectivity of a species' populations. The observed patterns are often complex. Signatures of historical processes, such as vicariant events, can be masked or eroded by contemporary mixing of populations (Taberlet *et al.*, 1998). Disentangling these signatures can allow us to better understand the processes that have historically facilitated or limited a species dispersal and distribution. In particular, phylogeographic structure can demonstrate where barriers have prevented historical and contemporary gene flow between populations (Maggs *et al.*, 2008).

Clibanarius erythropus is an intertidal hermit crab whose range has recently expanded to the southwest United Kingdom (UK), from Brittany. As such, *C. erythropus* has demonstrated the ability to disperse across the Western English Channel which is ~160km wide and dominated by strong oscillating tidal currents making it a prominent barrier to dispersal. *C. erythropus* has a pelagic larval stage that can survive for longer than 31 days (Harms, 1992), meeting the definition of Pascual *et al.*, (2017) that the species has a high dispersal ability. Long lived pelagic larvae may have allowed the species to be carried via ocean currents from Brittany to the southwest UK. Nothing is known about the phylogeographic structure of *C. erythropus* and by extension the genetic structure and diversity of the newly established populations. The appearance of *C. erythropus* in the southwest UK has been linked to the warming waters of the English Channel (Hawkins *et al.*, 2008b; Patterson *et al.*, 2020). If populations of *C. erythropus* have historically had high levels of gene flow between them, this would suggest the species has a high dispersal ability, and confirm the notion that the range of *C. erythropus* could readily shift with environmental change.

The Mer d'Iroise, off the coast of Brittany, is a biological transition zone and is the leading edge for several marine and intertidal species, including *C. erythropus* (Ingle & Clark, 2008; Gallon *et al.*, 2017; Deli *et al.*, 2019). For intertidal decapods, with similar geographic ranges to *C. erythropus*, studies of phylogeographic structure have predominantly focused on the Mediterranean with little attention further north than the Iberian Peninsula (García-Merchán *et al.*, 2012; Sá-Pinto *et al.*, 2012; Fratini *et al.*, 2016; Deli *et al.*, 2018, 2019). The phylogeographic structure of intertidal species is often particularly complex, with certain genetic breaks being distinctive in some species but absent in others (Maggs *et al.*, 2008; Pascual *et al.*, 2017). In the Bay of Biscay and the English Channel, intertidal species show phylogeographic structure (Roman & Palumbi, 2004; Denis *et al.*, 2009; Neiva *et al.*, 2014) but knowledge is limited to species with ranges that extend much further north than Brittany (Roman & Palumbi, 2004; Triantafyllidis *et al.*, 2005; Palero *et al.*, 2008). Species with dissimilar but intersecting ranges do not always show the same phylogeographic structure across the regions in which they overlap (Maggs *et al.*, 2008; Pascual *et al.*, 2017). Consequently, we cannot infer the phylogeographic structure of these leading-edge species from the existing known literature.

Here we investigate the phylogeographic structure of *C. erythropus* at the leading edge of its range, in Brittany and the southwest UK, and its historic range, covering the Mediterranean, Iberian Peninsula, and the Azores. The leading edge of a species' range is expected to have reduced genetic diversity as a consequence of genetic bottlenecks that occur during range expansions (Excoffier *et al.*, 2009; Peter & Slatkin, 2013), but this is not always the case if populations have been established from multiple historically isolated populations - such as glacial refugia (Maggs *et al.*, 2008; Provan & Bennett, 2008). There has been little investigation into the broad patterns of genetic diversity in European Paguroidea (hermit crabs) but globally Paguroidea trend towards panmixia (Negri *et al.*, 2012). As such, the genetic diversity of *C. erythropus,* at margins of its range, is expected to be low, but worthy of investigation as historical and contemporary processes, such as the reconnecting of multiple glacial refugia, could have added additional complexity. The genetic diversity of species in Brittany will strongly influence the genetic diversity of any species that undergo a range expansion to the UK, such as *C. erythropus*. The phylogeographic structure of *C. erythropus* in the UK and Brittany could also be used to infer the geographic origin of the larvae that reached the UK in 2016. This research will further our understanding of the phylogeography of the European seascape and the processes that led to the range expansion of *C. erythropus* to the UK.

Methods

Sample collection.

C. erythropus were collected from ten sites, three in the UK and seven in France, starting in February 2019 and ending in May 2019 (Figure 2). Samples were also received from three sites across Europe; two in Italy and one in Spain. Additional samples were also received from the Azores (Portugal) (Table 1).

Commencing two hours before low tide, the intertidal zone was searched for one hour or until 30 *C. erythropus* were collected from each UK site or 20 *C. erythropus* were collected from each French site.

To acquire tissue for DNA extraction, a bench vice was used to carefully crack open the gastropod shell exposing the carapace and abdomen of the residing *C. erythropus*. A scalpel was used to remove the dactyl and the propodus of the 2nd right-hand pereiopod (1st walking leg). The carpus and the merus were also obtained if cutting induced the moulting of the whole pereiopod. Tissue samples were preserved in individual 1.5 ml microcentrifuge tubes containing 70% ethanol. Each *C. erythropus* was then transferred to a plastic container with a range of empty gastropod shells for it to inspect and inhabit. Once all individuals had been processed and moved into new shells they were released back into the local area.

Table 1: The country, name, abbreviation given in Figure 2, and geographic coordinates of all sample sites included in this study. Followed by the number of *C. erythropus* samples collected/received, the number of samples processed for sequencing, the number of sequences extracted, and the number of haplotypes identified from each sample site.

Country	Site name	Abbreviation	Lat	Long	Samples collected	Samples processed for sequencing	Sequences extracted	Haplotypes identified
UK	Gyllyngvase	GL	50.14303	-5.067372	30	10	5	1
	Porth Meor	PM	50.08204	-5.321646	30	10	6	1
	Porthleven	PL	50.50542	-5.035261	29	10	6	1
France	Roscoff	Rc	48.71868	-4.015528	20	10	6	1
	Tremazan	TZ	48.55833	-4.727587	20	10	6	1
	Caramet sur Mer	CM	48.2846	-4.569664	20	10	5	1
	Plogoff	PO	48.02668	-4.637787	20	10	6	1
	St Guenole	St	47.80556	-4.375553	20	10	10	2
	Pointe de Kerjean	PK	47.79541	-3.827048	20	10	7	1
	Kerroc'h	Ke	47.69753	-3.455062	20	10	6	1
Spain	Cadiz	CD	36.578772	-6.285505	20	10	5	2
Italy	Messina	MA	38.235896	15.579537	28	10	7	1
	Livorno	Lc	43.527438	10.304467	24	10	6	1
Azores (Portugal)	Santa Maria	SM	36.979145	-25.104584	58	10	3	2

DNA extraction

DNA extraction was undertaken using the high salt method following Aljanabi & Martinez (1997). Samples were removed from storage and dried to remove excess ethanol. Each sample was placed in a 2 ml screw cap micro-centrifuge tube with a 5mm steel ball bearing and homogenized (Omi Bead Rupter 24) for 60 seconds. Once completed, 600 µl of TNES buffer and 15 µl of Proteinase-K (20 mg/ml) was added to each tube and incubated overnight for ~16 hours at 55 °C in a water bath.

The samples were removed from the water bath and 167 µl of 5M NaCl was added to each tube, which was mixed by shaking for 20 seconds, before being micro-centrifuged (13,500 rpm) for 10mins at room temperature. The supernatant was transferred into a new 1.5 ml micro-centrifuge tube and mixed with an equal volume of 100% ethanol (~700 µl). The samples were then micro-centrifuged (13,500rpm) for 45 minutes at 4 °C. The supernatant was removed, and the remaining DNA pellet washed in 700 µl of 100% ethanol before briefly centrifuged (13,500rpm). The 100% ethanol was removed and the pellet washed in 700 µl of 70% ethanol. The 70% ethanol was removed, and the tubes left to air-dry for 30 minutes after which the DNA was re-suspended in 100 µl of Tris-EDTA before freezing. DNA quality and quantity were assessed by visualisation on 1% agarose gels and using the Qubit® (Invetrogen) BR DNA assay.

A region of the mitochondrial cytochrome oxidase subunit gene (mtCOI) was amplified by PCR using the standard LCO1490 and HCO2198 primers (Folmer *et al.*, 1994) in 10 µl PCR reactions using GoTaq Green PCR master mix (Promega). Reactions contained 2 µg template DNA, and 3pmols forward and reverse primer and thermal cycling was performed using Veriti 96-well PCR machine (Life

Technologies) under the following conditions: initial denaturation of 4mins at 95 °C, followed by 35 annealing cycles of 30 s at 95 °C, 30s at 55 °C, and 30 s at 72 °C. PCR amplification was confirmed by visualization on 2% agarose gels and amplification products were capillary sequenced in forward and reverse directions using BigDye v3.1 sequencing chemistry. PCR products were treated with Exonuclease I and Alkaline phosphatase prior to sequencing and sequencing products were analysed using the Life Technologies 3500 genetic analyser.

Sequence data were generated for 84 isolates from 5 regions (Azores, France, Italy, Spain, and the UK), from 14 sample sites (one in the Azores, seven in France, two in Italy, one in Spain, and three in the UK). Consensus sequences for each isolate were generated in Geneious v9.1.5. Low-quality sequence and non-overlapping ends were trimmed from each consensus and sequences for all isolated aligned using the global alignment option in Geneious. The alignment consisted of 495 base pairs of which seven were polymorphic (1.41%). Four of the polymorphic sites were missing values in more than 5% of isolates leaving three di-morphic sites. All subsequent analyses were based on this alignment and were conducted in R using the packages “*ade4*” and “*pegas*” (Dray & Dufour, 2007; Paradis, 2010; R Core Team, 2013).

Results

The average nucleotide frequency across all samples was A - 26.6%, C - 20.7%, G - 19.4%, and T - 33.4%. For each of the three polymorphic sites, only one sample was found to carry a different variant. Meaning there were four haplotypes in total with one haplotype carried by 81 individuals (96.4%) and each of the three remaining haplotypes represented by a single isolate. One haplotype was found in the Azores, one in Spain, and one in St Guenole, France (Fig. 1).

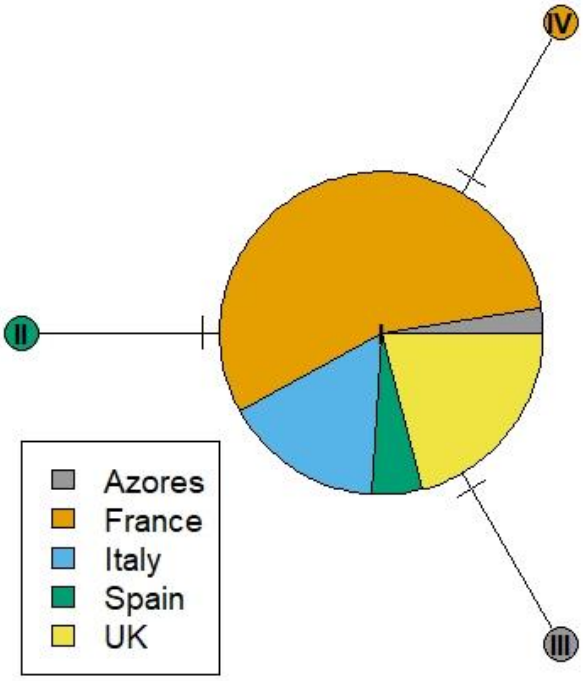


Figure 1: The haplotype network for 84 samples of *Clibanarius erythropus* from five regions of Europe. Radii of individual haplotype charts indicate the total number of samples carrying that specific haplotype. Haplotypes carried by a single individual are scaled up to increase visibility. 81 samples carried haplotype I, while haplotype II, III, and IV were carried by single individuals. The coloured fraction of each haplotype chart shows what percentage samples for that haplotype came from each geographical region.

A two-level analysis of molecular variance (AMOVA), indicated that there was a significantly greater amount of differentiation between regions than expected (18.7%, sig = 0.0136, p < 0.009, 9999 permutations). There was no significant variation between sample sites within regions (- 1.4%, sig = - 0.008, p = 0.635) and between the individuals within sample sites (92.7%, sig = 0.068, p = 0.18).

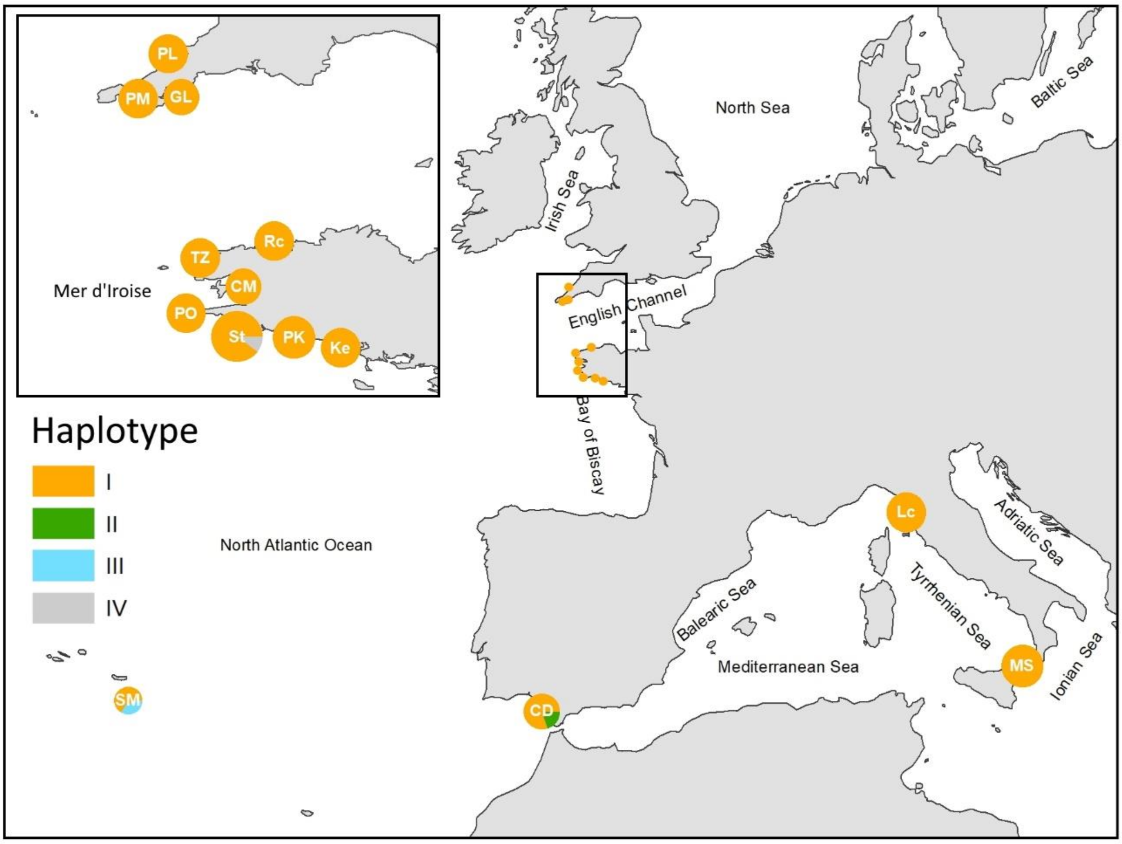


Figure 2: The distribution of haplotypes across populations of *Clibanarius erythropus* in Europe. The radii of charts indicate the sample size from each population (range = 3 to 10, mean = 6). The percentage of individuals from each population carrying each haplotype is represented by the fraction of chart shaded in each colour. Abbreviations of site names are given in Table 1. 81 samples carried haplotype I, while haplotype II, III, and IV were carried by single individuals.

Discussion

The haplotype network of *C. erythropus* was not clearly resolved and nearly all individuals, from all regions, carried the same haplotype (Fig 1, Fig 2). No further phylogeographic information could be inferred from the remaining haplotypes, which were represented by single individuals. There was little genetic differentiation between the surveyed populations of *C. erythropus,* including regions from the species historical and recently expanded range. While a two-level AMOVA suggested a significant genetic differentiation between regions this was associated with a singleton in the Azores where only three individuals were sequenced. The origin of the *C. erythropus* larvae that reached the UK in 2016 cannot be identified using our samples of mtCOI.

Panmixia in marine and intertidal species is thought to be rare with most species showing some signature of contemporary or historical restrictions to gene flow (Maggs *et al.*, 2008). For many species found across the European seascape, distinct phylogeographic breaks are seen between the Mediterranean and the Atlantic, as well as between the Mediterranean and the Black Sea. For example, the European littoral prawn, *Palaemon elegans,* has three distinct haplotype lineages of mtCOI exclusively associated with the NE Atlantic, the Mediterranean, and the Black sea (Reuschel *et al.*, 2010; Deli *et al.*, 2018). Further examples of heterogeneous genetic structure in the mtCOI of intertidal species across the European seascape can be seen in the Green shore crab, *Carcinus maenas*, (Roman & Palumbi, 2004) and gastropods *Nassarius nitidus* (Albaina *et al.*, 2012) and *Littorina saxatilis* (Panova *et al.*, 2011). This suggests limited historical and contemporary gene flow between these regions. As such, our findings contrast with the general pattern of phylogeographic structure seen in the European seascape, suggesting that the historical and contemporary gene flow in populations of *C. erythropus* is greater than other European intertidal species.

The phylogeography of decapods in the NE Atlantic and Mediterranean is highly variable and not always as clear and distinct as those seen in *P. elegans*, *C. maenas*, and *N. nitidus*. Atlantic and Mediterranean populations of *Eriphia verrucosa* and *Pachygrapsus marmoratus,* sequenced for mtCOI, contain a mixture of haplotypes from two lineages theorized to have originated from a late Pleistocene vicariant event followed by contemporary mixing of the two populations (Fratini *et al.*, 2016; Deli *et al.*, 2018, 2019). Populations of *C. erythropus* sequenced in this study contained haplotypes from a single lineage. *C. erythropus* appears to have a much lower level of genetic heterogeneity across the NE Atlantic and Western Mediterranean than other intertidal decapods. We are unable to identify any signatures of historical or contemporary restrictions in gene flow in *C. erythropus* among the populations sampled in this study.

The mechanisms that could have caused such a low level of genetic diversity in *C. erythropus* are unclear, but may be caused by the species high larval dispersal ability (Pascual *et al.*, 2017). For instance, species of intertidal invertebrates with long-duration pelagic larvae, suggesting high larval dispersal ability, have decreased genetic structure along the Pacific coast of America compared to those with short duration pelagic larvae (Kelly & Palumbi, 2010). Although a similar relationship is not seen along the South African coast (Teske *et al.*, 2007) or SE Australia (Ayre *et al.*, 2009). Pascual et al (2017) reviewed the effect of life-history traits on the level of gene flow in populations within and between the Mediterranean and the NE Atlantic. Species with long (>31 days) pelagic life stages and a highly motile adult life stage had decreased genetic differentiation between populations. *C. erythropus* larvae can survive for longer than 31 days (Harms, 1992) but once settled are benthic and are likely restricted to the local area (Benvenuto *et al.*, 2003). The high dispersal ability of *C. erythropus* larvae may have eroded or prevented any signatures of historical processes being seen in contemporary populations. However, panmixia is not seen in *C. maenas*, *E. verrucosa* and *P. marmoratus,* all of which are European decapods with long-lived pelagic larvae (< 30 days) (Lumare & Gozzo, 1972; Cuesta & Rodríguez, 2000; See & Feist, 2010).

García-Merchán *et al* (2012) studied populations of *Pagurus excavates* and *Pagurus alatus,* both sublittoral hermit crab species*,* across the Atlantic-Mediterranean transition zone using the same mtCOI gene used in our study. *P. alatus* and *P. excavates* had lower genetic diversity between sample sites compared to other decapod species and no genetic differentiation between the sample sites in the Atlantic and Mediterranean. For both *P. excavates* and *P. alatus* nearly all individuals carried the same dominant haplotype. Although García-Merchán *et al.* (2012) covered a smaller geographic area, the low genetic differentiation is similar to our findings for *C. erythropus* suggesting that Paguroidea may have lower genetic diversity than other Eastern Atlantic and Mediterranean decapods.

A lack of phylogeographic structure is not the case for all Paguroidea species globally. The genetic diversity of Paguroidea has been more extensively studied In the Western Atlantic. Genetic differentiation has been seen in the mtCOI of *Pagurus longicarpus,* between the Gulf of Mexico and the North Atlantic, with further genetic differentiation within the North Atlantic suggested to be caused by a northern glacial refugium (Young *et al.*, 2002). However, species more closely related to *C. erythropus* show less evidence of phylogeographic structure. *Clibanarius sclopetarius, Clibanarius vittatus,* and *Calcinus tibicen* show distinct genetic differentiation between the regions of the Caribbean and the South American coast of Brazil, likely caused by the formation of the amazon river basin 5 million years ago, but little intraspecific genetic variation within each region (Negri *et al.*, 2012; Mandai *et al.*, 2018). *Clibanarius tricolor* also shows panmixia across the Caribbean

(Stark *et al.*, 2018). The studies of *C. sclopetarius, C. vittatus*, and *C. tricolor*, and now our findings for *C. erythropus,* all suggest that species within the *Clibanarius* genus do not show complex genetic differences across large scale oceanographic regions, such as the Caribbean or European seascape.

The lack of distinct genetic diversity or differentiation across the historical range of *C. erythropus* means the lack of genetic structure in the leading edge of the species' range is unsurprising. Of the 63 individuals sequenced across the 10 UK and French samples sites, all but one carried the same haplotype that dominated all the other surveyed populations in Europe and the Azores. The Bay of Biscay and English Channel were of particular interest in this study because studies into the phylogeographic structure of European warm-water species have often lacked samples from the region (Fratini *et al.*, 2016; Deli *et al.*, 2019). The Mer d'Iroise is a biological transition zone and, as such, Brittany is the leading edge for several intertidal and marine species (Gallon *et al.*, 2017). As newly established northern populations will likely originate from Brittany, the level of contemporary genetic diversity in Brittany will strongly influence the genetic diversity of *C. erythropus* and other range expanding species in the future. With little genetic diversity present in the Brittany and UK populations, any new populations that establish further northwards will likely contain the same low level of genetic diversity. If the recent range expansion of *C. erythropus* to the UK has resulted in a founder effect, it cannot be seen within the region of the mtCOI gene sequenced here.

The ability for a species to overcome dispersal barriers and show high levels of panmixia has been suggested to predict which species will undergo rapid contemporary range expansion in response to climate change (Lourenço *et al.*, 2017). This study furthers the evidence that phylogeographic structure in Paguriodea is rare and that, in the absence of exceptionally strong and stable hydrological barriers, species of hermit crab will trend toward panmixia, with the noted exception of *Pagurus longicarpus* (Young *et al.*, 2002). This suggests that *C. erythropus* and other *Clibanarius* species can overcome most barriers to gene flow, seen in other intertidal and marine species, and may quickly take advantage of novel climatically suitable habitats. The recent rapid increase in abundance of *C. erythropus* seen in the southwest UK (Hawkins *et al.*, 2017; Patterson *et al.*, 2020) furthers the idea that the range of this species will be and is able to readily shift with environmental change.

Across the UK and French sites, 59 out of 60 individuals (98.3%) carried the same haplotype. The single unique haplotype was carried by an individual from St Guenole where a higher sample size of sequences (n = 10) was attained. Excluding St Guenole, the average sample size attained for each of the UK and French sites was 6, ranging 5 to 7 (Table 1). It is possible that more unique haplotypes exist at a low frequency across the UK and French sites which an expanded sample size would have identified. However, any additional low frequency haplotypes found in the UK and French populations would not suggest these populations were, or are, geographically isolated from the rest of *C. erythropus'* range sampled in this study.

Sequences of *C. erythropus* were not extensively sampled in the Mediterranean and we did not obtain samples from the Eastern Mediterranean or the Black Sea, so this study cannot conclude that *C. erythropus* is homologous across its entire geographic range. Genetic differentiation between the Black sea and Mediterranean is common in intertidal species (Reuschel *et al.*, 2010; Pannacciulli *et al.*, 2017) and any phylogeographic structure may not become apparent until a higher number of sample sites, over a wider geographic area, are included (Fratini *et al.*, 2016). In the

Azores, only three of the ten processed samples provided adequate sequence data and further research should be conducted to ascertain a clearer picture of genetic diversity found in the region. Investigation of *E. verrucosa* and *P. marmoratus*, and other species with a northern limit of Brittany, may be of particular interest as they are predicted to expand to the UK in the future (Ingle & Clark, 2008).

Sequencing more variable regions of *C. erythropus'* genome, such as the 5.8S ITS ribosomal DNA region, may allow the detection of finer-scale genetic differentiation across populations of *C. erythropus* at the boundary of its range. However, preliminary work conducted in this study did not yield a specific PCR product for the 5.8S ITS region using a range of primer pairs (CE_ITS_F and CE_ITS_Ri, CE_ITS_F and CE_ITS_Rii, CR_F3 and CR_R3, and CR_F4 and CR_R4). Without any PCR product, we could not attain any sequence data for 5.8S ITS region. Sequences of 5.8s ribosomal DNA on NCBI do not resolve into an unambiguous alignment and additional work may be required or an alternate marker sort. However, the lack of sequences from more variable regions of *C. erythropus'* genome does not negate the comparisons between our results other studies that used the same mtCOI gene.

Conclusion

Over the geographic area surveyed in this study, *C. erythropus* appears to have lower genetic diversity than other European intertidal species, which conforms to the panmixia seen in other Paguroidea globally. The recent range expansion of *C. erythropus* reinforces the hypothesis that panmictic species might be those most likely to expand their ranges under climate change. Our results suggest no genetic founder effects in the newly established UK populations of *C. erythropus* within the mtCOI gene sequenced here. Our sequences of mtCOI cannot shed any light on where the UK populations of *C. erythropus* originated. Our findings point towards a disparity between *C. erythropus* and the general phylogeographic structure of other European intertidal species. Further exploration of the phylogeographic structure in the Brittany and UK region should be conducted to ascertain if other warm-water species show the same low levels of genetic diversity seen in *C. erythropus*.

Chapter 2: The range expansion of *Clibanarius erythropus* to the UK was likely caused by unusual oceanic currents carrying larvae from North Brittany

Abstract

The ranges of species are shifting as a consequence of anthropogenic climate change. The English Channel may pose a major barrier to dispersal, preventing mainland European intertidal species from adequately keeping pace with the shifting climate. The hermit crab *Clibarnarius erythropus* appeared in the UK in 2016 suggesting the pelagic larvae of the species can overcome the barrier of the English Channel. Here, we model the dispersal of *C. erythropus* larvae in the English Channel in the years prior to its arrival. Simulations suggest the larvae of *C. erythropus* arrived in 2014, originated from North Brittany, experienced a mean temperature of around 16 °C, and took longer than 20 days to be transported across the sea. The English Channel may prevent species with pelagic larvae that settle within 20 days, such as many species of gastropod, annelids, and macroalgae, from successfully range expanding to the UK. As North Brittany was the only feasible landmass from where *C. erythropus* could have originated, species with long-lived pelagic larvae but without reproducing populations in North Brittany, such as *Pachygrapsus marmoratus* and *Eriphia verrucose,* may not appear in the southwest UK until the species are established in North Brittany. Our results suggest that the transportation of larvae from Brittany to the southwest UK is rare and driven by occasional, unusual ocean currents. The rarity of such currents could limit the ability of many intertidal species to adequately shift their range with climate change.

Introduction

Globally the ranges of many species are shifting towards the poles, as a consequence of anthropogenic climate change (Hawkins *et al.*, 2008b; Thomas, 2010). Yet not all species and communities will be able to keep pace with climate change (Sorte *et al.*, 2010; Burrows *et al.*, 2011). In the closely studied southwest United Kingdom (UK), the ranges of many intertidal species have increased northwards while other species have become locally extinct in the southern edge of their range (Southward *et al.*, 1995; Helmuth *et al.*, 2006; Hawkins *et al.*, 2008b, 2017). In the UK, it appears that the number of species becoming locally extinct is greater than the number of novel species arriving from further south (Burrows, 2017) and is causing climate 'debt' (Jackson & Sax, 2010). The lack of intertidal species' range-shifting into the UK may occur because the English Channel poses a major barrier to the expansion of species' ranges from further south (Salomon & Breton, 1993; Lefebvre *et al.*, 2003; Nicolle *et al.*, 2017). Determining which species will be able to overcome the barrier of the English Channel, and why, will further our understanding of how the intertidal community of the UK will change over the coming decades, and build our understanding of the processes that drive or limit range expansions (Hiscock *et al.*, 2004; Keith *et al.*, 2011; Wilson *et al.*, 2016).

Brittany is reported as a biogeographical transition zone for a number of benthic, intertidal, and marine species (Gallon *et al.*, 2017). Multiple crustaceans (Ingle & Clark, 2008; Dauvin, 2009; Deli *et al.*, 2019), nudibranchs (Grall *et al.*, 2015), and key commercially important species, such as the Green Ormer, *Haliotis tuberculata* (Roussel & Van Wormhoudt, 2017), have a northern limit on the north coast of Brittany or the Channel Isles. One species with a range that has expanded from mainland Europe into the southwest UK is *Clibanarius erythropus.* Records of

C. erythropus occurred in the UK in the 1950/60s (Carlisle & Tregenza, 1961) but due to a combination of an acute pollution event (The Torrey Canyon oil spill) and an apparent lack of further influx of larvae or successful reproduction in the UK, the species eventually disappeared (Southward & Southward, 1988). After 1985, no known records of *C. erythropus* occurred in the UK until 2016. Physical measurements of *C. erythropus* in autumn 2018 suggest that initially the UK population was a single cohort that arrived in the UK as one single transportation event (Patterson *et al.*, 2020). Thus, the successful arrival or recruitment of *C. erythropus* larvae to the UK appears to be rare, having occurred only twice in the last 60 years. Understanding the processes that facilitated or limited the species' arrival could inform us on the processes that allow range expansion across the English Channel, allowing predictions for *C. erythropus'* and other species distributions in the future.

In 2016 and 1959/60, *C. erythropus* simultaneously appeared at multiple sites not associated with intensive human activity. This suggests that the settlement of *C. erythropus* in the southwest UK, both in the 1950s and the 2010s, was caused by the species pelagic larval being transported across the Western English Channel by ocean currents rather than direct anthropogenic transportation (Southward & Southward, 1977, 1988; Patterson *et al.*, 2020). The population of *C. erythropus* with the highest proximity to the UK is in North Brittany. After the 1959/60 UK appearance of *C. erythropus,* Southward & Southward (1977) speculated that the most likely source of larvae was the southern coast of Brittany due to the lower population size and/or temperature-suppressed reproduction on the northern coast of Brittany. The Western English Channel is around ~160km wide and dominated by strong oscillating tidal currents. When these tidal cycles are taken into account the overall movement of water in the English Channel is slow (3cm/s) and weak - varying in directionality under different environmental factors; for instance wind direction (Pingree & Maddock, 1977; Salomon & Breton, 1993). While the successful transportation of *C. erythropus'* larvae between the southwest UK and Brittany appears to have occurred, previous studies modelling larval dispersal in the English Channel have found no connectivity between the southwest UK and Brittany (Lefebvre *et al.*, 2003; Nicolle *et al.*, 2017). These two prior studies may not be applicable because dispersal in Nicolle *et al.,* (2017) may not be biologically relevant to *C. erythropus* and analysis in Lefebvre *et al.,* (2003) was restricted to a limited set of oceanographic conditions. The average trajectory of water in the Western English Channel calculated by Salomon & Breton (1993) would allow freely drifting particles to be carried from Brittany to the southwest UK but the velocity of water would be insufficient for the live larvae of *C. erythropus* to reach to UK (Harms, 1992) and only occur under specific wind conditions (Salomon & Breton, 1993). Yet the appearance of *C. erythropus* in the southwest UK indicates the transportation of larvae via ocean currents can occur.

Here, we use larval dispersal simulations based on an archival hydrodynamic model to simulate the release and transportation of larvae in the Western English Channel in the years prior to 2016. We ask whether oceanographic conditions before the most recent recruitment of *C. erythropus* were unusual, only occurring once over the duration of our simulations. If this were the case, it could indicate that the transportation of larvae from Brittany to the southwest UK was due to a rare hydrological event, unlikely to be repeated frequently. Determining how frequently the hydrology of the Western English Channel permits the transportation of particles from Brittany to the UK will further our understanding of how often species could have their ranges expanded to the UK (Hiscock *et al.*, 2004).

The simulations allow us to determine when, and how often, larvae can be transported from Brittany to the southwest UK. We include simulation with and without vertical diel migration, a common pelagic behaviour whereby individual larvae vary their depth in the water column throughout the day (Williamson *et al.*, 2011). Little is known about the behaviour of *C. erythropus'* pelagic larvae and we include simulations with and without vertical diel migration to determine how sensitive the trajectory and velocity of larvae is to this unknown factor.

We also asked where the larvae of *C. erythropus* that reached the UK could have originated from. As North and South Brittany have noted differences in species composition (Helmuth *et al.*, 2006), determining where the larvae of *C. erythropus* that reached the UK originated could further our knowledge of which intertidal species could expand their range to the UK in the future.

Methods

To investigate the potential trajectory and velocity of *C. erythropus* larvae between Brittany and the southwest UK, we used the Lagrangian tool ichthyop v3.3 (Lett *et al.*, 2008). This tool uses archived hydrodynamic models to simulate the movement of individual particles over time and can track latitude, longitude, and depth in 3D. This can be coupled with organismal responses to temperature and salinity, as well as larval behaviour such as vertical diel migration, to build an individual-based model of larval transport for the species and system in question. Larval transport can be calculated both forwards and backwards in time.

Larval reproduction and survival

The first record of *C. erythropus* in the UK since 1985, was in March 2016 (Patterson *et al.*, 2020). Due to the active marine recording community in Cornwall the transportation and recruitment of *C. erythropus* to the southwest UK likely occurred within a few years prior to first recording (Hawkins *et al.*, 2017). To investigate when this recruitment event(s) was most likely to have occurred, we simulated the reproduction and dispersal of *C. erythropus* from Brittany to the UK between 2012 and 2016, inclusive.

Evidence suggests that, in the Mediterranean, *C. erythropus* reproduces in the summer (Southward & Southward, 1977; Harms, 1992) but in the Atlantic coast of Spain *C. erythropus* reproduces later in the year from August to September (Southward & Southward, 1977). At the northern limit of *C. erythropus'* range (in the UK) a gravid individual was recorded in October 2018 (Patterson *et al.*, 2020). As such, it seems possible that reproduction in Brittany could occur between August and November and we simulated larval dispersal between August and November of each year

Harms *et al*, (1992) concluded that *C. erythropus* larvae collected from the Adriatic could not fully develop at or below 15 °C but could at 18 °C. Water temperatures in the English Channel rarely exceed 18 °C and between 2012 and 2016 and no single month in our study period had a mean water temperature higher than 16.6 °C (Channel Coastal Observatory, 2020). The results of Harms *et al*, (1992) would suggest a full reproductive cycle of *C. erythropus* would not be possible in the English Channel. Nonetheless, this seems to have occurred. As such, we did not implement a lower or upper lethal temperature in our larval dispersal model but did track the sea surface temperature (SST) at each particle's location using the temperature data from MARS3D.

The geographic and temporal extent of the larval dispersal models

Our simulations of larval trajectory and velocity within Ichthyop were calculated using the hydrodynamics model MARS3D (3D hydrodynamic Model for Applications at Regional Scale, Ifremer (Lazure & Dumas, 2008)) with a resolution of 2.5km^2, 40 levels of depth (sigma-levels) between the sea surface and the seafloor, with an adaptive timestep between 200-400s and covers an area from 8°W to 5°E and 43°N to 53°N. MARS3D is not coupled to a wave model. Validation of MARS3D has been conducted using satellite measurements of SST and in situ measurements of sea surface elevation and currents (Lazure & Dumas, 2008; Lazure *et al.*, 2009). Differences between in situ measures and MARS3D we minable, producing accurate prediction of salinity and temperature. Due to the mesh size of the model some local structure are not fully resolved and MARS3D may underestimate currents within coastal areas (Lazure & Dumas, 2008). MARS3D has been used for a number of studies investigating the trajectory of pelagic larvae in the near shore waters of Brittany (Allain *et al.*, 2007; Ayata *et al.*, 2010; Huret *et al.*, 2010). We download the available MARS3D data with a temporal resolution of one hour from http://marc.ifremer.fr/en/. Within ichthypop, we subset the MARS3D data to a 210542 km^2 area covering Brittany and the Southwest Peninsula of the UK (51.0°N 7.5°W, 51.0°N 1.0°W, 47.0°N 1.0°W, 47.0°N 7.5°W; Figure 1). As larval trajectories could not be calculated beyond the subset of MARS3D data, any particle transported outside of the simulated area was permanently frozen in place (Figure 1). Due to the temporal resolution of the MARS3D data some particles paths could intersect with the coastline. Any particle that was transported onto land was frozen in place until ocean currents transported that particle in a direction not intersecting with the coastline.

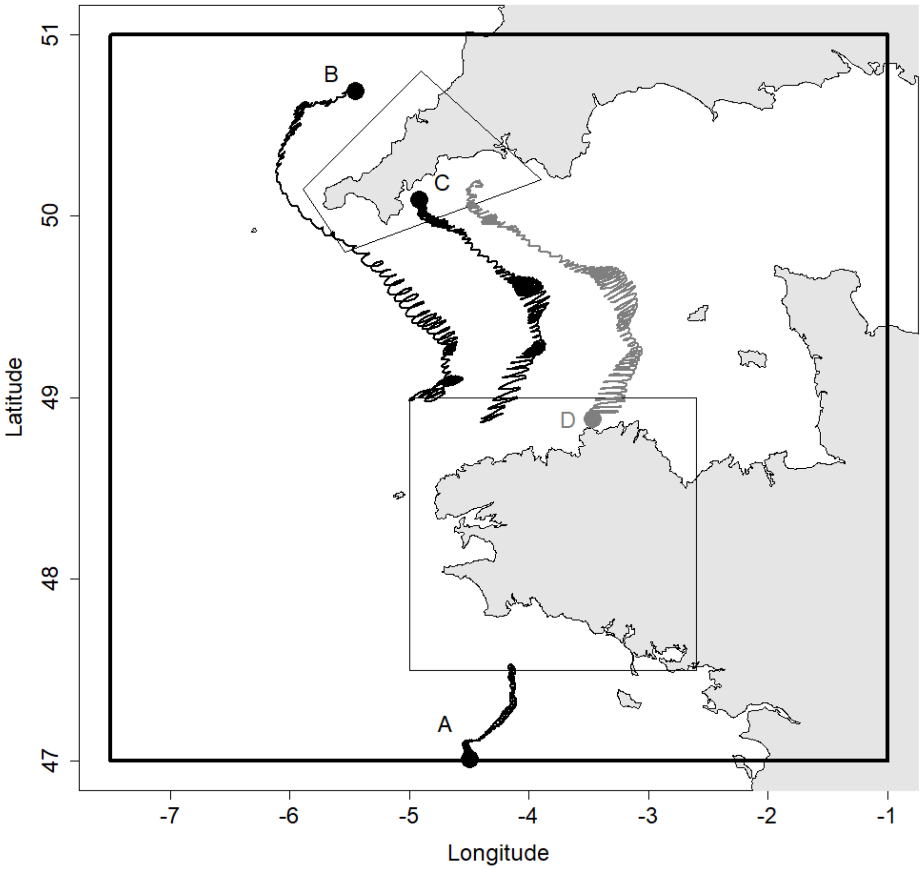


Figure 1: The extent of the simulated area (thick black outline) and the UK and Brittany polygons (thin black outlines). **A**, **B**, and **C** are the routes of individual particles selected from the forward simulations for illustration purposes. Particle **A** is transported outside of the simulated area and frozen in place. Particles **B** and **C** both represent potential recruitment events but under two circumstances. **B** the particle enters the UK polygon but is then transported outside of the UK polygon and **C** the particle enters and remains within the UK polygon. **D**, coloured grey, is the route of an illustrative particle selected from the backwards simulations.

Simulations of larval trajectory and velocity, in Icthypop, were run forwards in time, with 10,000 particles released at 10am (BST) each day from a polygon surrounding Brittany (4.9°W 50.8°N, 3.9°W 50.2°N, 5.54°W 49.8°N, 5.89°W 50.15°N). The initial position of each particle was randomly placed within the Brittany polygon. Due to the irregular shape of the coastline, 51.8% of particles were placed on the northern half of the Brittany polygon. Particle trajectory and velocity were calculated with time steps of 300 seconds (s) as a compromise between simulation stability (CFL ≤ 1) and computation time. The latitude, longitude, and depth for each particle were recorded every hour (3600s or 12 time-steps) for 40 days (3,456,000s, 11,520 time steps, 960 records). The first simulation of each year ran from the 2nd August to the 11th September and the final simulation of each year ran from the 21st of November to the 31st December. From here onwards these simulations are referred to as 'forward simulations.'

Simulations of larval trajectory and velocity, in Icthypop, were also run backwards in time, with 10,000 particles were released at 10am daily from a polygon surrounding the Southwest Peninsula of the UK (5.0°W 47.5°N, 5.0°W 49.0°N, 2.6°W 49.0°N, 2.6°W 47.5°N, Figure 1). Running simulations backwards will be used to confirm that the origin of *C. erythropus* larvae in the UK is restricted to the Brittany polygon. 35.3% of particles had an initial position in the northern half of the polygon. Particle trajectory and velocity were calculated with the same time step, recording frequency, and duration of transport as the forward simulations. The starting conditions of the backwards simulation was set as the end time of the forward simulations. For example, particles released on the 11th October were tracked backwards until the 2nd August. From here onwards these simulations are referred to as 'backwards simulations.'

C. erythropus lives intertidally and up to depths of 30 meters (Gherardi, 1990). The UK and Brittany polygons (Figure 1) extend to areas below 30 meters of depth and, as such, encompass unsuitable habitat of *C. erythropus*. However, these polygons were chosen because the hydrodynamic processes are more complex in nearshore water and maybe underestimated by MARS3D (Lazure & Dumas, 2008).

To investigate whether the tidal cycle strongly influenced the probability of recruitment, backwards simulations were run for 2015 with particles released at 4pm instead of 10am. Upon visual inspection of the data, no difference in dispersal or recruitment was observed, so we did not conduct any further analysis of tidal effects.

Variation in larval trajectory due to larval behaviour

Little is known about the larval behaviour of *C. erythropus*. Initial larval dispersal simulations were conducted with no forcing of diel vertical migration but migration has been shown to have a significant impact on the dispersal trajectory in other larval dispersal simulations (Ayata *et al.*, 2010). To conduct a sensitivity analysis, simulations were also run with larval diel migration. In the vertical migration simulations, all parameters not mentioned below were kept consistent with those of the forward simulations. Particles were forced to instantaneously move to -30m in the daytime and -10m at night-time, which conforms to the temporal variation seen in surveys of decapod larvae, including species of Paguroidea (Hermit crabs) (Dos Santos *et al.*, 2008). Vertical migration began at 3.6 days, after the start of the simulation and varied with the time of sunrise and sunset. The time of sunrise and sunset was calculated at the centre point of the simulated area (7.25°W, 49°N) for the first day of each simulation using the R package '*suncalc*' (Thieurmel & Elmarhraoui, 2019). From here onwards these simulations are referred to as 'vertical migration simulations.' Due to the constraints of ichthyop vertical migration cannot be conducted backwards in time.

Data analysis

In order to compare the potential for recruitment between each study year, we measured the number of recruitment events for each day particles were released, across all simulations. If a particle was transported into UK polygon at any point during the forwards and vertical migration simulations this was counted as a potential recruitment event (Figure 1). Similarly, if a particle was transported into the Brittany polygon during the backwards simulations this was also counted as a potential recruitment event.

In order to ask whether recruitment potential varied within and between study years, and whether the behaviour of vertical migration facilitates or restricts the level of recruitment, we compared seven general additive models (GAMs). GAMs are ideal for this approach as the relationships between the explanatory variables and the number of recruitment events are expected to be complex and non-linear. Data from the backward simulations was not included as the trajectory of particles was calculated from an initial position within the UK polygon, not the Brittany polygon.

The variables included in each of the seven GAMs are listed in Table 2. The seven models tested the following hypotheses: **1)** the number of recruitment events is seasonal and consistent year to year, with no effect of vertical migration. **2)** the number of recruitment events varies, is seasonal, with no effect of vertical migration, but with an additive effect of year. i.e. the seasonal pattern remains the same but with a higher or lower number of recruitment events for each individual year. **3)** the number of recruitment events is seasonal and consistent year to year but with an additive effect of vertical migration **4)** the number of recruitment events is seasonal with an additive effect of year and an additive effect of vertical migration. **5)** the number of recruitment events varies throughout the year but is not seasonal, i.e. temporal variation is independent between years. **6)** the number of recruitment events varies throughout the year but is not seasonal and there is an additive effect of vertical migration. **7)** the number of recruitment events varies throughout the year but is not seasonal and the effect of vertical migration varies with each year and over time.

For all models, the maximum number of knots (k') was set to 20. The complexity of a spline is determined by the number of knots, a higher number of knots allows for more complex splines. The edf is the number of knots needed to draw a specific spline produced by a model. If the edf is close to k' then it suggests the relationship is more complicated and cannot be adequately drawn with the maximum number of knots allowed under the current model. Smoothers were selected using REML.

As there is temporal autocorrelation in the oceanographic currents from the MARS3D data, and thus in particle trajectories calculated on adjacent release dates, temporal autocorrelation was included in all models, with the day of the year nested within each year and simulation type. Variation caused by the temporal autocorrelation was accounted for when assessing model fit. This was implemented using the *gamm* function in the R package '*mgvc*' (Wood *et al.*, 2016).

The number of recruitment events is count data bounded between 0 and 10,000 (the total number of particles release on each day), however, the maximum number of recruitment events is expected to be low (< 500 recruitment events or 5.0% of particles) this means the number of recruitment events is not restricted by the total number of particles. As such, we used a Poisson distribution in our models as this was the most adequate distribution currently supported under the *gamm* function of the *mgcv* package. All other data analysis was conducted in R v4.0.2 (R Core Team, 2013), using the packages ‘*tidyverse*’ (Wickham *et al.*, 2019), ‘*ncdf4’* (Piece, 2019), and ‘*lubridate*’ (Grolemund & Wickham, 2011).

Selection of the best-fitting GAM followed Pedersen *et al.*, (2019) using minimum AIC value and the highest pseudo-R-squared values. The selected model was evaluated through model diagnostics plots and the effective degrees of freedom (edf) for each spline reviewed. Pseudo-R-squared is calculated as the proportion of variance explained by the predicted values of each model and as such represents a rough goodness of fit for each model.

To determine where the *C. erythropus* in the southwest UK could have originated from, we visualized the density of initial starting positions for larvae that underwent a recruitment event in the forward and vertical migration simulation. In order to determine all possible locations that the larvae of *C. erythropus* could have originated from, we also visualized the density of particles in the final timestep of the backward simulations.

Results

Across all years and simulation types, potential recruitment events occurred. There was a significant correlation between the number of recruitment events in the forward and the backward simulations for each day of release (spearman’s rank correlation; $S = 967014$, $R = 0.894$, $p < 0.01$). There was also a significant correlation between the number of recruitment events in the forward and the vertical migration simulations for each day of release (spearman’s rank correlation; $S = 14082303$, $R = 0.494$, $p < 0.001$).

Across all days where forward simulations were initiated, the mean number of recruitment events, across all years, was 36.7 (i.e. on average, 0.37% of particles’ trajectories intersected with the UK polygon after being released in the Brittany polygon), the median was 9 (0.01%) and the maximum was 369 (3.7%), occurring on 2014-08-24. In the backward simulations, where particles were released in the UK polygon and simulations where run backwards in time, the mean number of recruitment events, across all years, was 57.9 (i.e. on average, 0.58% of particles' trajectories intersected with the Brittany polygon after being released from the UK polygon), the median was 15 (0.15%) and the maximum was 499 (5.0%), occurring on 2014-08-30. In the vertical migration simulations, the mean number of recruitment events, across all years, was 10 (0.1%), the median was 0 (0%) and the maximum was 449 (4.5%) - occurring on 2014-08-30. In the forward and backward simulations, 36% of days on which simulations were initiated resulted in zero recruitment events. In the Vertical Migration simulations, 74% of days on which simulations where initiated resulted in zero recruitment events (Figure 2).

Table 1: Summary of recruitment events for all years simulated. Values are given as the percentages of particles that underwent a recruitment event. Each simulation released a total of 10,000 particles. SD = standard deviation, Max = Maximum.

Year	**Forwards**				**Backwards**				**Vertical migration**			
	Mean	Median	SD	Max	Mean	Median	SD	Max	Mean	Median	SD	Max
2012	0.19	0.00	0.29	1.09	0.28	0.00	0.42	1.64	0.10	0.00	0.30	1.71
2013	0.29	0.32	0.28	1.12	0.49	0.28	0.57	2.29	0.09	0.00	0.27	1.56
2014	0.71	0.04	1.02	3.69	1.02	0.05	1.46	4.99	0.32	0.00	0.98	4.49
2015	0.23	0.07	0.33	1.61	0.30	0.05	0.64	3.73	0.22	0.00	0.48	1.90
2016	0.38	0.21	0.40	1.23	0.73	0.54	0.92	4.30	0.14	0.00	0.29	1.11
All years	0.36	0.09	0.57	3.69	0.56	0.15	0.92	4.99	0.18	0.00	0.54	4.49

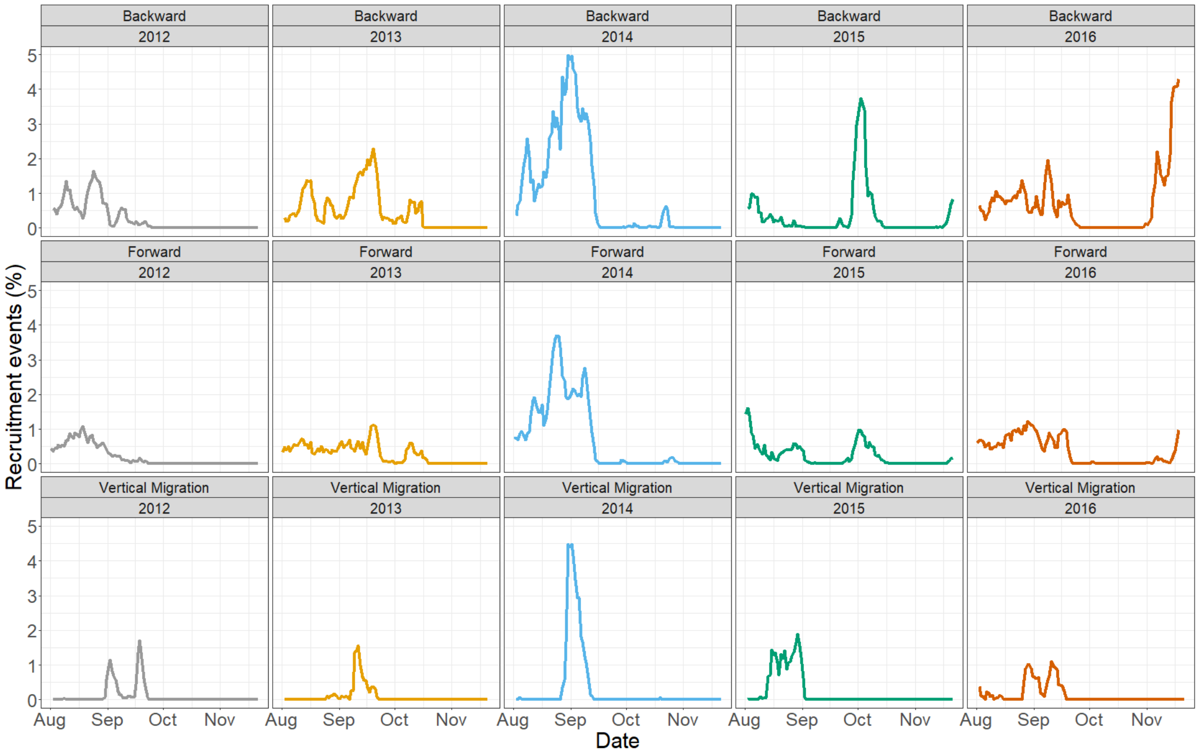


Figure 2: The percentage of recruitment events across all simulated years in both the backwards, forwards, and vertical migration simulations. One recruitment event is a single particle calculated to have a trajectory that intersects with the UK polygon (in the forward and the vertical migration simulations) or the Brittany polygon (in the backward simulations) at any time point within 40 days of release. Date corresponds to when a particle would have originated from Brittany: i.e. the first time-step of the forwards and vertical migration simulations and the final time-step of the backwards simulations.

For particles that underwent a recruitment event in the forward simulations with no vertical migration, the median length of time to reach the UK polygon was 34.7 days, ranging from 13.7 days to the maximum cut off value of 40.0 days. Very few particles took fewer than 20 days to reach the UK and this occurred only in 2013 and 2014, with 7 and 138 particles, respectively. In the forward simulations with vertical migration, the median length of time to reach the UK polygon was 36.3 days, ranging from 25.0 days to the maximum cut of value of 40.0 days. Across all years and simulation types, the number of particles arriving in the UK increased as the simulations progressed, the highest number of particles arriving on a single day occurring on the final day of each simulation (Figure S1). The median duration of larval transportation was close to the maximum duration of larval transportation allowed in in our simulations (40 days). Having an increased maximum duration of larval transportation may increase the number of particles able to reach the UK but this would not be biologically relevant for *C. erythropus* (Harms, 1992).

All models showed that the level of recruitment varied throughout the year, and there was a significant effect of year and simulation type ($p < 0.0001$). Model 7 (in which there are separate splines for each combination of year and simulation type) had the lowest AIC value and highest pseudo-R-squared value (Table 2). In model 7, all splines had a k-value that was not significantly different from 1 ($p > 0.05$) suggesting that the effective degrees of freedom (edf) was significantly below the maximum number of knots (k’) (Table 2). Therefore, our simulations indicate that the level of recruitment varied throughout each year, was not seasonal, and the behaviour of vertical migration significantly altered the level of recruitment (Table 3). In general, vertical migration decreased the number of recruitment events to zero, however, in

2012, 2013, 2014, and 2015 there were short periods where recruitment was higher in the vertical migration simulations than the forward simulations. (Figure 2).

Table 2: The output parameters for each proposed model. **df** – degrees of freedom, **AIC** - Akaike information criterion, **delta AIC** – the difference in AIC between the lowest AIC model and the given model, **Pseudo R-squared** – the proportion of variation in the data explained by predicted values of the model, **K'** – the set maximum number of knots, **median edf** – the median estimated degrees of freedom (**edf**) for each fitted spline, **min edf** – the minimum edf of all fitted splines, **max edf** – the maximum edf of all fitted splines, **F-value** and association **p-value** from anova.

	Model	df	AIC	delta AIC	Pseudo R-squared	k'	median edf	min edf	max edf	F-value	p-value
7	~ s(Day of Year, by Year * Vertical migration) + Year * Vertical migration	31	14030.48	0	0.98	19	9.9	6.62	18.4	4.3	< 0.0001
6	~ s(Day of Year, by Year) + Year + Vertical migration	17	15628.23	1597.76	0.6	19	16.81	14.26	18.63	91.5	< 0.0001
5	~ s(Day of Year, by Year) + Year	16	18641.55	4611.07	0.63	19	16.85	14.55	18.95	4.9	< 0.0001
2	~ s(Day of Year) + Year	8	18765.17	4734.69	0.47	19	16.96	NA	NA	722.4	< 0.0001
4	~ s(Day of Year) + Year + Vertical migration	9	19018.47	4987.99	0.5	19	16.93	NA	NA	806	< 0.0001
1	~ s(Day of Year)	4	20102.38	6071.90	0.27	19	16.97	NA	NA	1289.5	< 0.0001
3	~ s(Day of Year) + Vertical migration	5	20155.61	6125.14	0.29	19	16.93	NA	NA	1217.3	< 0.0001

Table 3: The summary statistics for Model 7. **edf** – estimated degrees of freedom. **Forw** – Forward simulations without vertical migration. **VM** – Vertical migration simulations.

Parametric coefficients				**Approximate significance of smooth terms**			
Predictor	Estimate	t-value	p-value	Predictor	edf	F-value	p-value
2012 Forw (Intercept)	-2.61	-1.71	0.09	s(Day of Year): 2012 Forw	6.97	90.55	< 0.0001
2012 VM	-9.89	-1.09	0.28	s(Day of Year): 2012 VM	10.55	726.45	< 0.0001
2013 Forw	0.37	0.04	0.97	s(Day of Year): 2013 Forw	6.62	12.6	< 0.0001
2013 VM	-79.8	-51	< 0.0001	s(Day of Year): 2013 VM	18.4	119085.3	< 0.0001
2014 Forw	1.63	0.33	0.74	s(Day of Year): 2014 Forw	14.76	2187.38	< 0.0001
2014 VM	-6.71	-0.1	0.92	s(Day of Year): 2014 VM	7.1	14435.14	< 0.0001
2015 Forw	3.63	1.6	0.11	s(Day of Year): 2015 Forw	7.17	417.55	< 0.0001
2015 VM	-141.43	-87.9	< 0.0001	s(Day of Year): 2015 VM	18.14	2053864	< 0.0001
2016 Forw	4.09	1.58	0.12	s(Day of Year): 2016 Forw	14.36	446.07	< 0.0001
2016 VM	-24.38	-1.15	0.25	s(Day of Year): 2016 VM	9.25	76.98	< 0.0001

The mean sea surface temperature (SST) for all particles throughout the forward simulations was 15.5 °C. The mean SST for all particles in the vertical migration simulations was also 15.5 °C. For particles that underwent a recruitment event in the forward simulations, the mean SST was 15.2 °C and ranged from 13.1 °C to 17.1 °C. For particles that underwent a recruitment event in the vertical migration simulations, the mean SST was 15.0 °C and ranged from 14.2 °C to 15.3 °C. The average SST a recruited particle experienced varied throughout and between years (Figure 3). From August to September 2014, the average SST experience by particles that underwent a recruitment event remain above 15 °C and reached 16 °C, in comparison to all other years that recorded much lower mean SST (Figure 3)

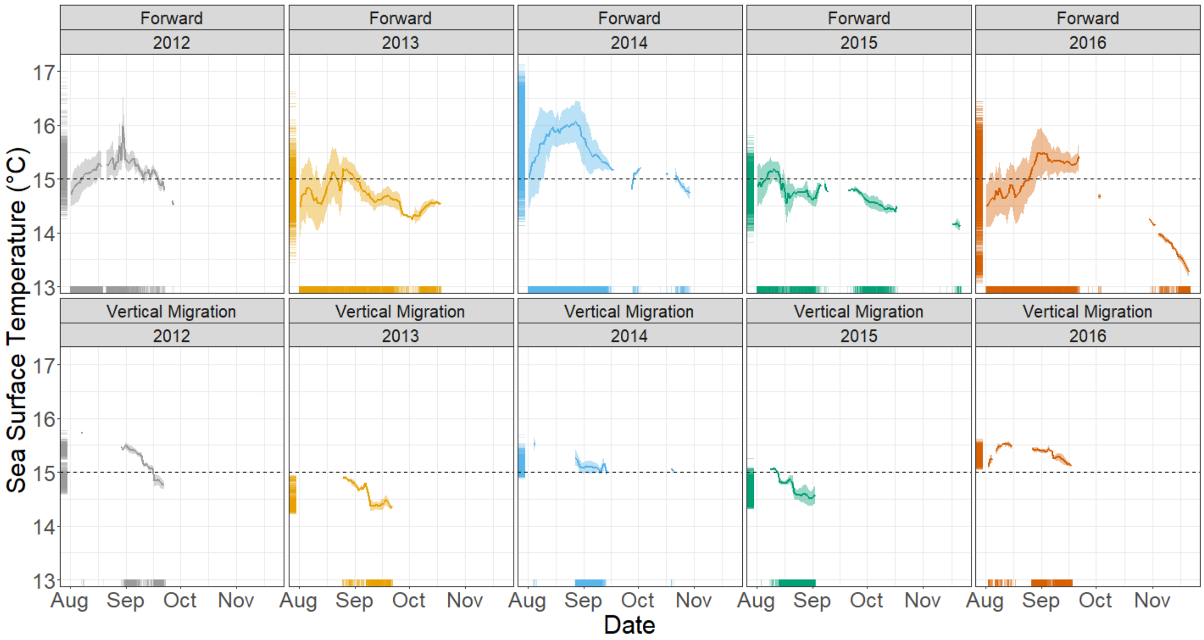


Figure 3: The average sea surface temperature (SST) experienced by particles that underwent a recruitment event (the trajectory of the particle intersected with the UK polygon), throughout the forwards and the vertical migration simulations. Breaks in the data show where no recruitment events took place. Thick coloured lines show the mean SST experienced by all particles released on the given date bounded by the standard deviation. Rug plots show the average temperature experienced by each individual particle. Date corresponds to the day particles were released. Dashed black line shows 15 °C, below which Harms (1992) showed C. erythropus larvae, from the Mediterranean, could not fully develop.

Looking at the trajectory of all particles in the forward simulations, including those that did not undergo a recruitment event, our simulations show that particles released from Brittany were carried to the southwest UK, the Channel Isles and the Cherbourg Peninsula, all locations where the species has been recorded (GBIF.org, 2019). In 2014 and 2015, particles were also projected to reach close to the coast of Dorset, as far east as Weymouth (Figure S2b). The vertical migration simulations also project larvae reaching the UK in all years but no particles were transported further East than the Lizard peninsula (Figure S2c).

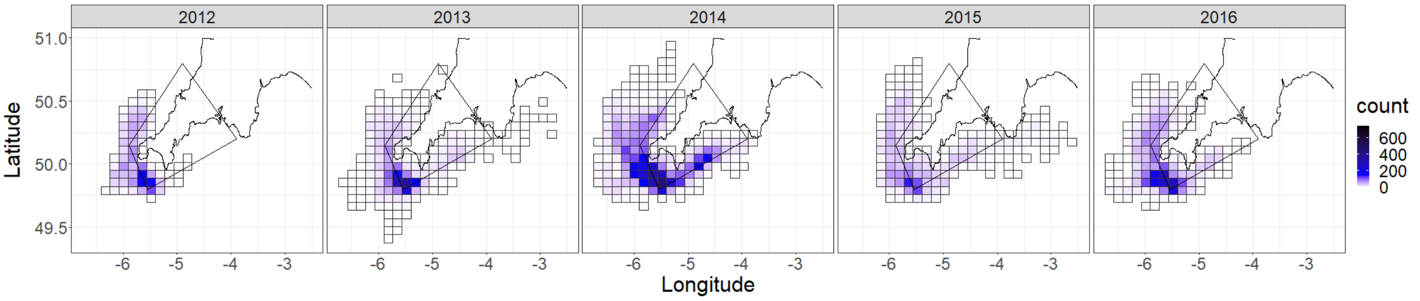
The majority of particles in the backwards simulations were projected to have originated from the northern half of the English Channel, close and often within the UK polygon, where they were initially placed (Figure S2a). Particles released in the backwards simulations were not projected to have originated from any coastline other than North Brittany. A number of particles in the backward simulations were projected to have originated from outside of the simulated area. However, the projected trajectory of the backwards particles only intersected with the western and northern boundaries of the simulation area where there is no feasible landmass from which *C. erythropus* larvae could have originated (Figure S2a).

In the forwards simulations, particles that were transported to the UK polygon were initially positioned in the northwest corner of the Brittany polygon (Figure 4b). After 40 days of transportation, these particles were mainly concentrated in the southwest corner of the UK polygon (Figure 4b), however, particles were projected to reach both the north and south coast of the Southwest Peninsula of the UK (Figure 4b). Similarly, in the backwards simulations, the initial starting positions of particles, that were projected to have originated from the Brittany polygon, were concentrated in the southwest corner of the UK polygon and, after 40 days of transportation, were projected to have originated in the northwest corner of the Brittany polygon (Figure 4c-d).

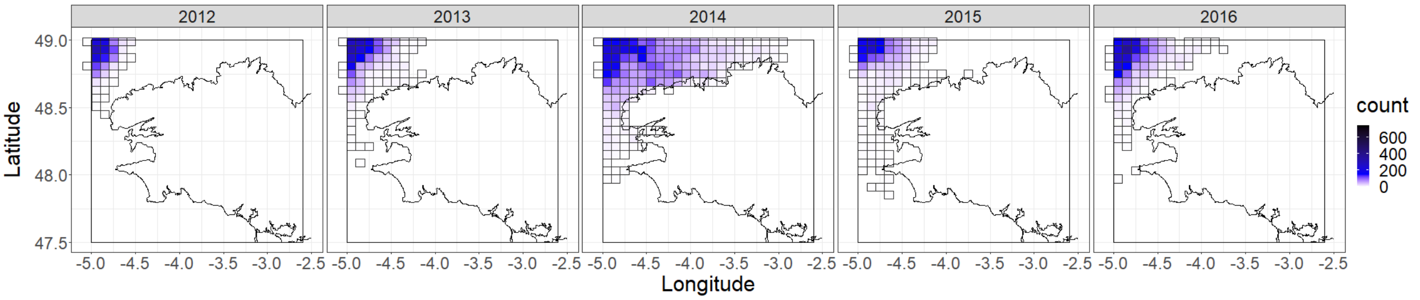
The calculated origin of particles is concentrated in the northwest corner of the Brittany polygon across all years, except for 2014 where the initial starting position of the forward simulations and the projected origin of the backwards simulations is more evenly distributed along the north coast of Brittany (Figure 4b). In the vertical migration simulations, all particles that underwent a recruitment event originated in the northwest corner of the Brittany polygon including in 2014. In the vertical migration simulations, the end point of particles is restricted to the southwest corner of the UK polygon, with little connectivity to locations where *C. erythropus* is known to be present (Figure 4e). There was no recorded connectivity between the south coast of Brittany and the southwest UK, across all years and simulation types (Figure 4).

Forwards

(a) Calculated final position

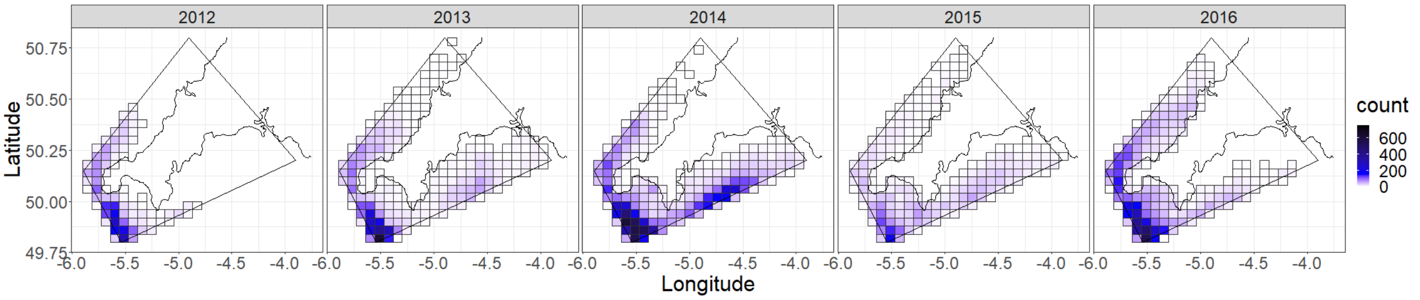


(b) Intial conditions

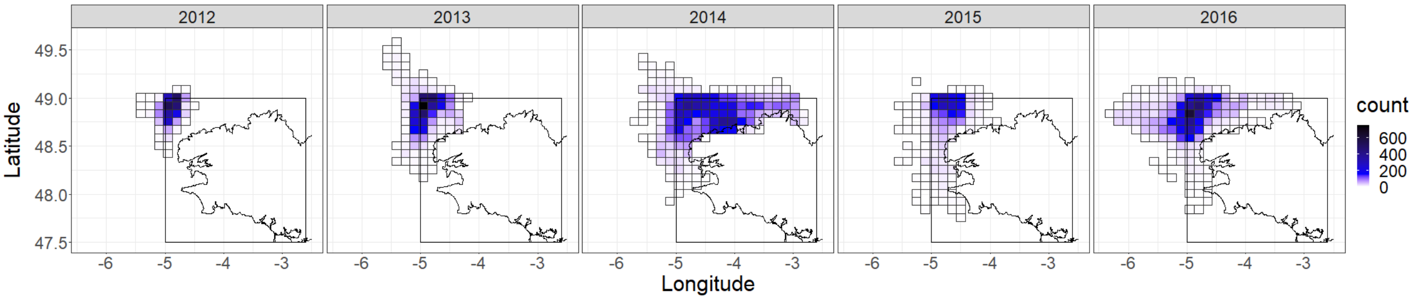


Backwards

(c) Intial conditions

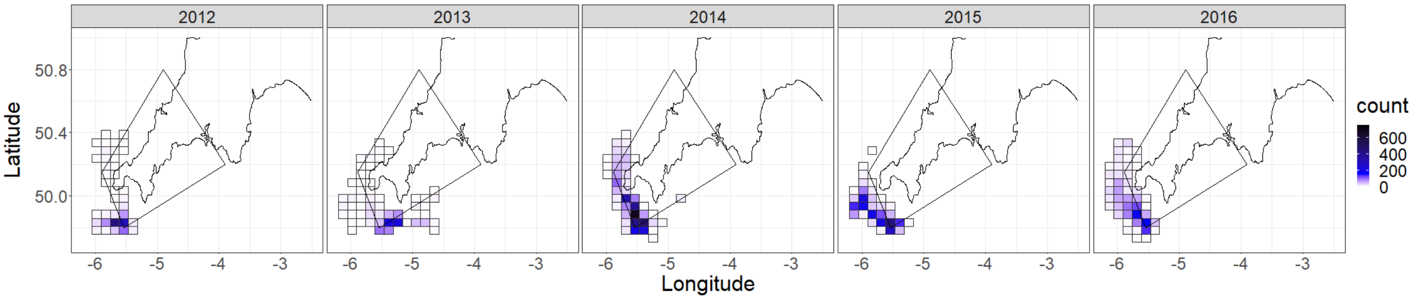


(d) Calculated final position



Vertical Migration

(e) Calculated final position



(f) Intial conditions

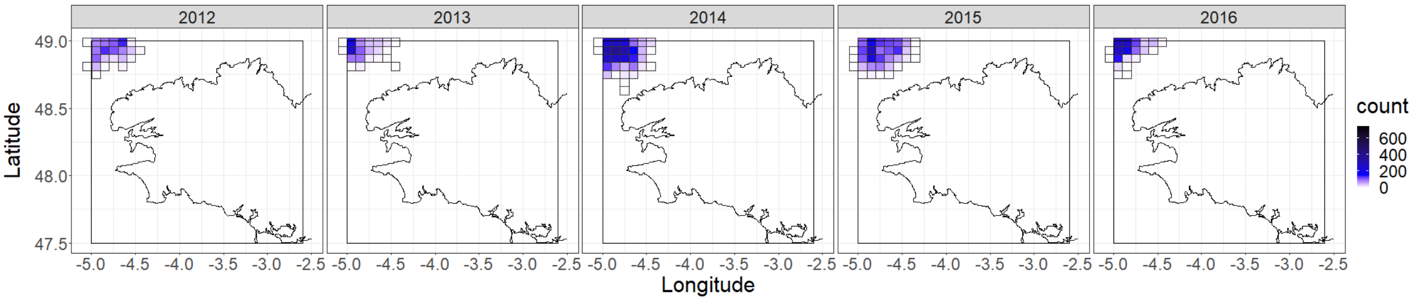


Figure 4: The colour of each grid-cell indicates the number of particles within each grid-cell under the following circumstances. The initial starting position **(b)** and the calculated final position, after 40 days **(a),** of all particles that recruited (i.e. entered the UK polygon at any time point) in the forwards simulations. The initial starting position **(c)** and the projected origin **(d)** of all particles that entered the Brittany polygon at any time point in the backward simulations. The initial starting position **(f)** and projected final position **(e)** of all particles that entered the UK polygon at any time point in the forwards simulations with vertical migration. Areas not enclosed within grid-cells did not contain any particles that underwent recruitment.

Discussion

This study used larval dispersal simulations to further understand the processes that led to the hermit crab *C. erythropus* arriving in the southwest UK prior to 2016. Simulations showed that, between 2012 and 2016, it was possible for larvae to reach the UK but with variation in the number and geographic origin of larvae arriving in each year. The only feasible landmass from which larvae could have originated was the north coast of Brittany. Larvae took at least 20 days to reach the UK in all but a few circumstances. The average temperature experienced by larvae that reached the UK, varied between years but was typically around 15 °C. In comparison to other years, the larvae that reached the UK in 2014 originated from closer to the coastline of Brittany (Figure 4) and the temperature experienced by those larvae was around 16 °C, one degree higher than in other years (Figure 3).

Since the first recording of *C. erythropus* in the UK, the species appearance was suggested to be caused by the natural transportation of pelagic larvae via ocean currents (Carlisle & Tregenza, 1961; Southward & Southward, 1977). However, models of larval dispersal show little connectivity between Brittany and the UK (Salomon & Breton, 1993; Lefebvre *et al.*, 2003; Nicolle *et al.*, 2017). Our results contrast with these findings, to show that the dispersal of *C. erythropus* larvae, from Brittany to the southwest UK, could be possible.

The transportation of larvae away from the coastline of Brittany and onwards to the southwest UK only occurred in 2014 (Figure 4). This is important because *C. erythropus* is predominantly intertidal with individuals only found in shallow water down to 30m (Gherardi, 1990). Our simulations show larvae reaching the UK polygon in all years, but the only time when large numbers of larvae originated from regions shallower than 30m was in 2014 (Figure 4). Particles that reached the UK in years other than 2014 originated further offshore, in waters deeper than *C. erythropus* is known to inhabit. This finding suggests that changes in hydrodynamics of the English Channel, specifically in the region off North Brittany, played an important role in the appearance of *C. erythropus* in the UK.

Our findings, suggesting that the larvae of *C. erythropus* arrived in a single recruitment event in August and September 2014, conforms with prior research on *C. erythropus* in the UK. In 2017 the UK population consisted of a single size cohort, suggesting it was founded by a single recruitment event (Patterson *et al.*, 2020). August and September 2014 is 18 months prior to the first recording of *C. erythropus* in March 2016 at Castle beach, Falmouth (Patterson *et al.*, 2020). A gap of 18 months between the arrival of *C. erythropus* and the first recording of the species is reasonable, as the final megalopa larval stage of *C. erythropus* is only 3mm in length (Bartilotti *et al.*, 2008) and would have initially gone unnoticed or misidentified as *Pagurus bernhardus*. Records indicate *C. erythropus* has only successfully inhabited the UK twice in the last 60 years, once before 1959/60 (Carlisle & Tregenza, 1961) and once before 2016 (Hawkins *et al.*, 2017). It appears that the oceanographic conditions needed to facilitate transportation of larvae between near-shore Brittany and the southwest UK are rare, occurring only once in the five years we simulated. It may be that *C. erythropus* did not return to the UK immediately after the effects of the Torrey Canyon oil spill had dissipated because the species pelagic larvae were not transported away from the north coast of Brittany until 2014. The MARS3D hydrological model has archival oceanographic data dating back to 2006. Further simulations to establish whether there was any connectivity between Brittany and the southwest UK over a longer time period could further substantiate this hypothesis.

After the arrival of *C. erythropus* in 1959/60, Southward & Southward (1977) suggested that, due to the lower population size and lower water temperatures found in North Brittany, the pelagic larvae that reached the UK must have originated from South Brittany. Given our results showed zero connectivity between South Brittany and the southwest UK, it is likely that the *C. erythropus* recorded in the UK in 2016 did not originate from South Brittany. In October 2018, a gravid individual was found in the UK suggesting that reproduction is possible further north than was previously thought (Patterson *et al.*, 2020). As such, we speculate that the origin of larvae before 1959/60 could also have been North Brittany.

The temperature experienced by the simulated larvae that arrived in the southwest UK during August and September 2014 was around 16 °C, one degree higher than in other years (Figure 3). Harms (1992) showed that the larvae of *C. erythropus,* from the Mediterranean*,* can develop at 18 °C but not at 15 °C. We cannot conclude that the one degree rise in temperature seen in 2014 would be enough to facilitate larval survival compared with other years however, in general higher temperatures increase larval survival (O’Connor *et al.*, 2007). The warmer water combined with the rare oceanic currents suggests 2014 was the ideal time for *C. erythropus* to arrive in the UK.

Our results further show that the behaviour of larval vertical migration can significantly alter the trajectory of larval dispersal and subsequently the connectivity between two sites (Ayata *et al.*, 2010). Vertical migration prevented simulated larvae from being transported to regions where *C. erythropus* is known to be present in the UK after 2016. For example, larvae in the vertical migration simulations did not reach water south of Falmouth, Fowey, or Plymouth (Figure 4e). Larvae undergoing vertical migration in our simulation would be prevented from reaching regions of the

Brittany and UK polygons shallower than 30m. However, the bathymetry of the Western English Channel does not match up with the regions of the UK or Brittany polygons larvae failed to reach. The presence of *C. erythropus* in Falmouth, Fowey, and Plymouth suggests that the vertical migration parameters chosen for this study do not accurately depict that of *C. erythropus.* It is likely *C. erythropus* has more behavioural flexibility during its larval development than allowed in our simulations, which permitted the species to overcome the final stretch of shallow water. For short periods of time, the number of particles reaching the UK polygon during the vertical migration simulations exceeded that seen in the equivalent simulations without vertical migration (Figure 3). The increase in connectivity during the vertical migration simulations indicates that larvae in the English channel may be able to alter the velocity and direction of transportation by actively controlling their position in the water column.

The parameters of our larval dispersal simulations were set using the best knowledge we could attain about the larvae of *C. erythropus*. As there have only been a couple of studies on the larvae of *C. erythropus* (Harms, 1992; Bartilotti *et al.*, 2008), we also inferred information from closely related species and widen the estimates of parameters where their remained uncertainty. For example, the spawning season in the North Atlantic. The simulations presented here may not depict the specific biology of *C. erythropus,* but the parameters chosen are likely to be roughly in line for decapods with long-lived pelagic larvae.

The dispersal of particles from Brittany to the southwest UK took longer than 20 days, with the absolute minimum number of days identified as 13.4 days (Figure S1). This suggests that the duration of a species’ pelagic larvae will strongly influence whether or not a species will expand its range to the southwest UK via ocean currents. Crustaceans, teleost, and echinoderms, commonly have pelagic larvae that require more than 30 days to develop (Bradbury *et al.*, 2008). For example, the larvae of the barnacle *Pollicipes pollicipes* takes 28 days to develop (Franco *et al.*, 2015) and the nearest breeding population is Brittany (Hawkins *et al.*, 2017). There are reports that there was a recruitment of *P. pollicipes* to southwest UK in 2015 suggesting that the species arrived with *C. erythropus* in 2014. The larvae of *Pachygrapsus marmoratus* and *Eriphia verrucose,* which are decapods currently restricted to Brittany, take 30 and 40 days to develop, respectively (Lumare & Gozzo, 1972; Cuesta & Rodríguez, 2000). Our results suggest *P. marmoratus* and *E. verrucose* may reach the UK via larval dispersal in the future. Species with shorter pelagic larvae, such the majority of gastropods, porifera, and macroalgae with larvae that typically develop and settle within 10 days (Bradbury *et al.*, 2008), may be unable to successfully disperse across the Western English Channel limiting these species' response to climate change.

An in-depth understanding of the life cycle of species' pelagic larvae will be key to predicting where range expansions of marine and intertidal species will occur (Keith *et al.*, 2011), yet, there exist key gaps in our knowledge. Most importantly the understanding of a species' pelagic larvae often come from studies conducted in the centre of a species' range. For warm-water species currently limited to the Bay of Biscay, studies of larval duration, spawning, and the interaction between these and temperature have been conducted in the Mediterranean (Fransozo, 1987; Harms, 1992; Cuesta & Rodríguez, 2000) where the SST is considerably higher than the English Channel. The findings from Harms (1992) would suggest that the SST of the English Channel would be lethal to the larvae of *C. erythropus*. Nevertheless, *C. erythropus* has successfully arrived in the UK twice suggesting that local adaptation has occurred. *C. erythropus* larvae require food during their larval development but can develop into the juveniles after a periods of starvation in the megalopae stage (Harms, 1992). The range of diet larvae of *C. erythropus* can utilise is unknown but Harms (1992) reared larvae of *C. erythropus* on freshly hatched Brine shrimp (*Artemia nauplii*) and kept individuals separate to avoid cannibalism. Our simulations of larval dispersal showed little connectivity between South Brittany and the southwest UK. This suggests that for a species with similar life-history to *C. erythropus* to successfully arrive in the southwest UK via larval dispersal, a reproducing population must be established in North Brittany. *P. marmoratus* and *E. verrucose,* may have not yet arrived in the southwest UK, because populations of are currently restricted to South Brittany even though they have pelagic larvae with a similar duration to *C. erythropus* (Ingle & Clark, 2008; Deli *et al.*, 2019). Monitoring changes in the intertidal community of North Brittany, particularly for the appearance of *P. marmoratus* and *E. verrucose,* could forewarn of the species arrival in the southwest UK.

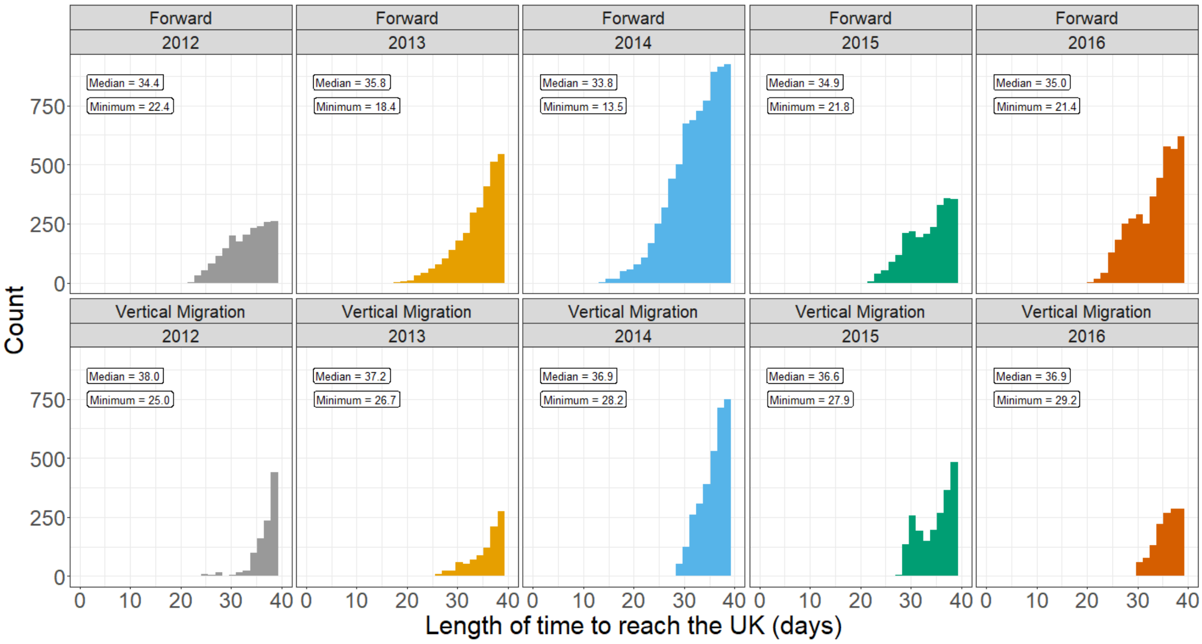
That we are aware of, this study is the first to demonstrate the possibility of connectivity between the southwest UK and Brittany using larval dispersal models. Other studies into larval dispersal models in the English Channel have found that the southwest UK is isolated from other potential sources of larvae in the English Channel, including Brittany. Nicolle *et al.*, (2017), found that scallop stocks of *Pecten maximus* in the southwest UK were isolated from all other stocks in the English Channel. Nicolle *et al.*, (2017), simulated larvae for two specific spawning dates each year and larvae settled precisely in the location where they reached maturity, around 35 days but dependent on SST. In our study, we ran simulations that released larvae daily for four months and counted connectivity as any particle reaching the general vicinity of the UK at any time point in the simulations. Our results show that the number of particles reaching the UK can fall from 5% to 0% within a few days. This means a single simulated spawning event, while potentially relevant for a specific species, will not show the connectivity between two regions for different spawning seasons. However, the finding that there was no connectivity between the southwest UK and Brittany, in the years Nicolle *et al.*, (2017) simulated (2000 – 2009), furthers the hypothesis that 2014 was an exceptionally rare year for dispersal.

Lefebvre *et al.*, (2003) also found that southwest UK populations of the Brittle Star, *Ophiothrix fragilis,* did not show any influx of larvae from other populations in the English Channel. Lefebvre *et al.*, (2003), based their connectivity on the general patterns of 2D oceanographic currents calculated by Salomon & Breton (1993) under various weather conditions. As such, Lefebvre *et al.*, (2003) methods may not have used as complex a variety of oceanographic circumstances than the daily oceanographic data produced by MARS3D. Indeed, preliminary results from our study using MARC2D also did not show any connectivity between the southwest UK and Brittany. Although, built of the work of Salomon & Breton (1993) newer more complex hydrodynamic models of the English Channel, such as MARS3D, may offer better predictions of larval dispersal.

Conclusion

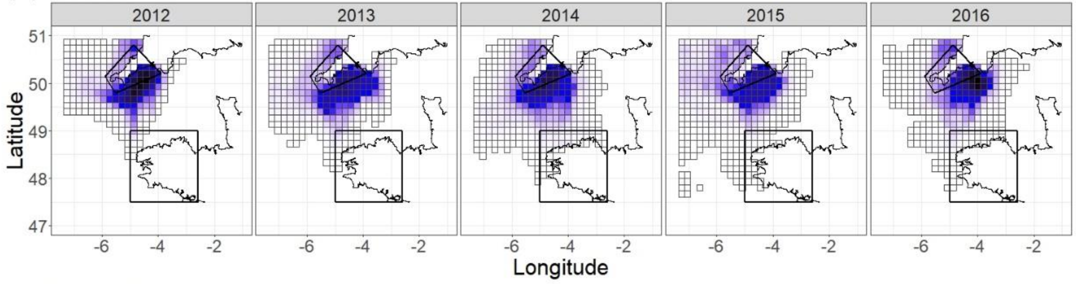
With anthropogenic climate change predicted to cause high levels of species extinction worldwide (Pereira *et al.*, 2010), understanding the processes that limit the geographic ranges' of species is key to predicting which species will expanded their range and where (Bellard *et al.*, 2012; Sorte, 2013). This study suggests that *C. erythropus* was able to overcome the barrier of the English Channel, expanding its range to the UK, because of its long-duration pelagic larvae and the rare hydrological and thermal conditions found in the English Channel in August and September 2014. The origin of these larvae is likely to be the north coast of Brittany. These results can be used to forecast which marine and intertidal species will arrive in the southwest UK in the coming decades.

Supplementary material

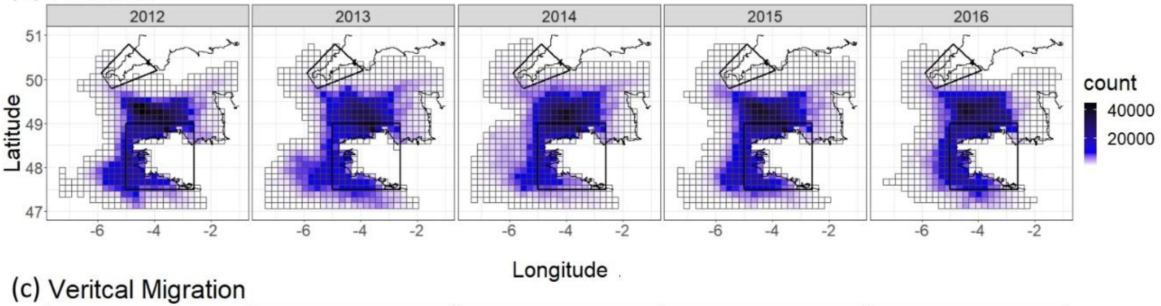


Supplementary Figure 1: The length of time particles took to be transported from their initial starting position (in the Brittany polygon) to the UK polygon during both the forward simulation and the vertical migration simulations. Simulations were terminated at 40 days.

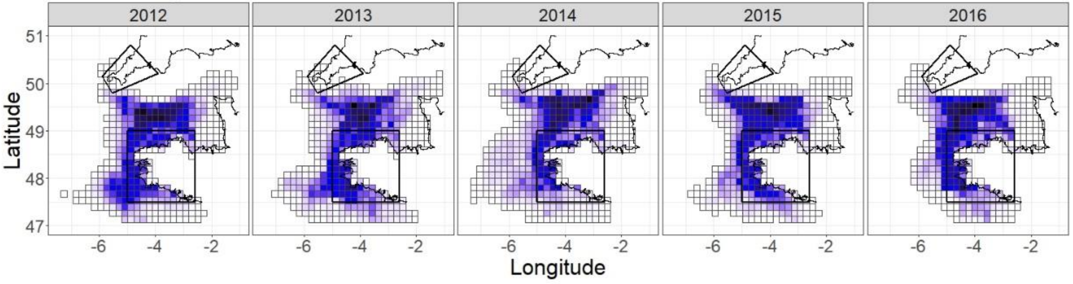
(a) Backwards



(b) Forwards



(c) Veritcal Migration



Supplementary Figure 2: The colour of each grid-cell indicates the number of particles within each grid-cell under the following circumstances. **(a)** The final position of all particles in backward simulations after 40 days. Particles in the backward simulation were initially placed within the UK Polygon. The final position of all particles in the **(b)** forward and **(c)** vertical migration simulations. Particles in the forward and vertical migration simulated where released from the Brittany polygon. Areas not enclosed within grid-cells did not contain any particles.

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