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Marine sublittoral benthos fails to track temperature in response to climate change in a biogeographical transition zone

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Species ranges are shifting globally to track temperature changes in response to climate warming, with substantial variability among taxa. In the English Channel, a biogeographical transition zone between the cold temperate and warm temperate provinces of the North-East Atlantic, distribution shifts have been relatively well documented for plankton, fish and intertidal benthic organisms, but little information is available on sublittoral benthos. Following a description of the magnitude of the sea bottom temperature (SBT) rise, the changes in the distribution and occupancy of 65 benthic invertebrate species were analysed by comparing data collected throughout the English Channel at more than 200 stations sampled during a cool period in the 1960s–1970s and at present in 2012–2014. A non-uniform rise in SBT for the last three decades was observed at the regional scale, varying from 0.07 to 0.54°C per decade. This rise differs from that reported for sea surface temperature (SST) in stratified areas suggesting that SBT should be used rather than SST to analyse responses of subtidal organisms to climate change. Despite shifts in both minimum and maximum sea bottom isotherms (2.5 and 3.2 $km.year^{-1}$, respectively), the distribution centroid shift of most species remained <1.0 $km.year^{-1}$, regardless of the average temperatures they usually experience. Conversely, decreases were observed in the occurrence of most cold-water species and increases were found in the occurrence of most warm-water species. These results suggest that ongoing climate change could lead to a decrease in benthic biodiversity at range limits, especially where connection routes are lacking for new migrants.

Keywords: benthos, biogeographical transition zone, climate change, distribution shifts, English Channel, range limits, sea bottom temperature, species occupancy

Introduction

Global warming has intensified over the last few decades constituting a major threat to living systems (Parmesan and Yohe, 2003; Parmesan, 2006; Urban, 2015; Pecl *et al.*, 2017). One of the most striking lines of evidence of the impact of climate change on biodiversity are the distribution shifts reported worldwide across lands and oceans (Parmesan and Yohe, 2003; Perry *et al.*, 2005; Helmuth *et al.*, 2006; Chen *et al.*, 2011; Burrows *et al.*, 2014;

Hiddink *et al.*, 2015). According to the climate variability hypothesis, species latitudinal ranges are expected to reflect their thermal tolerance (Sunday *et al.*, 2012). With climate warming, species' ranges are then predicted to expand to their poleward boundaries (i.e. leading-edges), and to contract to their equatorward boundaries (i.e. trailing-edges). Analysing the links between thermal tolerance and latitudinal range boundaries of marine and terrestrial ectotherms, Sunday *et al.* (2012) supported these predictions, showing that marine ectotherms could be qualified as thermal-range conformers. Further meta-analyses on marine species reported that most of them have responded in a manner consistent with the expected impacts of climate change, shifting towards previously cooler waters (poleward or towards deeper waters), but at different rates and directions within and between regions (Pinsky *et al.*, 2013; Poloczanska *et al.*, 2013). Additionally, noticeable differences in distribution change rates and response consistency were highlighted among taxonomic or functional groups, raising questions on the ability of sessile or slow-moving organisms (i.e. benthic species) to respond or adapt to warming compared with dispersive or highly mobile organisms (i.e. pelagic species). Besides effects on the distribution of species, climate change could also alter local population abundances. For example, in central Europe, long-term temperature change has recently been shown to have significant effects in the terrestrial communities but more variable effects in the aquatic communities (Bowler *et al.*, 2017). Changes in local abundances of species could then indirectly influence their distribution and ultimately their extinction risk.

Biogeographical transition zones, defined as geographical areas of overlap between different biotic components at their range margins (Ferro and Morrone, 2014), are particularly sensitive to climate change (see Thuiller *et al.*, 2005 for plants; Mieszkowska and Sugden, 2016 for a review on marine benthic habitats). At the biogeographical boundary between the northern cold temperate Boreal region and the Southern warm temperate Lusitanian region, the western English Channel benefits from a long history of oceanographic and ecological investigations (reviewed in Southward *et al.*, 2005). It is therefore particularly suited to detect biological fluctuations in relation to changes in temperature (Hawkins *et al.*, 2003). During the last century, climatic conditions in the English Channel underwent considerable variability with (i) a period of warming in the 1920s and 1930s, (ii) a cooling in the 1940s, (iii) a pronounced warming from the mid-1950s to 1962, (iv) a period of cooling until the mid-1980s, and (v) the present warming period with a rapid annual temperature increase (Smyth *et al.*, 2010). The consequences of these changes have been relatively well documented for plankton (Beaugrand *et al.*, 2009), fish (Genner *et al.*, 2004, 2010) and intertidal benthic organisms (Southward *et al.*, 2005; Mieszkowska *et al.*, 2007, 2014; Hawkins *et al.*, 2008, 2009). Conversely, studies reporting the response of sublittoral benthos to climate change in this biogeographical transition zone are rare (but see Hinz *et al.*, 2011).

Yet, from two large-scale surveys of the benthic fauna carried out throughout the English Channel between 1958 and 1962, Holme's seminal work resulted in the classification of macrobenthic species according to their patterns of distribution in relation to the longitudinal temperature gradient and climatic conditions (Holme, 1961, 1966). This classification includes: (i) the stenothermal cold-water Western species distributed west of a line between Start Point (UK) and Guernsey (UK); (ii) the stenothermal cold-water West Channel species generally distributed throughout the western half of the Channel; (iii) the eurythermal cold-water Eastern species which are commonest in the eastern part of the Channel; and (iv) the warm-water Sarnian species centred around the Channel Islands and in the inner parts of the nearby gulf where annual temperature ranges may be as high as in the eastern end of the Channel. In addition to these biogeographical groups, he proposed two other groups: (i) species distributed throughout the length of the Channel and supposed to be insensitive to the reported thermal gradient and, (ii) species with "miscellaneous distributions" which exhibited patchy distributions at the scale of the Channel according to an insufficient sampling effort and/or in relation to specific edaphic factors. Later, during the 1960s and 1970s, Cabioch *et al.* (1977) investigated the macrofauna distribution across the entire English Channel and, taking sessile epifauna as an example, concluded that species distribution was due to complex interactions between temperature, current speed, and sediment grain size and highlighted that certain species had their eastern-most range limits within the Channel related to climatic gradients.

Generally, the assessment of benthic macrofauna responses to climate change is performed using sea surface temperature (SST) data from remote sensing or gridded datasets (Hawkins *et al.*, 2003; Southward *et al.*, 2005; Hawkins *et al.*, 2008; Hinz *et al.*, 2011; but see Sims *et al.*, 2001 and Hiddink *et al.*, 2015) which do not necessarily reflect the temperatures experienced by marine benthic macrofauna. On the example of the English Channel, our aims were to: (i) assess the magnitude of the rise in monthly mean sea bottom temperature (SBT) and its heterogeneity at a fine scale, (ii) report the differences generated by the use of SST instead of SBT in the description of the degree of exposure of the benthic macrofauna to climate change, (iii) assess changes in the distribution of a selection of macrobenthic species regarding climate change by comparing rare and valuable unpublished data on the occurrence of benthic species collected in the 1960s–1970s (during the last cool period) throughout the English Channel with those collected in 2012–2014, and (iv) relate these changes to the actual increase in temperature experienced by the different benthic organisms.

Material and methods

Recent SBT changes along the English Channel

To assess the relative magnitude of temperature changes that benthic organisms experience, interpolated monthly mean SBT data on a 1/15° lat by 1/9° lon grid from the "North West European Shelf Reanalysis" performed by the UK Met Office were studied. This reanalysis is based upon the Forecasting Ocean Assimilation Model 7 km Atlantic Margin Model (FOAM AMM7) and covers the period from January 1985 to July 2012. Although not covering the forty years period elapsing between the past surveys and our resurveys, the reanalysis was conducted from years prior to the beginning of the last warming period in the Channel (Supplementary Figure S1) and is therefore expected to reflect the main long-term changes experienced by the benthic organisms since the beginning of the 1970s. For each pixel of the grid, the slope of the regression line between temperature and time was calculated for the warmest month (September) and for the coldest month (March). Results were then multiplied by 10 to get a value of temperature change per decade. To judge the differences that would have brought the use of SST instead of SBT in the assessment of the climate changes experienced by benthic organisms, an identical calculation was carried out on SST data from the same model. Furthermore, to estimate the longitudinal distance and direction of benthic isotherm shifts between the 1970s and the 2000s, nodes were extracted from the monthly averaged maximum and minimum isotherms, separated by a 0.5°C lag, over the first 10-year period (1985–1994) and the last 10-year period (2002–2011 for September and 2003–2012 for March) using QGIS 2.14.3-Essen (QGIS Development Team, 2016). The distance was then calculated in a World Mercator + lat 49.5° projection between the average longitudinal positions of nodes belonging to the same isotherm at the two periods. To test if changes in the longitudinal position of isotherms between the two periods were significantly different from zero, one-sample Student *t*-tests were used.

Sampling procedures adopted in the 1960s–1970s and in 2012–2014

From 1959 to 1968, Louis Cabioch started the exploration of the benthic communities of the western Channel, off the northern coast of Brittany, between 3°15'W and 5°00'W, by sampling 1691 stations (Cabioch, 1968). In collaboration with other French scientists, he extended the exploration to the whole Channel and sampled 2776 more stations from 1971 to 1976. This produced the largest available dataset on benthic populations throughout the English Channel (see Cabioch *et al.*, 1977 for results on sessile epifauna). Sampling was done using a 0.65-m diameter Rallier du Baty anchor-dredge, a semi-quantitative circular gear designed to penetrate all types of soft bottoms from mud to cobbles. At each station, sediment was dredged for 3–5 min and a sub-sample of 30 l was sieved over a 2-mm mesh size (Gentil, 1976). Most species were sorted and identified on board, reporting information on the distribution of about 300 species for the whole of the English Channel. Species not immediately identifiable on board were preserved in 70% ethanol for later analysis in the laboratory, along with a control batch of previously identified species (as large as possible). Available data for the present study included only endofauna immediately identifiable on board.

In 2012 and 2014, 228 stations were sampled along three transects from the Ushant Sea to the central Channel. These transects were defined so as to cross the distribution limits of many species for which the distribution was described by Holme (1961, 1966) (Figure 1). At each station, a sampling procedure strictly identical to the one previously adopted by Cabioch and co-workers was applied. Thus, a similar Rallier du Baty anchor-dredge was used and dragged onto the seabed for 5–10 min. A 30 l sub-sample of the collected sediment was then sieved through a 2-mm mesh. The remainder was sorted on board and the species fixed in 96% ethanol for later identification in the laboratory. To enable comparison between the two datasets and to avoid the lack of suitable habitats for species to track temperature changes, samplings were focussed on the most extensive and continuous habitat of the Channel: the circalittoral coarse sediment (Coggan and Diesing, 2011).

Treatment of 1960s–1970s and 2012–2014 survey data

Only mollusc, echinoderm, and decapod crustacean species were considered in this study as: (i) they are best sampled by the

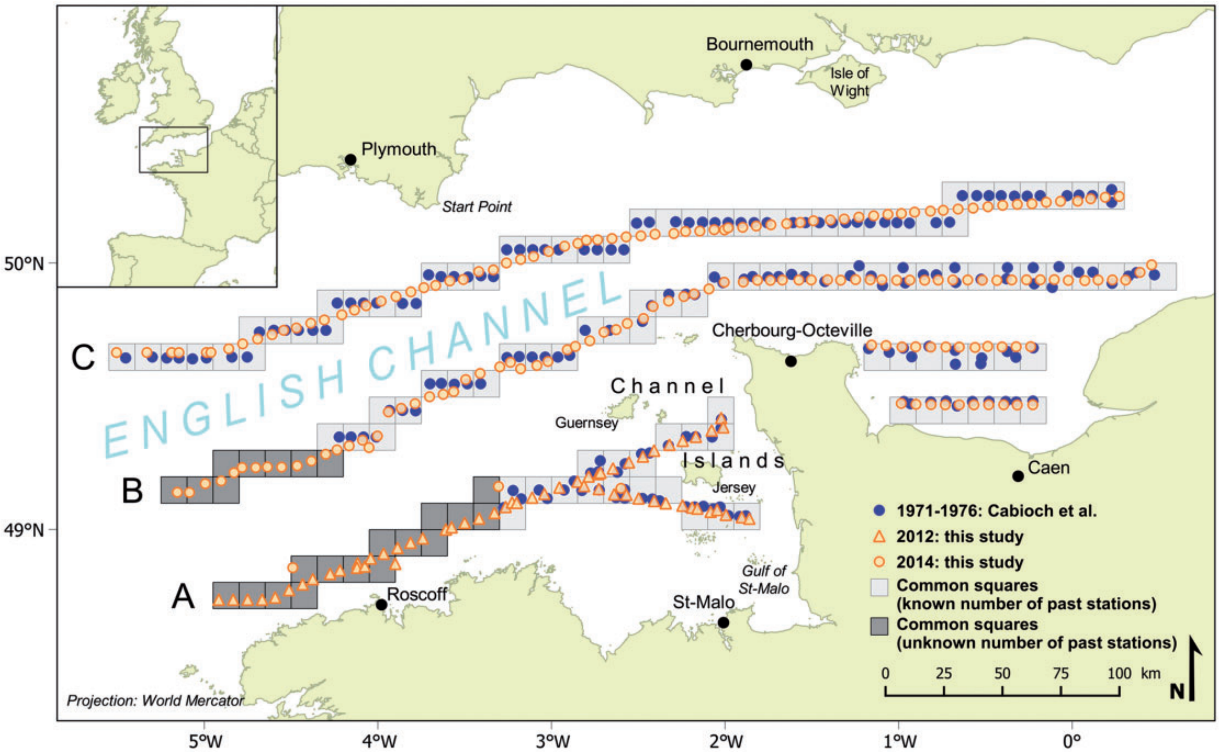

Figure 1. Location of the 184 stations sampled by Cabioch *et al.* from 1971 to 1976 and of the 228 stations sampled in 2012 and 2014. Squares used for comparison of presence/absence data are represented. Dark squares, off the northern coast of Brittany, are those where only presence/absence data from 1959 to 1968 were available. Capital letters A, B and C refer to the three transects.

Rallier du Baty anchor-dredge; (ii) they were those mainly recorded and classified in terms of distribution patterns by Holme (1961, 1966) and; (iii) taxonomic uncertainties are limited. For the period 1971–1976, data were available as number of individuals per station while, prior to 1968, only presence/absence data per 6 square nautical miles were available, each square containing several sampling stations.

To allow spatial comparison of species' occurrence, the sampling stations of the past and present surveys were grouped into 131 squares (each 6 nautical miles^2) common to both periods (Figure 1). The number of sampling stations per square varied between 1 and 3 stations for the contemporary surveys and between 1 and 13 for the historical surveys, except off the northern coast of Brittany where only presence/absence data per square were available. To avoid bias in the assessment of range shifts resulting from different sampling effort between periods (Bates *et al.*, 2015), the number of historical stations per square was limited to the number of contemporary stations where it exceeded our sampling effort of one to three stations per square, keeping only stations which were the closest to the ones we sampled. Off the northern coast of Brittany, 23 squares incorporating an unknown number of stations sampled in the 1960s and 38 stations sampled in 2012 and 2014 were compared (Figure 1). For the rest of the English Channel, 108 squares incorporating 184 and 190 stations, sampled in the 1970s and in 2012–2014, respectively, were considered. Both past and contemporary sets of species were updated to the currently accepted names using the World Register of Marine Species.

Differences in the distribution of the benthic macrofauna

To compare historical and contemporary datasets, and avoid artefacts of detectability due to the rarity of some species, we selected and analysed the data for species sampled in at least 10 squares out of the 131 in the 1960s–1970s or in 2012–2014 (i.e. the most common species). These species were assigned to a biogeographical group (i.e. Western species, West Channel species, Eastern species, Sarnian species, species present throughout the length of the Channel) according to Holme's classification (Holme, 1966). For species with "miscellaneous distributions" or not classified by Holme, we used Cabioch and co-workers unpublished records to assign them to one of the other groups where possible. If not, species remained in a "not classified" group.

Distributional changes of species were investigated through two metrics: the spatial distribution and the spatial occurrence. Since thermal gradients are longitudinal in the Channel and benthic species subsequently expected to move preferentially along a West-East axis with rising sea temperature, changes in spatial distribution were assessed by calculating the longitudinal distribution centroid and the longitudinal distribution range of each species transferred along the line of latitude 49.5° in a World Mercator + lat 49.5° projection. To test if changes in the longitudinal distribution centroid between the two survey periods were significantly different from zero, one-sample Student *t*-tests or non-parametric Wilcoxon tests were used. Changes in spatial occurrence were analysed based on the number of occurrences recorded out of the 131 squares sampled at both survey periods and detailed for each transect to get a representation of the latitudinal component of these changes. To enable greater confidence in identifying changes in species occurrence, only changes in the number of occurrences by a minimum divisor or factor of 1.5 were considered as meaningful (Callaway *et al.*, 2007). The following categories were thus defined:

(i) Decreasing spatial occurrence: the total number of squares where a species was recorded was at least divided by 1.5 (33% decrease) from the 1960s–1970s surveys to the 2012–2014 surveys.

(ii) Increasing spatial occurrence: the total number of squares where a species was recorded was at least multiplied by 1.5 (50% increase) from the 1960s–1970s surveys to the 2012–2014 surveys. Some species, present in at least 10 squares in the contemporary surveys but absent from the historical ones may have been either not recorded or recorded out of the endofauna dataset used in this study. These species were therefore not considered in our analyses.

(iii) Unchanged spatial occurrence: the total number of squares where a species was recorded changed by $<$20% from the 1960s–1970s surveys to the 2012–2014 surveys. This represents a conservative threshold.

Finally, to check if the observed spatial occurrence changes are linked to temperature changes, the relative change in species occurrence (expressed as the ratio of the number of contemporary records against the number of historical records of cold-water species on the one hand and warm-water species on the other hand) was plotted as a function of decadal SBT increases experienced at squares centroid between 1985 and 2012 in September and in March. Following Holme's original classification, cold-water species included all the Western, West-Channel and Eastern species except the bivalve *Gouldia minima*. This species contrasts with the other Western species in the fact that it is a warm-water species near its northern limit (Holme, 1966). The warm-water species thus included *G. minima* and all the Sarnian species.

Results

Recent SBT changes along the English Channel

Modelled SBT data for the period 1985–2012 showed a noticeable warming trend along the English Channel (Figure 2). This warming was more prominent in coastal waters (e.g. in the Channel Islands—St-Malo area) and in the central and eastern parts of the English Channel where the greatest decadal increases in temperature reached 0.50°C in September and 0.54°C in March. The western-most areas (deeper and under direct Atlantic influence) experienced far smaller temperature changes, with minimal increases by 0.07°C per decade for the warmest month and by 0.13°C per decade for the coldest month. The magnitude of the warming is also lower along the Southern coast of England in March but not in September, increasing the temperature range experienced by benthic organisms in this part of the English Channel. This spatial heterogeneity in the warming experienced by benthic organisms differed from that observed when using SST (Supplementary Figure S2). In particular, in the western-most areas, increases in maximum SST were almost as important as in the central and eastern parts inducing strong differences in decadal changes in temperature between the sea surface and the seabed (Supplementary Figure S2).

As a consequence of this warming, sea bottom isotherms moved significantly. Between 1985–1994 and 2002–2012, maximum isotherms longitudinally shifted, on average, 54 km towards the west (one-sample *t*-test, $t = 3.664$, $p < 0.01$), while minimum isotherms longitudinally shifted 42 km towards the east

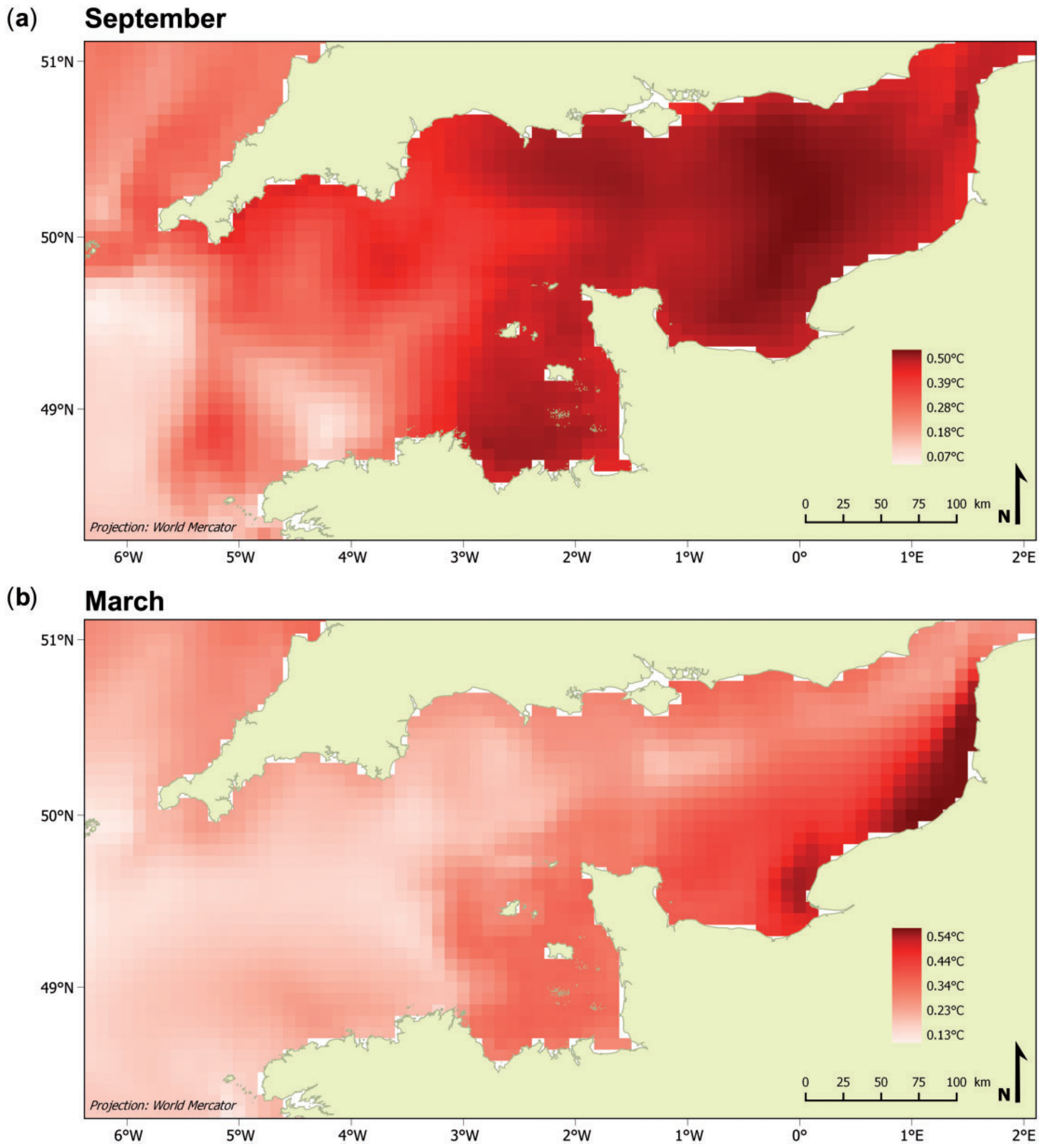

Figure 2. Decadal changes in SBT along the English Channel calculated (a) for the period 1985–2011 for the warmest month (September) and (b) for the period 1985–2012 for the coldest month (March).

(one-sample *t*-test, $t = 8.652$, $p < 0.001$), i.e. at mean rates of 3.2 and 2.5 km.year^{-1}, respectively. Some variations were, however, observed throughout the Channel, especially for the highest maximum isotherms which shifted a greater distance than the others (e.g. 142 km for the 16.5°C isotherm from the eastern to the central Channel, Supplementary Table S1).

Spatial distribution changes of the benthic macrofauna

A total of 65 mollusc, echinoderm, and decapod crustacean species were present in at least 10 squares at one of the two sampling periods. Regardless of their biogeographical group, these species showed only few longitudinal distribution shifts (Figure 3). On average, they covered a significant shift of 23 km to the East (one-sample Wilcoxon test, $V = 1691$, $p < 0.001$), i.e. 0.6 km.year^{-1} assuming a 40 years period between the two surveys. The maximum eastward distribution centroid shift of 207 km (5.2 km.year^{-1}) was observed for the bivalve *Arcopagia crassa* and the maximum westward distribution centroid shift of 80 km (2.0 km.year^{-1}) for the sea star *Crossaster papposus*. Taken individually, each biogeographical group displayed an average longitudinal shift to the East which is significant for the Western species,

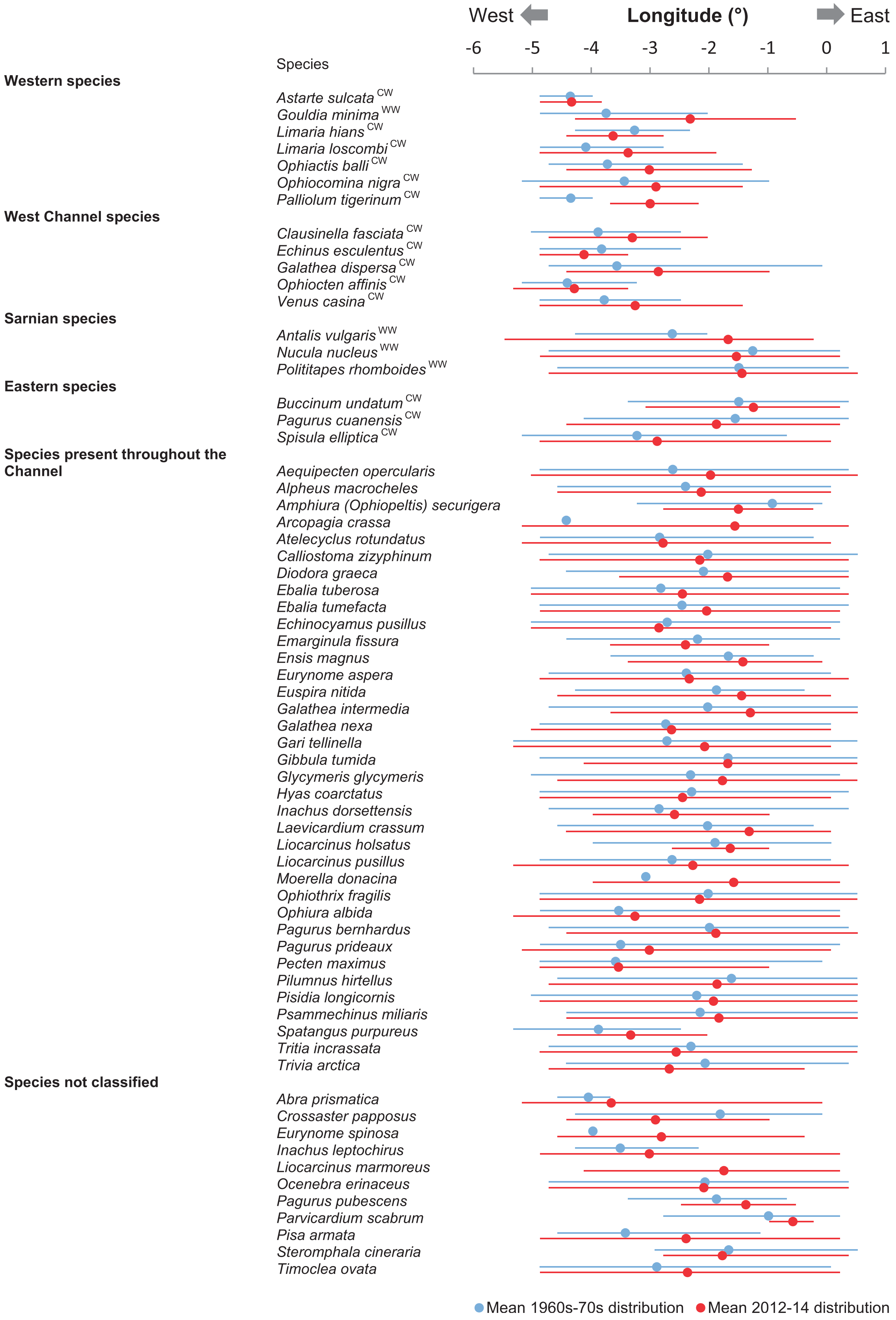

Figure 3. Trends in spatial distribution along a West-East axis. Points represent longitudinal distribution centroids of the species and horizontal bars their distribution range. The exponents "CW" and "WW" indicate whether the species are regarded as cold-water or warm-water species, respectively.

for the species present throughout the Channel and for those not classified. Western species shifted 45.6 km (one-sample *t*-test, $t = 2.560$, $p < 0.05$, 1.1 km.year^{-1}), West Channel species 23.7 km (one-sample *t*-test, $t = 1.767$, $p = 0.15$, 0.6 km.year^{-1}), Sarnian species 17.5 km (one-sample *t*-test, $t = 0.660$, $p = 0.58$, 0.4 km.year^{-1}), Eastern species 6.6 km (one-sample *t*-test, $t = 0.437$, $p = 0.70$, 0.2 km.year^{-1}), species present throughout the Channel shifted 21.0 km (one-sample *t*-test, $t = 2.672$, $p < 0.05$, 0.5 km.year^{-1}) and species not classified shifted 23.8 km (one-sample *t*-test, $t = 2.735$, $p < 0.05$, 0.6 km.year^{-1}). For 71% of the 65 commonly sampled species, the distribution centroid shift remained <40 km (Figure 4).

At the species level, some distributional range changes were particularly remarkable regardless of their biogeographical group as defined by Holme (1961, 1966). In the Western species group, the range edges of the warm-water bivalve *G. minima* and cold-water bivalve *Palliolum tigerinum* both moved eastward with distribution centroid shifts > 80 km, without overlap in distribution between the two periods in the case of *P. tigerinum* (Figure 3). Contractions of the distribution range to the west were observed for West Channel cold-water species like the sea urchin *Echinus esculentus* but also for some species present throughout the Channel (e.g. *Emarginula fissura*) or not classified (e.g. *Parvicardium scabrum*) (Figure 3). Conversely, extensions of the distribution range were observed as expected for Sarnian warm-water species like the scaphopod *Antalis vulgaris* but also for species present throughout the Channel (e.g. *Moerella donacina*) and for those not classified (e.g. *Abra prismatica*) (Figure 3).

Spatial occurrence changes of the benthic macrofauna

The presence of 7 cold-water species out of 14 was reduced by one third or more between the two survey periods (Figure 5, Table 1). These decreases mostly affected species from the stenothermal Western and West Channel species groups (e.g. *Astarte sulcata* and *Ophiocomina nigra*). The three eurythermal Eastern species also showed slight decreases (by 27–32%). Overall, the number of occurrences of cold-water species decreased throughout the English Channel. Moreover, of the 39 widely distributed species, 14 (belonging to multiple taxonomic groups) saw the number of squares in which they were observed reduced by one third or greater. Decreases in spatial occurrence equally affected the three transects studied, with the exception of increases in the number of occurrences of the West Channel cold-water squat lobster *Galathea dispersa* and the widely distributed echinoderms *Spatangus purpureus* and *C. papposus* along the Southern transect (Table 1).

The spatial occurrence of three of the four warm-water species increased by more than 50% between the historical survey and the contemporary survey (Figure 5, Table 1). Seven of the 39 species present throughout the Channel and four of the eight species

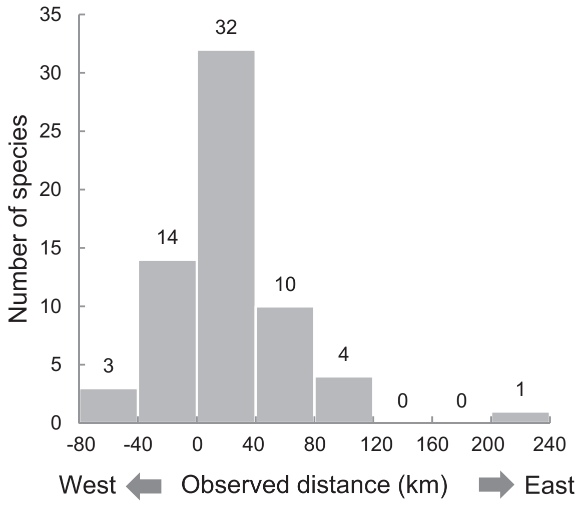

Figure 4. Observed distance and direction of shifts of the distribution centroid of the 64 benthic invertebrates sampled at the two survey periods in at least 10 squares at one of them. The crab *Liocarcinus marmoreus*, present in more than 10 squares in 2012–2014 was absent in 1959–1976. Therefore, no shift calculation was possible for this species.

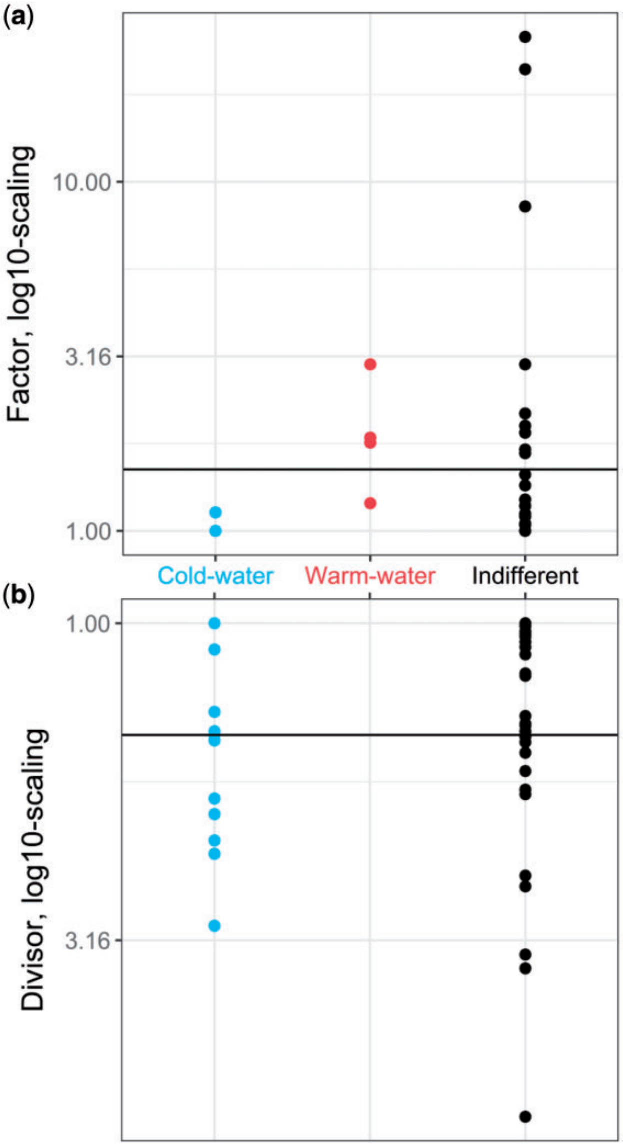

Figure 5. Spatial occurrence changes in benthic macrofauna between the two surveys (historical: 1959–1976; contemporary: 2012–2014) according to their affinity for cold or warm waters following Holme's original classification. (a) Increases in the number of occurrences. (b) Decreases in the number of occurrences.

Table 1. Trends in spatial occurrence. A total of 131 squares were sampled in each of the two surveys (historical: 1959–1976; contemporary: 2012–2014). Values are the number of squares in which the species was recorded.

Species	1959–1976				2012–2014				Observed change			
	Total	T A	T B	T C	Total	T A	T B	T C	Total	T A	T B	T C
Western species												
A. sulcata^{CW}	11	6	3	2	5	5	0	0	↓ **≥33% reduction**	↓	↓	↓
Limaria loscombi^{CW}	10	8	1	1	5	4	1	0		↓	↔	↓
Ophiactis balli^{CW}	23	7	8	8	15	5	6	4		↓	↓	↓
O. nigra^{CW}	30	18	12	0	13	10	2	1		↓	↓	↑
P. tigerinum^{CW}	12	8	4	0	4	4	0	0		↓	↓	↔
G. minima^{WW}	14	11	1	2	25	22	3	0	↑ **≥50% increase**	↑	↑	↓
Limaria hians^{CW}	11	9	2	0	10	10	0	0	↔ **<20% change**	↑	↓	↔
West Channel species												
E. esculentus^{CW}	17	13	3	1	9	7	1	1	↓ **≥33% reduction**	↓	↓	↔
G. dispersa^{CW}	18	3	9	6	12	7	3	2		↑	↓	↓
C. fasciata^{CW}	27	12	9	6	27	17	6	4	↔ **<20% change**	↑	↓	↓
O. affinis^{CW}	10	0	1	9	10	0	4	6		↔	↑	↓
V. casina^{CW}	31	18	8	5	35	22	7	6		↑	↓	↑
Sarnian species												
A. vulgaris^{WW}	4	4	0	0	12	11	0	1	↑ **≥50% increase**	↑	↔	↑
N. nucleus^{WW}	26	12	3	11	48	20	17	11		↑	↑	↔
P. rhomboides^{WW}	51	28	11	12	61	26	20	15	↔ **<20% change**	↓	↑	↑
Eastern species												
Buccinum undatum^{CW}	37	17	8	12	25	9	6	10	**Unclear trend**	↓	↓	↓
Pagurus cuanensis^{CW}	29	17	5	7	20	13	5	2		↓	↔	↓
Spisula elliptica^{CW}	33	18	11	4	24	13	10	1		↓	↓	↓
Species present throughout the Channel												
Amphiura (Ophiopeltis) securigera	12	4	5	3	2	1	0	1	↓ **≥33% reduction**	↓	↓	↓
E. fissura	15	5	6	4	6	5	0	1		↔	↓	↓
G. intermedia	63	20	20	23	41	12	13	16		↓	↓	↓
Gari tellinella	20	11	3	6	6	1	1	4		↓	↓	↓
Gibbula tumida	53	17	20	16	35	14	10	11		↓	↓	↓
Inachus dorsettensis	10	6	2	2	4	4	0	0		↓	↓	↓
Laevicardium crassum	13	10	1	2	7	4	1	2		↓	↔	↔
L. holsatus	13	3	4	6	7	3	1	3		↔	↓	↓
Ophiothrix fragilis	86	37	28	21	57	30	14	13		↓	↓	↓
Pagurus prideaux	26	11	11	4	10	7	1	2		↓	↓	↓
S. purpureus	36	11	12	13	21	12	4	5		↑	↓	↓
C. papposus	16	4	5	7	10	6	1	3		↑	↓	↓
Pagurus pubescens	21	5	9	7	6	1	2	3		↓	↓	↓
P. scabrum	11	6	1	4	6	5	1	0		↓	↔	↓
A. crassa	1	1	0	0	21	10	7	4	↑ **≥50% increase**	↑	↑	↑
Euspira nitida	7	6	0	1	14	5	2	7		↓	↑	↑
G. nexa	30	13	10	7	50	28	12	10		↑	↑	↑
M. donacina	1	0	0	1	26	8	11	7		↑	↑	↑
Pecten maximus	7	6	1	0	12	9	2	1		↑	↑	↑
Tritia incrassata	18	11	6	1	39	27	10	2		↑	↑	↑
Trivia arctica	11	4	4	3	21	12	3	6		↑	↓	↑
Aequipecten opercularis	73	28	27	18	67	26	23	18	↔ **<20% change**	↓	↓	↔
Atelecyclus rotundatus	28	8	8	12	27	13	9	5		↑	↑	↓
Calliostoma zizyphinum	41	19	15	7	43	23	11	9		↑	↓	↑
Diodora graeca	17	5	7	5	19	7	6	6		↑	↓	↑
Ebalia tuberosa	72	28	27	17	70	29	23	18		↑	↓	↑
Ebalia tumefacta	32	18	11	3	30	13	11	6		↓	↔	↑
Ensis magnus	14	8	0	6	14	6	3	5		↓	↑	↓
Eurynome aspera	34	14	7	13	28	18	5	5		↑	↓	↓
G. glycymeris	71	26	23	22	69	32	17	20		↑	↓	↓
Hyas coarctatus	45	21	15	9	47	25	10	12		↑	↓	↑
Liocarcinus pusillus	48	14	20	14	40	17	17	6		↑	↓	↓
Ophiura albida	29	11	8	10	26	12	8	6		↑	↔	↓
Pilumnus hirtellus	38	13	17	8	45	19	16	10		↑	↓	↑
Pisidia longicornis	73	23	28	22	72	35	22	15		↑	↓	↓

Continued

Table 1. continued

Species	1959–1976				2012–2014				Observed change			
	Total	**T A**	**T B**	**T C**	**Total**	**T A**	**T B**	**T C**	**Total**	**T A**	**T B**	**T C**
Alpheus macrocheles	20	11	5	4	29	12	10	7	**Unclear trend**	↑	↑	↑
Echinocyamus pusillus	49	26	17	6	66	35	20	11		↑	↑	↑
Pagurus bernhardus	46	21	13	12	31	13	11	7		↓	↓	↓
Psammechinus miliaris	49	29	14	6	34	16	15	3		↓	↑	↓
Species not classified												
A. prismatica	4	0	0	4	12	1	3	8	↑ **≥ 50% increase**	↑	↑	↑
Eurynome spinosa	2	2	0	0	17	11	0	6		↑	↔	↑
Inachus leptochirus	9	8	1	0	15	10	4	1		↑	↑	↑
L. marmoreus	0	0	0	0	13	1	5	7		↑	↑	↑
Steromphala cineraria	20	7	8	5	22	7	9	6	↔ **<20% change**	↔	↑	↑
T. ovata	64	33	21	10	61	38	14	9		↑	↓	↓
O. erinaceus	49	26	12	11	35	17	11	7	**Unclear trend**	↓	↓	↓
Pisa armata	13	12	0	1	16	7	5	4		↓	↑	↑

CW, Cold-water species; WW, Warm-water species; T, transect.

not classified also increased in their presence by >50% between the two surveys. With a few negligible exceptions, these increases in spatial occurrence equally affected the three studied transects.

Across the English Channel, just 4 cold-water species out of 14 (e.g. *Venus casina*) showed <20% change in spatial occurrence from the 1960s–1970s to 2012–2014 (Table 1). Similar results were obtained for 1 warm-water species out of 4 (i.e. the bivalve *Polititapes rhomboides*), for 14 of the 39 species present throughout the English Channel (e.g. *Glycymeris glycymeris*), and for 2 of the 8 species not classified (e.g. *Timoclea ovata*). Most of these species slightly increased their number of occurrences along the southern transect while they decreased or increased their number of occurrences more erratically along the other two transects.

The magnitude of the changes in the number of occurrences of the 14 species regarded as cold-water species and of the 4 species regarded as warm-water species varied according to the intensity of the decadal SBT increases (Figure 6). Indeed, the number of squares where cold-water species were recorded decreased between the historical surveys and our resurveys regardless of the magnitude of the decadal September and March warming, with the exception of squares where minimum SBT warmed by >0.40°C per decade. Conversely, the number of squares where warm-water species were recorded increased for a warming >0.20°C per decade in both September (Figure 6a) and March (Figure 6b).

Discussion

SBT changes along the English Channel

Previous descriptions of climatic conditions in the English Channel during the 20th century have been based on different methods including *in situ* measurements, remote sensing and abstractions from gridded SST datasets (Hawkins *et al.*, 2003; Saulquin and Gohin, 2010; Smyth *et al.*, 2010). Covering different periods and scales, these methods were more or less suitable to assess the effects of climate change on the benthic macrofauna at a regional scale. Although very useful to depict the long-term trend in climatic conditions, *in situ* measurements only provide local observations. Since the mid-1980s, remote sensing have provided monthly climatologies at a larger spatial scale (Saulquin and Gohin, 2010; Smyth *et al.*, 2010), but have also displayed systematic differences from *in situ* observations (Parker *et al.*, 1995). Therefore, interpolated SST data on a 1° geographic grid from the HadISST1 dataset (Rayner *et al.*, 2003) have often been used in studies on the effects of climate variability on benthic communities at regional scales in the NE Atlantic (Hawkins *et al.*, 2003, 2008; Southward *et al.*, 2005; Hinz *et al.*, 2011; but see Hiddink *et al.*, 2015). Mainly based on quality controlled *in situ* SST observations, SST datasets provide widely available data used as a proxy for bottom temperature over larger geographical areas than the extremely sparse and access limited long-term *in situ* time-series (Hughes *et al.*, 2009). However, they only offer a relatively coarse resolution when working at the regional or local scale and may overestimate the temperature in waters that can experience stratification during summer months as reported in the westernmost part of the English Channel (Smyth *et al.*, 2010; Marrec *et al.*, 2013).

Reflecting the climate change really experienced by benthic organisms at a regional scale and with a rather fine resolution, our results showed a clear warming trend of SBT between 1985 and 2012 for both minimum and maximum temperatures, in broad agreement with results obtained for SST using previously mentioned methods. A non-uniform warming was also highlighted, with September temperature increases ranging from 0.07°C per decade in the western end of the Channel to 0.50°C per decade in the eastern part. This difference between the most western areas and the eastern half of the Channel has previously been noted by Saulquin and Gohin (2010) who attributed it to the interplay between local physical and hydrodynamic conditions on the observed warming of the water masses. Generally in the English Channel, September and March isotherms longitudinally shifted at mean rates of 3.2 [0.2–8.4] km.year^{-1} to the west and 2.5 [1.4–3.4] km.year^{-1} to the east respectively which is more than the value reported by Hiddink *et al.* (2015) in the North Sea for the maximum temperature (mean 1.2 km.year^{-1}) and slightly less than the one reported for the minimum temperature (mean 3.3 km.year^{-1}).

These changes in temperature could partly be associated with the changes in climatic conditions reported in the NE Atlantic over the last decades (Dippner *et al.*, 2014). These include the climate regime shift that occurred in 1988–1989 in response to a shift in the North Atlantic Oscillation (NAO) from a persistent negative phase, characterized by cold winters, starting in 1977, to a persistent positive

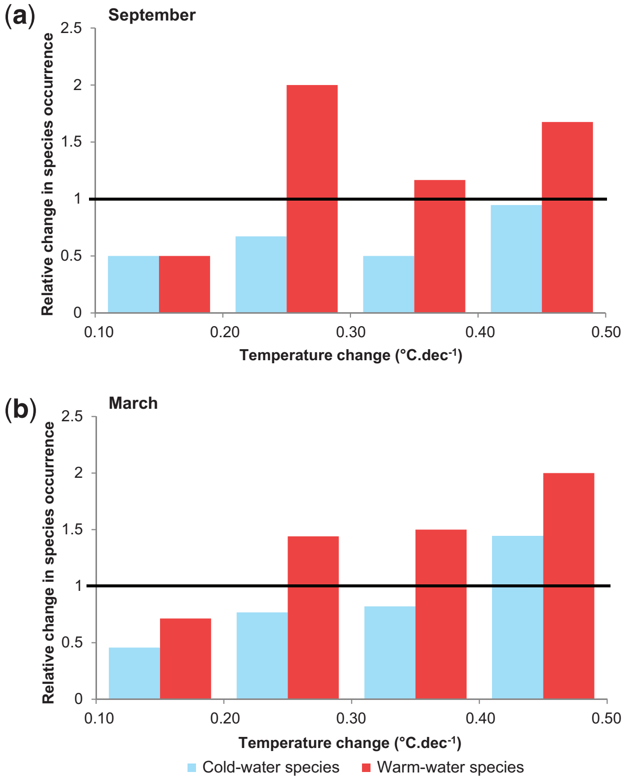

Figure 6. Relative changes in the spatial occurrence of cold- and warm-water species with decadal SBT increases in (a) September and (b) March. The ratio is the number of contemporary records against the number of historical records.

phase, characterized by warm winters, which ended in 2000. In parallel, over longer temporal scales, the switch from a negative to a positive phase of the Atlantic Multidecadal Oscillation in the mid-1990s was accompanied by a sharp increase in temperature up to the 2000s (Sutton and Hodson, 2005; Alexander *et al.*, 2014).

Linking observed distribution changes of the benthic macrofauna to climate change

For different biogeographical groups of macrobenthic species, Holme (1966) attempted to describe the main trends in distribution which could occur during a period of rising sea temperature in the English Channel. Assuming that species distribution reflects their temperature tolerance, he postulated that (i) stenothermal cold-water Western species' ranges retracted off the Plymouth area, either westward towards cooler waters or towards mid-Channel into deeper waters, (ii) cold-water Eastern species' ranges retracted up-Channel, and (iii) warm-water Sarnian species' ranges spread northward from the Channel Islands and extended both east and west. Most of the historical data used in this paper were recorded between 1971 and 1976, i.e. during a cooler period than that experienced for the twenty-four years preceding our resurveys (Supplementary Figure S1; Smyth *et al.*, 2010). This can then be used to test Holme's hypotheses and to assess changes in species distribution in response to climate change.

As the warming was found to be more prominent in the central and eastern parts of the English Channel, greater distribution changes were expected for the cold-water Eastern species and the warm-water Sarnian species. However, despite average distribution centroid shifts clearly lagging behind shifts in SBT isotherms for all biogeographical groups, our analyses revealed a slightly greater shift for the Western species group. Paradoxically, the direction of this shift was opposite to the one postulated by Holme (1966). The stenothermal cold-water Western species were expected to retreat westward with rising sea temperatures. Instead, their distribution centroids moved slightly to the east in the same direction as the March isotherms. Although these species are now located in areas with higher minimum temperatures, and therefore potentially more favourable winter conditions than in the 1960s–1970s, they are also located in areas with higher summer temperatures. This may be the reason for the decrease in spatial presence of five of the six cold-water Western species, four of which displaying decreases >50% of their 1960s–1970s occurrence and, subsequently, for the fragmentation of their distribution. Observations for the warm-water bivalve *G. minima* were more consistent with expectations. Its distribution centroid and distribution range shifted eastward towards warmer waters in summer and its presence increased by >78% in the area between the two periods, probably in response to the rise in SBT. *G. minima* could therefore constitute a good indicator species of climate change. Following Holme's hypotheses and the low magnitude of warming in the western Channel, distribution centroids of the West Channel species did not move significantly despite a slight eastward shift for all the species of this group apart from the sea urchin *E. esculentus*. The cold-water Eastern species hypothesised to retreat eastward up the Channel due to the rise in SBT observed in their distribution area were those displaying the lesser spatial distribution changes despite some slight but not meaningful decreases in their occurrence. Overall, while only a few minor changes were observed in terms of distribution centroids and distribution ranges for the 14 species considered as cold-water species, major decreases in occurrence were highlighted between the two surveys regardless of the magnitude of the decadal summer and winter warming.

In accordance with Holme's hypothesis, the scaphopod *A. vulgaris* is the only warm-water Sarnian species to have seen its range extended both west and east. This range extension was accompanied by a sharp increase in occurrence. Such an increase was also observed for the Sarnian bivalve *Nucula nucleus*. Although two of the four species considered as warm-water species have seen their range extended (i.e. *G. minima* and *A. vulgaris*), all species displayed an increased number of occurrences, particularly in areas coinciding with the greatest increases in SBT. Finally, distributional range and spatial occurrence changes of species present throughout the Channel, or of those showing patchy distributions, were highly variable among species and difficult to interpret in the light of climate change.

With few exceptions, our resurveys of the sublittoral benthic macrofauna in the English Channel, 40 years after Cabioch and colleagues' surveys, did not reveal major distribution centroid shifts and/or range shifts despite warming of sea bottom waters. A similar absence of broad-scale distribution changes of sublittoral benthic species has already been described along the southern coast of England (Hinz *et al.*, 2011). The authors reported range extension and increased occurrence of the sting winkle *Ocenebra erinaceus*, which they regarded as a warm-water species. In our study, this gastropod did not increase its range, and even tended to decrease in occurrence at the scale of the whole English Channel between the two periods. This constitutes a good example of the difficulty of unravelling local and regional scale impacts from global climate driven changes (Firth and Hawkins, 2011), and of the importance of considering large scales when assessing distribution changes in response to climate change. Such absences of sustained distribution changes of sublittoral benthic macrofauna with increases in sea temperature in the English Channel contrasts with observations carried out on other groups of organisms. For example, plankton have displayed shift rates reaching 23.2 km.year^{-1} (Beaugrand *et al.*, 2009); fish have displayed increases in species abundance (Genner *et al.*, 2004); and intertidal organisms have shown distribution shifts of between 3.4 km.year^{-1} for the warm-water trochid gastropod *Phorcus lineatus* (Mieszkowska *et al.*, 2007) and 28.3 km.year^{-1} for the barnacle *Perforatus perforatus* (Southward *et al.*, 2005). The slow life cycle and low mobility of sublittoral benthos compared with those of plankton and fish respectively, as well as the influence of factors such as air temperature and coastal currents on intertidal organisms, could explain much of this variation (Poloczanska *et al.*, 2013). Due to stronger warming of surface and coastal waters, especially in stratified areas, plankton, intertidal organisms, pelagic, and coastal fish may also experience greater temperature changes, therefore exhibiting greater distribution changes than benthos from the circalittoral coarse sediment.

Nevertheless, the impact of climate change on sublittoral benthos is probably not null since our study revealed that, between the 1960s–1970s and 2012–2014, most cold-water species decreased in occurrence while most warm-water species increased in occurrence. Similar results were obtained by Kröncke *et al.* (2011) in the North Sea where only one cold-temperate species (i.e. the polychaete *Ophelia borealis*) was observed to decrease in abundance between 1986 and 2000. Furthermore, an increase in abundance and a spatial range extension within the core distribution areas of various species with a southern distribution were recorded. Also in the North Sea, the range extension of non-native species such as the angular crab *Goneplax rhomboides* was found to be facilitated by climate change through an increase in water temperature and an enhanced inflow of Atlantic water through the English Channel caused by the switch from a negative to a positive NAO pattern in 1988–1989 (Neumann *et al.*, 2013; Dippner *et al.*, 2014). Although our observations on species distribution changes may partly result from this regime shift and the one identified in 2000–2001 over the NE Atlantic (Dippner *et al.*, 2014), they are more difficult to interpret in the light of these shifts than continuously sampled site-specific data on species composition (e.g. Meyer *et al.*, 2016). Instead, they provide a comprehensive background on long-term changes in the distribution of sublittoral benthic species in response to climate change in a biogeographical transition zone, which may help interpreting results obtained from long-term time-series.

The diversity of species' responses to changes in climatic conditions among marine taxa, particularly in the sublittoral benthos, can be explained by an extensive range of hypotheses (Hiscock *et al.*, 2004; Harley *et al.*, 2006). Besides the direct effects of sea temperature on the physiology of the different life stages (for which SST may be relevant), many other factors may influence the responses of the different organisms. These include hydrodynamic characteristics of water masses which may alter transport processes, geographical barriers to spread and specific differences in life history characteristics (reproductive mode, dispersal capability and longevity) (Sunday *et al.*, 2015). On the other hand, supposed species' thermal tolerances were based on distributions and classification into biogeographical groups, not on direct observations of their thermal response curves which may vary among species and even among populations within species (Pörtner and Farrell, 2008; Sorte *et al.*, 2011), potentially altering our understanding of species' responses to climate change. Habitat changes and modifications in the magnitude of biotic interactions are also factors likely to influence species' distribution in response to climate change (Heikkinen *et al.*, 2007; Wisz *et al.*, 2013).

In addition to climate change, other anthropogenic impacts including mainly commercial demersal fishing and eutrophication may have influenced changes in the occurrence of benthic invertebrates at large spatial scales. Increased fishing effort and fishery expansion since the early 1970s have been shown to alter food webs of the Channel ecosystem by replacing demersal finfish with invertebrates (Molfese *et al.*, 2014). Chronic bottom-fishing disturbance was also found to cause significant and widespread changes in the structure of shelf sea benthic communities and habitats (Kaiser *et al.*, 2000; Callaway *et al.*, 2007). For instance, trawling and dredging have been shown to severely affect species with fragile tests or shells, as well as long-lived species, while favouring scavenger and predator species. Although it could be difficult to disentangle the impact of climate change from the impact of trawl fishery, increased fishing effort is unlikely to explain the decrease in occurrence of most cold-water species and the sharp increase in occurrence of most warm-water species, particularly because no generalized scavenger outburst has been evidenced in our study.

Towards a loss of benthic biodiversity

Despite apparent absence of generalized distribution changes of sublittoral benthos in response to climate change, our study revealed a decrease in the spatial occurrence of most cold-water species and an opposite change of most warm-water species in a biogeographical transition zone. Following the stage-based framework proposed by Bates *et al.* (2014) to define climate-mediated range shifts in marine systems, these observations could be identified as the second stage of a geographic range contraction (i.e. population decrease) of cold-water species and as the second stage of a range extension of warm-water species (i.e. population increase). These stages immediately precede local extinction for the first and persistence for the others. Although the actual range was not yet significantly altered, the distribution of species displaying decreases in occurrence has become increasingly patchy in response to warming, and potentially other stressors. Fragmentation of the distribution of sublittoral benthic invertebrates may lead to isolation of populations no longer linked through dispersal, which may, in turn, exacerbate their decrease in occurrence. As suggested on metapopulation studies, benthic species can go extinct when distances between refugia become greater than the scale of larval dispersal (Quinn *et al.*, 1993). Furthermore, within species, recolonization of areas of high mortality by populations having higher thermal tolerances or able to acclimate to new thermal conditions can only happens if populations are connected via dispersal (Sorte *et al.*, 2011). Given these observations and potential effects due to rising seawater temperatures on key biological mechanisms, we postulate that fragmentation of the distribution, increased dispersal distances and reduced survival of both larvae and adults at the limits of their range will continue decreasing the occurrence of cold-water species and facilitate the extinction of some of them within the English Channel. As no introduction of warm-water species was observed to counteract this potential decline in biodiversity, the English Channel may act, as suggested by Burrows *et al.* (2014), as a climate source area, i.e. an area where "locally novel conditions are not connected to areas where similar climates previously occurred". Benthic biodiversity may therefore decrease in the Channel as sources lack connection routes for new migrants and as unadapted sessile or lowly mobile cold-water marine sublittoral benthos go extinct instead of migrating to convergence areas. Although maintaining long-term series is challenging in terms of logistics and resources, routine large scale spatial surveys sampling different ecosystem components in parallel over time are crucial to improve our understanding of the relationships between climate change and biodiversity, but also our understanding of the ecosystem functioning and of the nature's benefits.

Conclusions

Effects of global warming on the distribution of marine organisms cannot be assessed regardless of the changes in temperature they really experience. This study provides the first fine scale full-coverage picture of the decadal changes in SBT that occurred in the English Channel for the last three decades. It showed a clear but non-uniform warming trend, ranging from around 0.2 to 1.6°C between 1985 and 2012, and highlighted the need for SBT rather than SST data to properly describe the thermal conditions to which sublittoral benthic organisms are exposed when stratification happens. Our resurveys of the sublittoral seabed of the English Channel, 40 years after past surveys, showed a great heterogeneity of benthic species' spatial distribution shifts, which makes it very complex to draw general responses to climate change. The distribution of some species have shifted in agreement with our expectations, while for others it has moved in the opposite direction to that expected. However, for 71% of the studied species, the distribution centroid has remained within a 40-km distance west or east from its initial position, clearly lagging behind shifts in both minimum and maximum isotherms. This contrasts with the changes reported in the study area for other marine taxa, such as plankton and fish, but also with those reported for intertidal benthos, and in general with the distribution shifts reported worldwide for marine, freshwater, and terrestrial species. Besides, we showed that most cold-water species importantly decreased in occurrence while most warm-water species importantly increased in occurrence with rising SBT, giving support to an ongoing loss of benthic biodiversity related to climate change in areas where the arrival of the new migrants is absent. Identifying the factors limiting the distribution of marine benthos, from local populations to species as a whole, understanding their combined action, and predicting future shifts in response to climate change through species distribution modelling (e.g. Weinert *et al.*, 2016), may help at identifying potential refugia to protect from other disturbances in order to keep them as suitable as possible for species to maintain their populations as long as possible.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the article.

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