



The range expansion of *Clibanarius erythropus* to the UK suggests that other range-shifting intertidal species may not follow

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Abstract

The ranges of species are shifting as a consequence of anthropogenic climate change. In the marine realm biogeographic transition zones could form barriers to dispersal and inhibit range-shift, but little is known about this potential effect. The hermit crab *Clibanarius erythropus* appeared in the UK in 2016 with the nearest reproducing population being on the northern coast of Brittany. This raises questions of which conditions may have permitted *C. erythropus* to cross the English Channel (7.25°W, 49.00°N) and whether this barrier could be overcome by other intertidal species. Dispersal 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 channel. The transportation of larvae from Brittany to the southwest UK appears to be rare and driven by occasional, unusual ocean currents. The English Channel may continue to 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. North Brittany was the only landmass from which it is feasible the UK population of *C. erythropus* could have originated. Therefore, species with long-lived pelagic larvae but without reproducing populations in North Brittany may not appear in the southwest UK until the species are established in North Brittany. The English Channel could continue to limit the ability of many intertidal species to shift their range with climate change.

Keywords Range shift · Larval dispersal · Intertidal · Decapoda · Global change · English channel

Introduction

Globally, the ranges of many species are shifting towards the poles, as a consequence of anthropogenic climate change (Hawkins et al. 2008; 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. 2008, 2017). In the southwest UK, it appears that the number of intertidal species becoming locally extinct is greater than the number of novel species arriving

from further south (Burrows 2017) resulting in climate ‘debt’ (Jackson and 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 and 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).

The Iroise Sea, west of Brittany, is reported as a biogeographical transition zone for a number of benthic, intertidal, and marine species (Gallon et al. 2017). Multiple crustaceans (Ingle and 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 and Van Wormhoudt 2017), have a northern limit on the coast of Brittany or the Channel Isles. However, one species with a range that has expanded

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from mainland Europe into the southwest UK is *Clibanarius erythropus*. Records of *C. erythropus* occurred in the UK in the 1950/60 s (Carlisle and 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 and Southward 1988). After 1985, no known records of *C. erythropus* occurred in the UK until 2016. Given that intertidal sites in the southwest UK, such as Wembury, have been surveyed consistently between 1985 and 2016, *C. erythropus* is unlikely to have been present in the UK during this time (Hawkins et al. 2017). 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 and Southward 1977, 1988; Patterson et al. 2020). In 2018, the UK population of *C. erythropus* consisted of a single size cohort suggesting the species 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 been observed 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 other species' distributions in the future—particularly those with populations around the Iroise Sea, a noted biogeographic transition zone (Gallon et al. 2017).

The population of *C. erythropus* with the closest 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, since the population on the northern coast of Brittany had a smaller population and likely experienced water temperatures too cold for reproduction. Whether or not the larvae originated from northern or southern Brittany, the larvae would have been transported across the Western English Channel, which is around ~160 km 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 (3 cm/s) and weak—varying in directionality under different environmental factors; for instance, wind direction (Pingree and Maddock 1977; Salomon and Breton 1993). Therefore, 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). Yet, the appearance of *C. erythropus* in the southwest UK suggests the transportation of larvae via ocean currents can occur.

Here, we use larval dispersal simulations based on a hydrodynamic model to simulate the release and transportation of larvae in the Western English Channel in the years prior to the appearance of *C. erythropus* in the UK—2006–2016. We ask whether oceanographic conditions between 2006 and 2016 are consistently conducive for larval transport between Brittany and the southwest UK or if transportation between Brittany and the UK is unusual, only occurring once over the duration of our simulations. If the latter is 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.

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). Vertical diel migration has been shown to have a significant impact on the trajectory of larvae and as such the connectivity between locations (Ayata et al. 2010). 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. Our simulations could also narrow down which sub-population of *C. erythropus* was the likely source of the larvae that reached the UK, which will help us understand which sub-populations of other species could be important for the mediation of future range expansions.

Methods

To investigate the potential trajectory of *C. erythropus* larvae in the Western English Channel and the potential variation in inter-annual connectivity between Brittany and the southwest UK, we used the Lagrangian tool *ichthyop* v3.3 (Lett et al. 2008). This tool uses 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, to estimate locations of larval settlement/recruitment and origin, respectively.

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 2006 and 2016, inclusive.

Water temperature is likely a limiting factor in the species distribution of *C. erythropus* by preventing reproduction at colder temperatures (Harms 1992). Evidence suggests that, in the Mediterranean, *C. erythropus* reproduces in the summer (Southward and Southward 1977; Harms 1992) but in the Atlantic coast of Spain, *C. erythropus* reproduces later in the year from August to September (Southward and Southward 1977). At the northern limit of *C. erythropus*' range (the southwest UK), a gravid individual was recorded in October 2018 (Patterson et al. 2020). As such, it seems possible that water temperature could permit reproduction in Brittany between August and November and we simulated larval dispersal between these months 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 2007 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) suggest a full reproductive cycle of *C. erythropus* should 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 and Dumas 2008) with a spatial resolution of 2.5 km², 40 levels of depth (sigma-levels) between the sea surface and the seafloor, with an adaptive time-step between 200 and 400 s and covers an area from 8 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 and Dumas 2008; Lazure et al. 2009). Differences

between in situ measures and MARS3D were minimal, producing accurate prediction of salinity and temperature. 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 downloaded the available MARS3D data with a temporal resolution of 1 h from <http://marc.ifremer.fr/en/>. To improve computation time within Ichthyop, we subset the MARS3D data to a 210,542 km² 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; Fig. 1a). 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 (see A in Fig. 1a). Due to the 1-h temporal resolution of the MARS3D data, the paths of some particles could cross the coastline. Any particle that was transported onto land was frozen at the boundary between land and sea until the calculated trajectory of ocean currents it experienced would transport the particle in a direction away from the coastline. We did not remove these particles from the simulations as their approximate location was known.

Identifying recruitment events and possible larval origins

Simulations of larval trajectory and velocity, in Ichthyop, were run forwards in time, with 10,000 particles released at 10 am (GMT) 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 and was independent for each simulation. 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 s (s), as a compromise between simulation stability (Courant–Friedrich–Lewy ≤ 1) and computation time. The latitude, longitude, and depth of each particle was recorded every hour (3600 s or 12 time-steps) for 40 days (3,456,000 s, 11,520 time-steps, 960 records). 40 days is the maximum time length *C. erythropus* larvae survived in the laboratory (Harms 1992). 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. Henceforth, these simulations are referred to as ‘forward simulations.’

To identify whether or not particles could have originated from a location outside of the Brittany polygon, we conducted “backward” simulations where particles were released from around the UK and their potential trajectory calculated backwards in time. We simulated

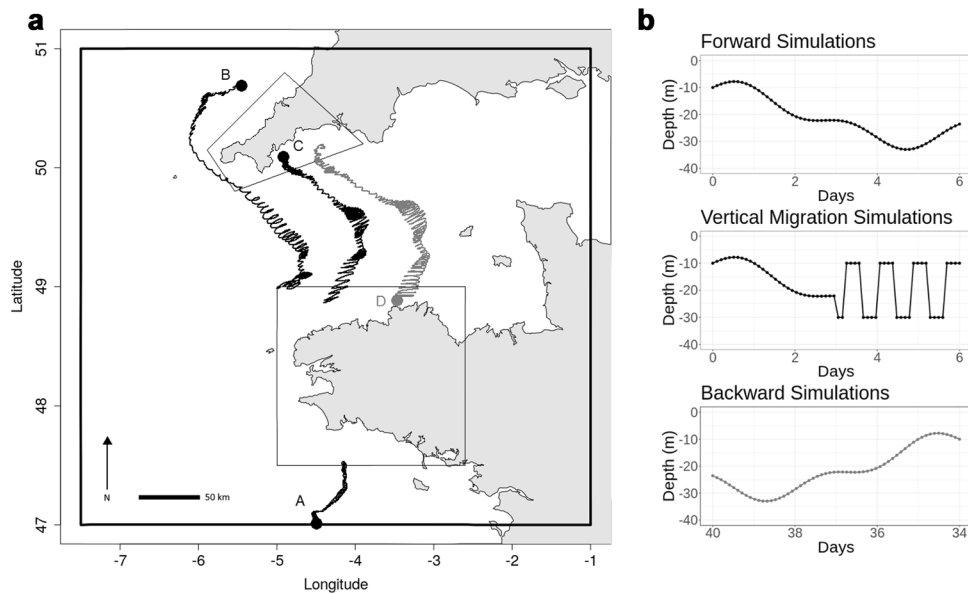


Fig. 1 Panel **a** the extent of the simulated area (thick black outline) and the extent of UK and Brittany polygons from where particles were initially placed at the start of each simulation and to determine if recruitment events occurred (thin black outlines). **A**, **B**, and **C** are the routes 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** 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. Particles are illustrative only and do not necessarily originate from areas of suitable habitat for *C. erythropus*. Panel **b**, example depth profiles for an individual virtual particle cover the first 6 days of a simulation, for each of the three simulation types. From top to bottom, forward simulations without vertical migration, forward simulations with vertical migration, and backwards simulations without vertical migration

larval trajectory and velocity backwards in time, with 10,000 particles released at 10am (GMT) 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, Fig. 1a). To reduce computational costs, backwards simulations were only conducted for the years surrounding the identified period of potential recruitment (2012–2016) 35.3% of particles had an initial position in the northern half of the UK polygon, while 64.7% had an initial position in the southern half of the UK polygon. Particle trajectory and velocity were calculated with the same time-step, recording frequency, and duration of transport as in the forward simulations. The starting conditions of the backwards simulation were 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.’

To investigate whether the tidal cycle strongly influenced the probability of recruitment, backwards simulations were run for 2015 with particles released at 4 pm 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 were kept consistent with those of the forward simulations unless stated here. Particles were forced to instantaneously move to -30 m in the daytime and -10 m at nighttime (Fig. 1b), 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 (the default within Ichthyop), 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*’ (Thieurmél and 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.

The UK and Brittany polygons, which were used to identify where particles originated or arrived (Fig. 1a), encompass areas where the seabed is deeper than 30 m which is unsuitable for *C. erythropus* settlement (Gherardi 1990). For the duration of this paper, we define suitable habitat as any region of sea with a depth less than 30 m; however, other factors such as salinity, substrate, and temperature will likely restrict the actual distribution of suitable habitat for *C. erythropus* further. The UK and Brittany polygons were initially designed to include areas of water deeper than ~30 m, because a polygon that only contained water below ~30 m is too complex to be implemented within Ichthyop. As such, in the forward simulations and the vertical migration simulations, we retrospectively excluded particles that were initially placed in water deeper than 30 m using the bathymetry data set from EMODnet (EMODnet Digital Bathymetry (DTM) 2020). The EMODnet bathymetry data have a resolution of 1/16 arc minutes (~113 m²) which is higher than the MARS3D oceanographic data (2.5 km²). We determined whether a particle was initially positioned in water deeper than 30 m exclusively using the EMODnet data. This reduced the total number of particles in each simulation from 10,000 to a mean of 1369 (range 1247–1478). Having trajectory data for virtual particles within and outside shallow water allows us to determine how sensitive our results are to dispersal from and into near-shore waters.

Recruitment events

If a particle was transported into the UK polygon at any point during the forwards and vertical migration simulations, this was counted as a potential recruitment event (Fig. 1a). Similarly, if a particle was transported into the Brittany polygon during the backwards simulations, this was also counted as a potential recruitment event. To compare the potential for recruitment between each study year, we recorded the number of recruitment events for each day particles were released as a proportion of particles initially placed in suitable habitat (water with a depth less than 30 m) at the start of each simulation. This allows us to compare the number of potential recruitment events across each year, between years, and between different simulation types.

All data analysis was conducted in R v4.0.2 (R Core Team 2013), using the packages ‘tidyverse’ (Wickham et al. 2019), ‘ncdf4’ (Pierce 2019), and ‘lubridate’ (Grolemund and Wickham 2011).

Results

Connectivity between Brittany and the southwest UK

Across all 1110 days where forward simulations with no vertical migration were initiated, 91 (8.2%) recorded at

least one virtual particle being transported from suitable habitat in Brittany to the UK (Fig. 2). Meaning that 1019 (91.8%) of our forward simulations recorded zero recruitment events. The maximum number of recruitment events in the forward simulations was 30 (2.1%), occurring on both August 22nd and 24th, 2014. Of the 1,693,919 particles released from suitable habitat in the forwards simulations, 570 (0.03%) underwent a recruitment event. In the forward simulations without vertical migration, 2014 had a much higher level of recruitment in comparison to all other years. From August 19th to September 5th, the percentage of particles undergoing a recruitment event stayed above 1.0% (Fig. 2). Over the ten years of vertical migration simulations, only one particle underwent a recruitment event on the 2009-09-12. (Fig. 2).

Including all particles, regardless of whether they originated from areas unsuitable for *C. erythropus*, increased the number of particles reaching the UK polygon. Notably, in the simulation without vertical migration, we see particles being transported from the Brittany polygon to the UK polygon in all years. We also see particles being transported from Brittany to the UK in the simulations with vertical migration, except for 2006. In the forwards simulations, the highest number of particles arriving in the UK occurred in August and September 2014, regardless of whether particles underwent vertical migration or not (Fig. 2; Fig. S1).

Larval duration and temperature

In the forward simulations with no vertical migration, the mean length of time to reach the UK polygon from suitable habitat in the Brittany polygon was 34.9 days, with a median of 35.7 and a range of 22.1 days–40.0 days (the maximum length of the simulations). Very few particles took fewer than 30 days to reach the UK and this occurred only in 2014 and 2016, with 69 and 1 particles, respectively. In 2014, particles took a mean of 34.7 days to be transported to the UK polygon (median 36.1 days, ranging from 22.1 to 40.0 days). Excluding particles from 2014, the mean length of time to reach the UK was 38.3 days; the median was 38.8, days and ranged from 29.0 to 40.0 days. Across all years, the number of particles arriving in the UK increased as the simulations progressed with the highest number of particles arriving on a single day occurring on the final day of each simulation.

For particles that underwent a recruitment event from suitable habitat in the forward simulations with no vertical migration, the mean SST particles experienced was 15.8 °C and ranged from 13.4 to 17.1 °C. The average SST of particles that were transported to the UK varied throughout and between years (Fig. 3). The 2 years in which a significant number of arriving particles experienced SST above 15°C were 2009 and 2014. In 2009, a small number

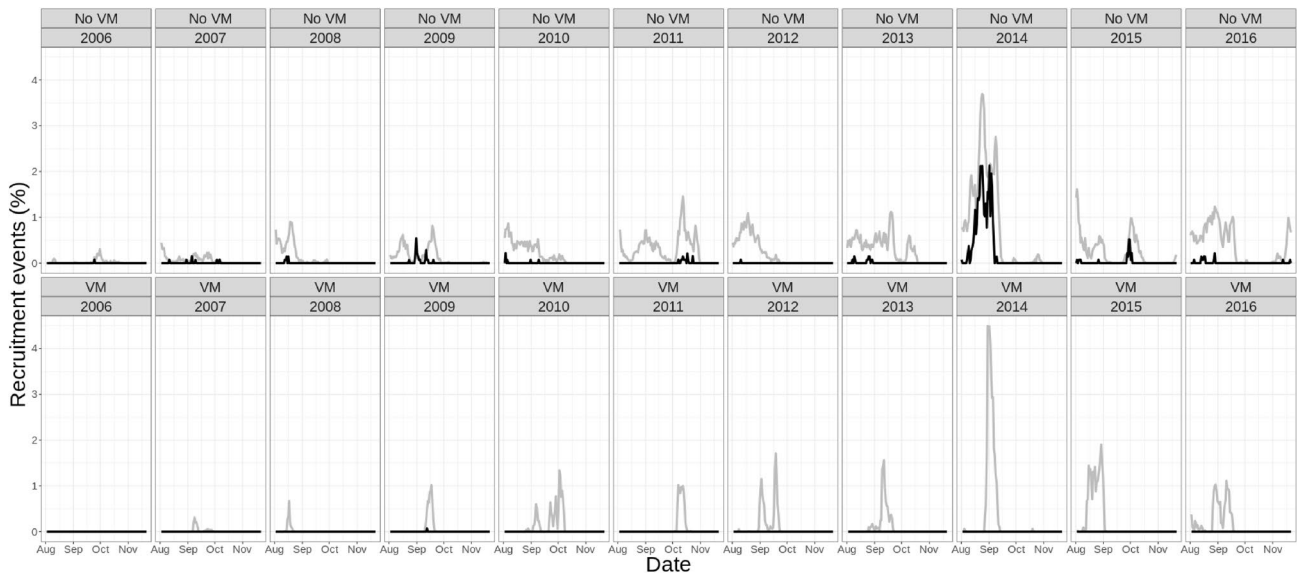
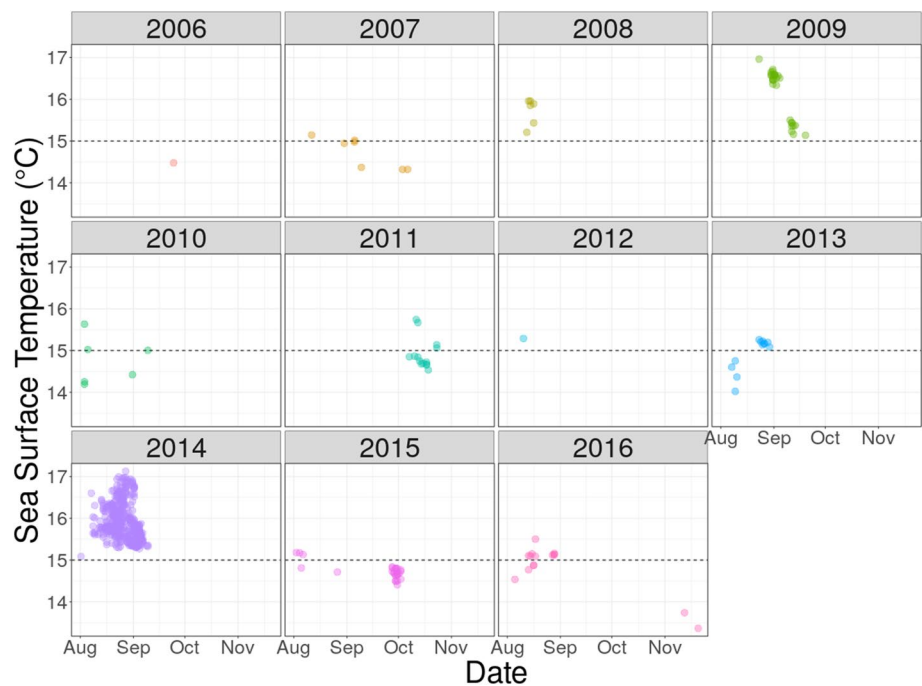


Fig. 2 The percentage of recruitment events across all simulated years for both forwards (No VM) and vertical migration simulations (VM). One recruitment event is a single particle calculated to have a trajectory that intersects with the UK polygon at any time point within 40 days. The black line corresponds to the percentage of particles that reached the UK polygon and were initially placed within suitable habitat for *Clibanarius erythropus* within the Brittany poly-

gon—defined as water with depth of less than 30 m. The grey line corresponds to the percentage of particles that reached the UK polygon that were initially placed anywhere within the Brittany polygon. Date corresponds to when a particle would have originated from Brittany, i.e., the first time-step of the forwards and vertical migration simulations

Fig. 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 and where initially placed in suitable habitat for *Clibanarius erythropus*—defined as water with a depth less than 30 m), throughout the forwards simulations. Breaks in the data show where no recruitment events took place. Individual points 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 that *C. erythropus* larvae, from the Mediterranean, could not fully develop



of particles (< 0.5%) reached the UK polygon had a mean SST of 16.2 °C (Fig. 3). In 2014, the mean SST experienced by all arriving particles and which originated in suitable habitat was 16.0 °C, ranging from 15.4 to 17.1 °C.

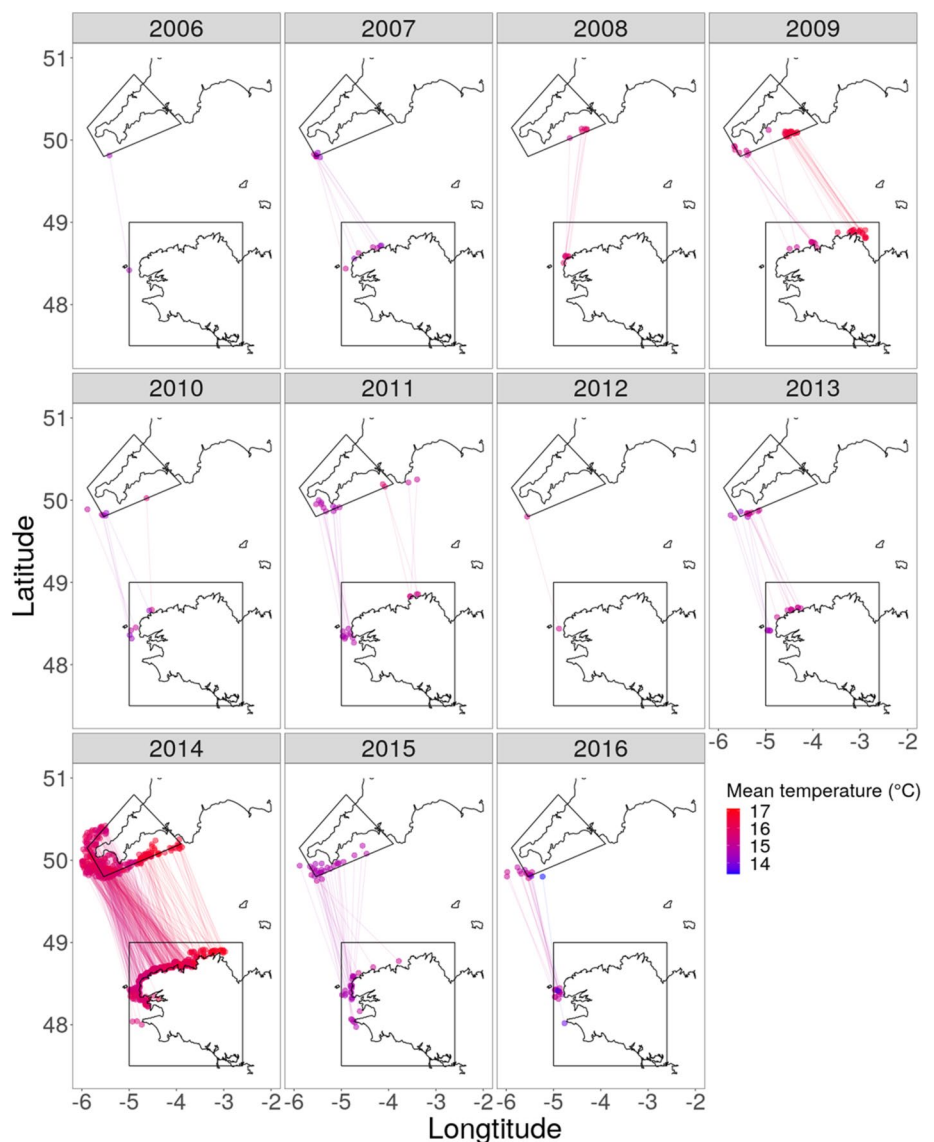
The geographical origin of larvae

In the forwards simulations with no vertical migration, particles that were transported to the UK polygon were initially positioned near the north coast of the Brittany polygon (Fig. 4). After 40 days of transportation, particles that recruited in 2014 were mainly concentrated in the southwest corner of the UK polygon, but were projected to have reached both the north and south coast of the south-west (SW) peninsula of the UK (Fig. 4). Only in 2014 did simulations show connectivity between Brittany and the north coast of the SW peninsula (Fig. 4). Across all years, we found no

connection between the UK and the south coast of Brittany, regardless of simulation type or whether the particles were restricted to have originated from suitable habitat (Figs. S1, S2, S3).

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 substantially away from suitable habitat for *C. erythropus*. In the backwards simulations, no particles were projected to have originated from any location other than North Brittany (Fig. S3). In the backwards simulations, several particles were transported beyond the western edge of the simulation where there is no feasible landmass from which particles could have originated.

Fig. 4 The initial starting position and projected final position of all particles that entered the UK polygon at any time point in the forwards simulations without vertical migration. Only particles that were initially placed in suitable habitat within the Brittany polygon are shown. Suitable habitat is defined as any region of ocean with a depth less than 30 m. The joining line indicates the initial and final position of each particle. Colour corresponds the average sea surface temperature (°C) experienced by each particle over the entire duration of the simulation



Looking at the trajectory of all particles in the forward simulations with no vertical migration across all years, including those that did not undergo a recruitment event and did not originate from suitable habitat, 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 (Fig. S2a). The vertical migration simulations also project larvae reaching the UK in all years, but no particles were transported further east than the Lizard peninsula and did not originate from habitat suitable for *C. erythropus* (Fig. S2b).

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 2006 and 2016, it was possible for larvae to reach the UK but with variation in the number arriving in each year. The only feasible landmass from which larvae could have originated was the north coast of Brittany. Larvae took at least 30 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 (Fig. 4) and the temperature experienced by those larvae was around 16 °C, one degree higher than in other years (Fig. 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 transporting a larger number of propagules to the UK suggests that 2014 was the ideal time for *C. erythropus* to arrive in the UK.

In our simulations, the transportation of larvae away from the coastline of Brittany and onwards to the southwest UK occurred only in large numbers in 2014 (Fig. 4). This is important, because *C. erythropus* is predominantly intertidal with individuals only found in shallow water down to 30 m (Gherardi 1990). The majority of particles that reached the UK in years other than 2014 originated further offshore, in waters deeper than *C. erythropus* is known to inhabit. The UK population seems to have been founded by a single recruitment event before 2016 (Patterson et al. 2020). Our results suggest that it is most likely that *C. erythropus*'

larvae founded populations in the UK following a period of larval transportation in August and September 2014.

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 3 mm in length (Bartilotti et al. 2008) and could have initially gone unnoticed or misidentified as *Pagurus bernhardus*. Records indicate that *C. erythropus* has only successfully inhabited the UK twice in the last 60 years, once before 1959/60 (Carlisle and 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 11 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 window of transportation opportunity did not re-open until 2014. However, we note that some transportation could have occurred in years other than 2014, but did not result in the founding of a viable population in the UK and was not detected.

After the arrival of *C. erythropus* in 1959/60, Southward & Southward (1977) suggested that the water temperatures in North Brittany were too low for *C. erythropus* to reproduce at all, and the population was likely a sink population fed by warmer South Brittany. Therefore, they suggested the 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, and thus in colder temperatures (Patterson et al. 2020). As such, reproduction in North Brittany seems likely in the present day, and possibly in the 1950s. We speculate that the origin of larvae before 1959/60 could also have been North Brittany. The appearance of *C. erythropus* in 1959/60 has been linked to a period of higher than average sea surface temperature in the English Channel (Carlisle and Tregenza 1961; Hawkins et al. 2017). After 1960, the sea surface temperature fell and did not return to same level until the 2000s (Hawkins et al. 2017). Our results suggest that the return of *C. erythropus* to the UK lagged behind the rise in sea surface temperature, because the transportation of larvae from Brittany to the UK did not occur until 2014. Larval vertical migration has been shown to alter the trajectory of larval dispersal and subsequently the connectivity between two sites (Ayata et al. 2010).

Vertical migration simulations did not prevent larvae from dispersing across the English Channel, and did not

substantively alter the inter-annual variation in connectivity between Brittany and the southwest UK (Fig. 2). Thus, the diel migration behaviour of larvae may not be important for crossing the English Channel. We note that vertical migration simulations may not accurately represent the behaviour of larvae in shallow water or the variability of diel migration over larval development. Larvae undergoing vertical migration in our simulation could not have reached regions of the UK polygon shallower than 30 m, because larvae were forced to instantaneously move to 30 m in the daytime. Larvae forced to be at or below the depth of their current position would have been temporarily frozen in place, severely limiting their dispersal ability. For instance, vertical migration prevented simulated larvae from being transported to water south of Falmouth, Fowey, or Plymouth (Fig. S1) where *C. erythropus* has been recorded since 2016. 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*, and that programmes like Ichthyop would be improved if they could adjust migration near to the shore. 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. Our simulations with no vertical migration show particles entering the near-shore water around the southwest UK, suggesting that if larvae stopped undergoing vertical migration in shallower water, after being transported across the English Channel, they could reach the coastline of the southwest UK.

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 been only two studies on the larvae of *C. erythropus* (Harms 1992; Bartilotti et al. 2008), we also inferred information from closely related species and widened the estimates of parameters where their remained uncertainty. For example, we extended the spawning season to be later in the year, because successful reproduction of *C. erythropus* could occur at substantially lower water temperatures than that seen in studies conducted in the Mediterranean (Harms 1992; Patterson et al. 2020). The simulations presented here may not depict the precise biology of *C. erythropus*, but the parameters chosen are likely to be in line for decapods with long-lived pelagic larvae.

The dispersal of particles from Brittany to the southwest UK took longer than 30 days, with the absolute minimum number of days identified as 22.1 days. Across all years, the majority of particles that recruited to the southwest UK arrived in the final week of our simulations (after 33 days). At 33 days, the larvae of *C. erythropus* would develop into the magalopa stage and be competent to settle (Harms 1992). Restricting recruitment to the final week of simulations had no bearing on the inter-annual variation in recruitment,

because nearly all recruited particles remained within the southwest UK until the end of the simulations (Fig. 4). The number of particles arriving may have continued to increase after 40 days (the maximum number of days simulated). 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). This may mean that many such species could cross to southwest UK from northwest France. The larvae of the barnacle *Pollicipes pollicipes* takes 28 days to develop (Franco et al. 2015) and the nearest breeding population to the UK is Brittany (Hawkins et al. 2017). There are reports that there was a recruitment of *P. pollicipes* to southwest UK in 2015. It is therefore possible that *P. pollicipes* arrived with *C. erythropus* in 2014, following the same hydrological conditions. The larvae of *Pachygrapsus marmoratus* and *Eriphia verrucosa* are decapods whose range currently extends no further north than Brittany, and take 30 and 40 days to develop, respectively (Lumare and Gozzo 1972; Cuesta and Rodríguez 2000). Our results suggest that *P. marmoratus* and *E. verrucosa* may reach the UK via larval dispersal in the future. Species with shorter-duration pelagic larvae, such as 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. Our simulations of larval dispersal showed little connectivity between South Brittany and the southwest UK. This suggests that for a species to successfully arrive in the southwest UK via larval dispersal, it must have a reproducing population in North Brittany. *P. marmoratus* and *E. verrucosa* have pelagic larvae with a similar duration to *C. erythropus* (Ingle and Clark 2008; Deli et al. 2019) so might be expected to cross the channel, but may have not yet arrived in the southwest UK, because they are currently restricted to South Brittany. Monitoring changes in the intertidal community of North Brittany, particularly for the appearance of *P. marmoratus* and *E. verrucosa*, could forewarn of the species arrival in the southwest UK.

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. The relative contributions of more rapid transportation, higher temperature experienced during transportation (both of which could affect survival), or a larger quantity of propagules transported between the coasts of north Brittany and southwest UK to establishment are not known. Importantly, the understanding of a species' pelagic larvae often come from studies conducted far from the edge of a species' range. For

warm-water species whose northern range limit is in 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 and 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 at its range margin, the species can tolerate cooler temperatures. Given the likelihood of local adaptation to cooler temperatures at poleward range margins, tolerances measured in warmer conditions should not be used to indicate a species' potential for poleward range expansion. In addition, larval development is normally longer in colder climates (Giménez 2006; McLeod et al. 2015), which could allow some species to be carried from Brittany to the southwest UK more regularly than our result would suggest. However, preliminary analysis of the phylogeographic structure of the mitochondrial cytochrome oxidase of *C. erythropus* in Brittany, the UK, and the Mediterranean shows that there is little genetic divergence between populations in the European seascape (Patterson 2020).

This study is the first we are aware of 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 4 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 species that spawn over several days, weeks, or even months. However, Nicolle et al., (2017), finding that there was no connectivity between the southwest UK and Brittany in 2000–2009, could also support our suggestion that the high potential for dispersal in 2014 may have been exceptionally rare.

Lefebvre et al. (2003) also suggested that the southwest UK was isolated from other biogeographic regions, finding 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 and Breton (1993) under various weather conditions. As such, Lefebvre et al.'s (2003) methods may not have used as complex a variety of oceanographic circumstances as the daily oceanographic data produced by MARS3D and which we used. Indeed, preliminary results from our study using 2D data (MARC2D) also did not show any connectivity between the southwest UK and Brittany (data not shown). 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 expand 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, and suggest that many species will not be able to make the jump. Improving predictions of marine range-shifts across biogeographic transition zones requires better representation of diel migration behaviour and three-dimensional representation of oceanic currents in models, as well as more accurate measurement of temperature tolerances and pelagic duration at range margins.

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Author contributions CP, RE, and CL all identified the research to be of interest. Study design was planned by CP and RE, with guidance from CL. Data download, programming, and the running of simulations was conducted by CP, with guidance from RE and CL. Data analysis was conducted by CP, with guidance from RE and CL. The manuscript was written by CP with guidance and editing by RE and CL. All authors read and approved the final manuscript.

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Data availability All oceanographic data used in this study are archived at <http://marc.ifremer.fr/en/>. All parameters used within the programme Ichthyop v3.3 are the default unless otherwise stated within the text.

Code availability Upon publication code will be published on Github.

Declarations

Conflicts of interest The authors declare no conflict of interest.

Ethics approval Not applicable.

Consent for publication All authors consent for publication.

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