



How climate warming impacts the distribution and abundance of two small flatfish species in the North Sea

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ABSTRACT

Climate change, specifically temperature, affects the distribution and densities of species in marine and terrestrial ecosystems. Here, we looked at the effect of temperature during winter and spawning period on latitudinal range shifts and changes in abundance of two non-commercial North Sea fish species, solenette (*Buglossidium luteum*) and scaldfish (*Arnoglossus laterna*). Both species have increased in abundance and moved to the north since the late 1980s, coinciding with a series of mild winters. In 1996, following a very cold winter, the abundance of both species temporarily decreased as they retracted to the south. The shift in temperature affected adult habitat conditions, allowing them to immigrate into new areas where they subsequently reproduced successfully. We can conclude this because recruitment improved following the increase in abundance. The recruitment relates significantly to the higher adult stock and higher temperatures. The predictions of higher average temperatures and milder winters in the North Sea make it likely that these species will increase further in abundance and move northward. The observed increase in abundance of these small flatfish species will affect the North Sea food web and therefore commercial species, e.g. plaice, by predation on juveniles and competition for benthic food resources.

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1. Introduction

Abundance and geographic distribution of species are continuously changing in response to temperature variation in the environment. In the North Sea, as elsewhere, temperature has increased lately and a continuing increase is predicted (IPCC, 2007). This predicted increase will result in a poleward movement among species, and an increase in abundance on the northern boundaries of distribution of terrestrial (Walther et al., 2002; Hickling et al., 2006) and marine species (Roessig et al., 2004).

In the North Sea, temperature has increased since the late 1980s (Becker and Pauly, 1996; Edwards et al., 2002; MacKenzie and Schiedek, 2007), particularly the minimum winter temperature (Wiltshire and Manly, 2004). This coincided with fish species spreading northward (Perry et al., 2005; Rindorf and Lewy, 2006) and into deeper waters (Perry et al., 2005; Van Keeken et al., 2007; Dulvy et al., 2008; Hiddink and ter Hofstede, 2008). At the same time, the prevalence of species formerly rare in the area has increased (Beare et al., 2004). These changes in fish distribution correlate to the temperature affinity of the species. Species with an affinity to warm water (Lusitanian) are more likely to increase in abundance, whereas

species with an affinity for cooler water (Boreal) are likely to decrease in abundance (Rijnsdorp et al., 2009).

Most previous studies of how climate change influences fish distributions and abundance have been descriptive and have not attempted to determine the underlying mechanisms. Furthermore, other factors may affect the distribution and abundance of fish species, such as commercial fishing, which may have contributed to the observed increase in small bodied fish species (Heessen and Daan, 1996; Daan et al., 2005).

Here, a process oriented approach is used to disentangle the mechanism(s) responsible for the observed changes in abundance and distribution. These mechanisms (survival, recruitment and immigration) are explored to determine the effect of climate on two non-commercial small sized, Lusitanian flatfish species; solenette and scaldfish.

Solenette (*Buglossidium luteum*), the smallest species of Soleidae in Europe, reach a mean length of 7 cm at the start of their second winter (Baltus and Van der Veer, 1995) and a maximum length of 13 cm (Wheeler, 1969). Scaldfish (*Arnoglossus laterna*), Bothidae, also reach a mean length of 7 cm at the start of their second winter (Baltus and Van der Veer, 1995) but a maximum length of 19 cm (Gibson and Ezzi, 1980). Both species occur in the open North Sea in waters deeper than 15 m, lack specific nursery areas, overlap in spatial distribution of juveniles and adults (Baltus and Van der Veer, 1995) and are residential without a clear seasonal migration. Both species have also recently expanded their habitat (Perry et al., 2005; Hiddink and

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ter Hofstede, 2008) and increased in abundance in the North Sea (Jennings et al., 2008; Tulp et al., 2008).

2. Methods

2.1. Fish data

Data from two annual Dutch beam-trawl surveys in the North Sea were used. The Sole Net Survey (SNS) and the Beam-Trawl Survey (BTS) cover different geographical areas with a considerable overlap in the coastal zone. The SNS has been carried out in September–October from 1969 to the present, excepting 2003. It covers approximately fixed stations on transects which run parallel or perpendicular to the continental coast. The survey uses two 6-m beam trawls with a standard ground rope and four tickler chains with a cod-end stretched mesh size of 40 mm, haul duration of 15 min and a towing speed of approximately 2.0 ms^{-1} . The BTS has been carried out annually in August–September since 1985 with the RV 'Isis' and covers the southeastern North Sea (Figs. 1 and 2), with the sampling stations stratified by ICES rectangle ($30'$ latitude $\times$ 1° longitude). It uses two 8-m beam-trawls with eight tickler chains and a cod-end stretched mesh size of 40 mm, haul duration of 30 min and a towing speed of approximately 2.0 ms^{-1} . Since 1996, the BTS has been expanded to the western, central and northern North Sea using RV "Tridens II", which has gear similar to that on RV "Isis" with the exception of a flip-up rope to allow fishing on rougher grounds (Wageningen IMARES, 2008).

Because the surveyed area varied over time, an area that was surveyed each year was chosen for analysis. For the BTS-Tridens, this study area is south of 57° N and for the BTS-Isis and the SNS, this is south of 55.5° N and east of 3° E . In both surveys the total catch is sorted and the size distribution (cm below) of each species is measured for each tow. Otoliths were collected together with the length (mm below) of the specimens. In the lab, the otoliths are coloured with a Neutral red solution, after which the rings are counted for age determination (1 January birthday). Because only a relatively small number of otoliths were collected during the described surveys and during a selection of years, otoliths collected during incidental trips in the southern North Sea extended the dataset used to calculate length–age keys (Table 1).

2.2. Temperature data

Mean temperatures (1st quarter and 2nd quarter) were calculated from a time series of monthly mean sea surface temperature (SST) for the period of 1969–2008 (Fig. 3) (Van Aken, 2003). The 1st quarter temperature, the coldest period of the year was used because low temperatures may constrain the Lusitanian species with an affinity for warmer water. Second quarter temperature was used as environmental condition during the spawning period. This data describes the Marsdiep inlet of the western Wadden Sea, which has been shown to be representative of the changes and inter-annual variation in temperature in the waters of the southeastern North Sea (Teal et al., 2008).

A second source of temperature data was those measured at the start of each haul. For the SNS this was SST, and for the BTS this was bottom temperature. Temperature data were missing for some hauls (SNS: 14%; BTS-Isis: 38%; and BTS-Tridens: 22%), owing to measurement errors and weather conditions.

2.3. Distribution and abundance estimates

The presence–absence of the species was used as a first proxy of the changes in distribution. As a next step, the relative abundance was estimated according the following model.

$$\text{Log}(N) \sim Y + S + V + s(D) + s(L) + \varepsilon.$$

The model allowed us to correct for the effect of depth (D), latitude (L), distribution of the tows among the surveys (S) and vessel (V) in each year (Y). Depth and latitude were modelled as a regression smoothed spline (Hastie and Tibshirani, 1990; Wood, 2006). The year effect from the model was used as an index of relative abundance of the two species, because no estimate of gear efficiency was available for these species. All modelling was done using the software package R (version 2.9.2) and the libraries mgcv (version 1.5-6) and nlme (version 3.1-94). Indices for recruitment and adult stock were calculated in the same way both for the total study area as well as for two sub-areas chosen to indicate the order of increase in adults and recruits in an area where both species were common at the start of the time series in a southern area (south of 53.5° N) and a northern area which they occupy later in the time series (north of 53.5° N and east of 5° E).

Recruitment was defined as all fish $<7 \text{ cm}$ for solenette and $<8 \text{ cm}$ for sculdfish. Based on the derived length–age keys, these fish represent 1-year olds. Fish above these thresholds represent 2-year and older fish that are mature (Gibson and Ezzi, 1980). Recruitment and adult stock for the years prior to 1975 could not be separated, because the species were counted but not measured.

2.4. Thermal preferences

The thermal preferences of the two species were assessed by contrasting the probability distribution function of temperatures sampled across the survey grid with the probability distribution function of the actual temperatures occupied by the fish (Dulvy et al., 2008). For BTS-Tridens, 476 hauls over the range of 4 to 20° C , for BTS-Isis 1119 hauls over the range of 8 to 22° C and for the SNS, 1834 hauls over the range of 11 – 20° C were used. For each survey-species combination, the probability distribution function was used to calculate a cumulative distribution function (cdf) (Perry and Smith, 1994). The maximum difference between the cdf of the sampled temperatures (predicted) and the cdf of the temperatures occupied by the fish (observed) was calculated (Perry and Smith, 1994). This maximum difference was compared to the maximum difference between the predicted cdf and 2001 random cdfs. Random cdfs were created by randomly distributing the number of fish observed at each haul over the temperatures, keeping the same number of hauls at each temperature (Perry and Smith, 1994). The maximum difference between the predicted cdf and all 2001 random cdfs was compared to the observed maximum difference. If the observed maximum difference was significantly larger, the fish were showing a significant preference for a specific temperature.

2.5. Temperature analyses

The effect of temperature in the 1st quarter (winter temperature) on the abundance (the year effect of the previous model) was analyzed using a linear model. Because a simple linear model would violate the rule of independence with one year influencing the next, our linear model incorporates autocorrelation between the abundance of successive years through an autoregressive model of order 1, modelling the residuals at time x as a function of the residuals of time $x - 1$ along with noise (Zuur et al., 2009). For example, a year with low abundance is most likely followed by a year with low abundance, while under similar temperatures a year with high abundance will be followed by a year with high abundance.

For both species, the effect of temperature on recruitment at age 1 was modelled with a linear model for each sub-area. The explanatory variables used were the adult stock in the year of spawning, along with the spawning temperature, April–June, and the succeeding winter temperature, January–March. Spawning temperature is considered a proxy for the development of the eggs and larvae, while the

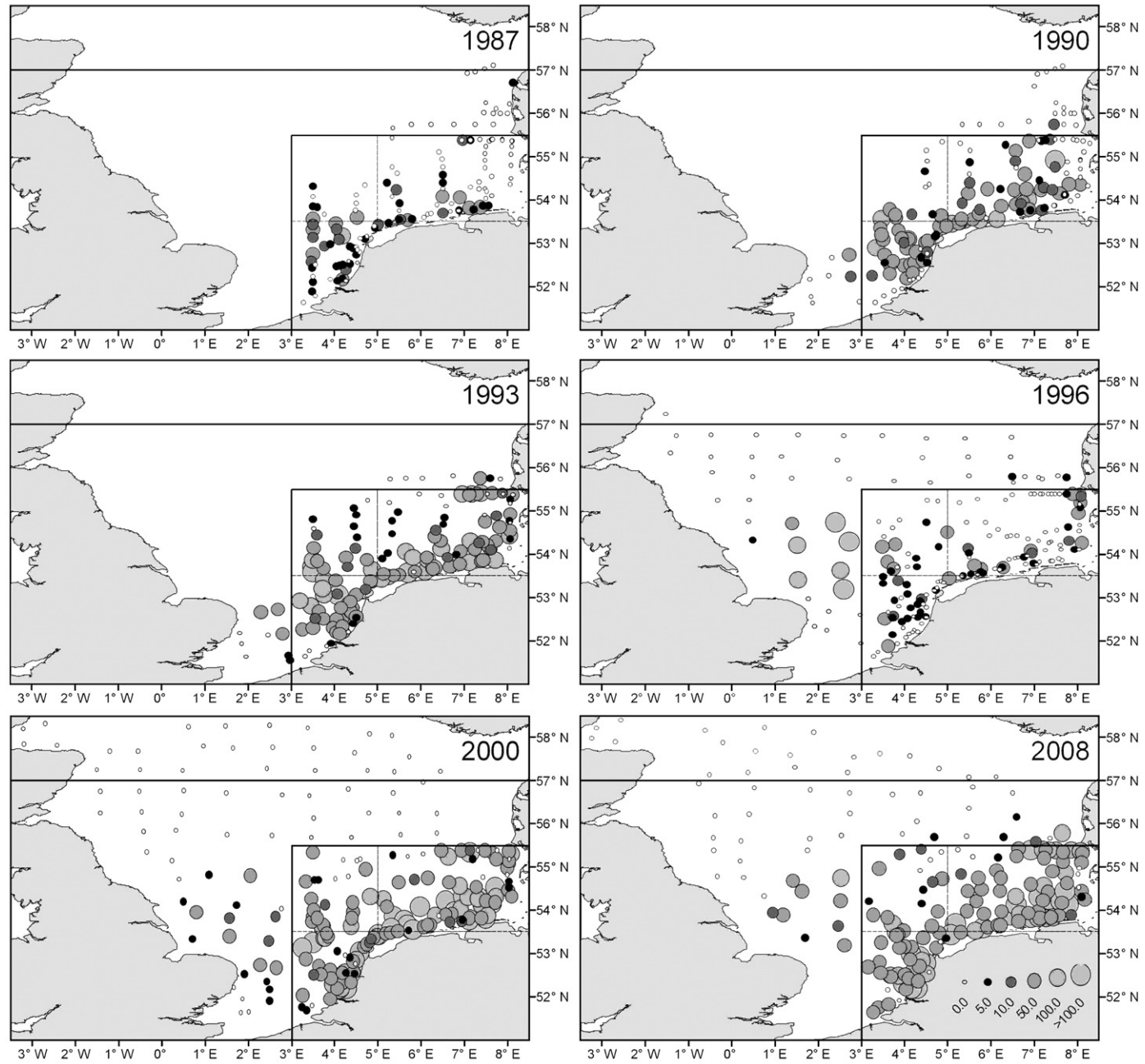


Fig. 1. Distribution of solenette in the BTS and SNS in the years 1987, 1990, 1993, 1996, 2000, and 2008. BTS-Tridens area below the horizontal line, SNS and BTS-Isis area within the lines along the Dutch, German and Danish coasts. The dotted lines mark the sub-areas.

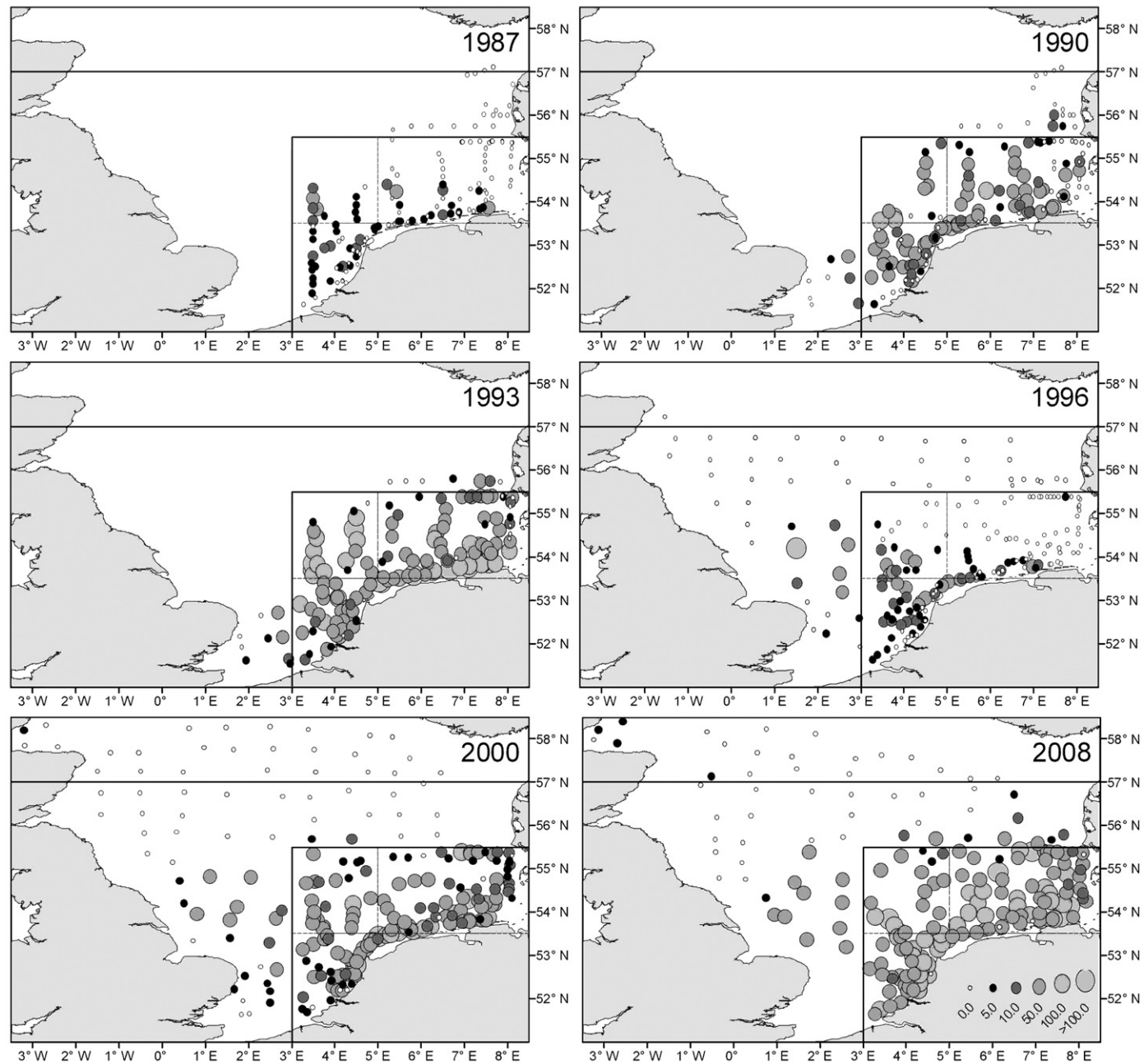


Fig. 2. Distribution of scadfish in the BTS and SNS in the years 1987, 1990, 1993, 1996, 2000, and 2008. BTS-Tridens area below the horizontal line, SNS and BTS-Isis area within the lines along the Dutch, German and Danish coasts. The dotted lines mark the sub-areas.

Table 1

Number of otoliths collected per year by age for both species, together with their year class.

Age	Scaldfish										Solenette									
	year										year									
	1993	1994	1997	1998	2000	2005	2006	2007	2008	Total	1993	1994	2000	2005	2006	2007	2008	Total		
1	44	64	11	3	10	5		91	2	230	6	39	3	2		43		93		
2	1992	1993	1996	1997	1999	2004		2006	2007		1992	1993	1999	2004		2006				
	24	237	3	12	21	40	1	142	14	494	15	152	6	15		29		217		
3	1991	1992	1995	1996	1998	2003	2004	2005	2006		1991	1992	1998	2003		2005				
	17	61	1	8	26	40	9	106	13	281	13	76	8	3	3	26	3	132		
4	1990	1991	1994	1995	1997	2002	2003	2004	2005		1990	1991	1997	2002	2003	2004	2005			
	13	21		1	4	11	9	117	8	184	29	55	4	12		67		168		
5	1989	1990		1994	1996	2001	2002	2003	2004		1989	1990	1996	2001	2002	2003				
	2	30			5	12	3	42	10	104	17	88	6	10		44	3	168		
6	1988	1989			1994	2000	2001	2002	2003		1988	1989	1995	2000		2002	2003			
	7					12		12	2	33	3	33	5	15	1	32	2	91		
7	1988					1999		2001	2002		1987	1988	1994	1999	2000	2001	2002			
	3				1		1	4	3	12	1	20	4	11	1	24	5	66		
8	1987				1992		1999	2000	2001		1986	1987	1993	1998	1999	2000	2001			
					1				2	3	5	1	14	2	35			57		
9					991				2000			1986	1992	1997	1998	1999				
											1	7	3	2	15	2	30			
10												1985	1991	1996	1997	1998	1999			
											2	3	1	1	14	1	22			
11											1984	1990	1995	1996	1997	1998				
											2	5	1		6		14			
12											1983	1989	1994		1996					
											1		1				2			
13											1982		1993							
14													1							
													1988							
Total														2		3				
														1991		1993				
	100	423	15	24	68	120	23	514	54	1341	84	474	53	90	11	338	16	1066		

winter temperature is considered as a possible bottleneck for surviving of the pre-recruits.

3. Results

The presence–absence data show an expansion of both species in the study area since the start of the time series, when both species occurred in 20% to 50% of the SNS and BTS-Isis hauls. This increased from the late 1980s to above 90% by 2000 (Fig. 4). An exception was the year 1996, when coverage decreased to 50%, comparable to the

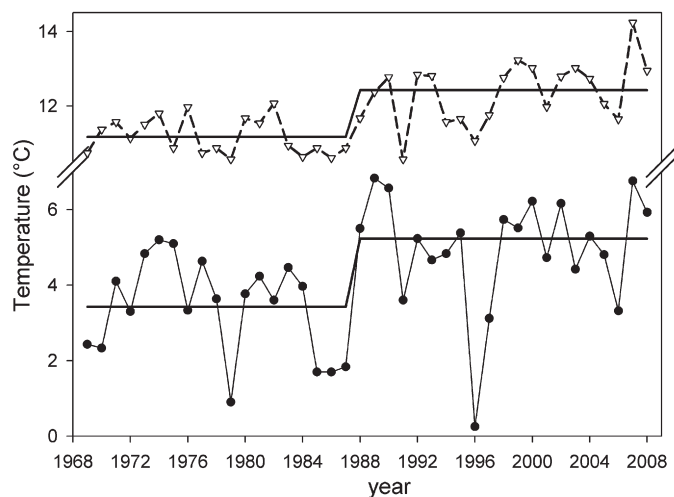


Fig. 3. Mean winter temperatures in the 1st quarter (solid line and circles) and mean temperature in the 2nd quarter (dashed line and triangle) from a time series of monthly mean sea surface temperature (SST) in the Marsdiep inlet in the western Wadden Sea (Van Aken, 2003) in the period 1969–2008.

1970s. Maps of fish densities (Figs. 1 and 2) show that both species occupied the southern area of the North Sea throughout the study period, expanding their range northward into the northern area beginning in the late 1980s. In 1996, both species disappeared from most of the northern parts of the study area and still occurred in their original range, but returned to the northern parts in subsequent years. Relative abundance calculated over all survey data results in a year effect comparable to the trend in presence (Fig. 4), showing an increase since the end of the 1980s and a temporary decrease in 1996. The increase in abundance thus seems to reflect the expansion. The numbers per haul show that local densities increased between the period before 1988 (solenette: median: 4.4 n/ha, 3rd quartile: 12.0 n/ha; scaldfish: median: 4.4 n/ha, 3rd quartile: 8.9 n/ha) and the later period excluding 1996 (solenette: median: 24.3 n/ha, 3rd quartile: 53.4 n/ha; scaldfish: median: 21.1 n/ha, 3rd quartile: 40.4 n/ha). This local increase in densities can also be seen in the density maps (Figs. 1 and 2).

The relative abundance of both species was slightly higher in the 1970s coinciding with milder winters. Lower abundances were found in the winter of 1979, which was severe with sub-zero temperatures in a large part of the German Bight. The major increase in abundance occurred beginning in the late 1980s, with a series of very mild winters in which temperatures, even in the German Bight, did not fall below 4 to 5 °C. The decrease in 1996 occurred following the severe winter in the beginning of that year, when temperatures in the German Bight and along the northern part of the Dutch coast dropped below 0 °C and those along the southern Dutch dropped below 4 °C (BSH, 2008). After 1996, abundance increased again, although the winter temperatures were colder than those in the beginning of the 1990s.

Analyses show a significant positive relationship between winter temperatures, Jan–March, and the relative abundance of both species (solenette: t -value: 3.127881 $P < 0.01$; scaldfish: t -value: 3.817167

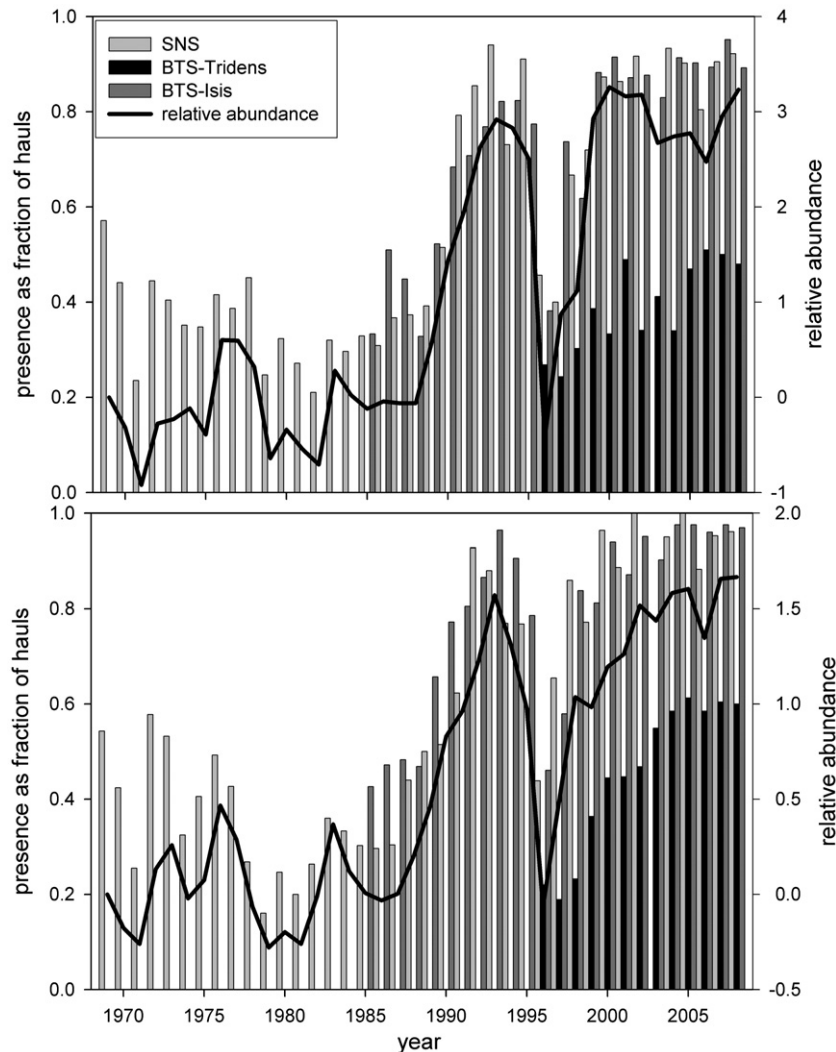


Fig. 4. The fraction of hauls in each survey in which the species was present, represented by the bars (left axis) and the overall modelled relative abundance (the year effect of the statistical model relative to the first year of the time series, right axis). Above solenette and below scaldfish.

$P < 0.001$). The model used, incorporated the abundance of previous years in an autocorrelation structure, in which the correlation parameter was 0.68 for solenette and 0.74 for scaldfish. Thus the correlation between residuals of two successive years is high, meaning that the abundance in one year determines the abundance in the following year, adjusted positively by the milder winters. The relation between temperature and the abundance of the species is visualised as the residuals of the statistical model incorporating only the autocorrelation plotted against the temperature (Fig. 5).

The probability of occurrence of both species was higher at higher temperatures. This was most explicit in the BTS-Tridens, which covered the largest range of temperatures (Fig. 6). In the randomization procedure, the maximum difference between the actual cdf and the predicted cdf was larger in 99% of the 2001 runs. This means that all but one survey-species combination showed a distribution that differed from a random distribution, both species occurred thus significantly more often in areas with higher temperatures. The single exception is the combination BTS-Isis–scaldfish, which was not significantly different from random, indicating a small difference between the two species: scaldfish seems to occur more often between 10–14 °C than do solenette (Fig. 6).

Comparing the changes in abundance in the southern area and the northern area revealed small differences between areas and species (Fig. 7). The start of the increase in abundance at the end of the 1980s is more pronounced in the northern area. Here, the reaction of the two

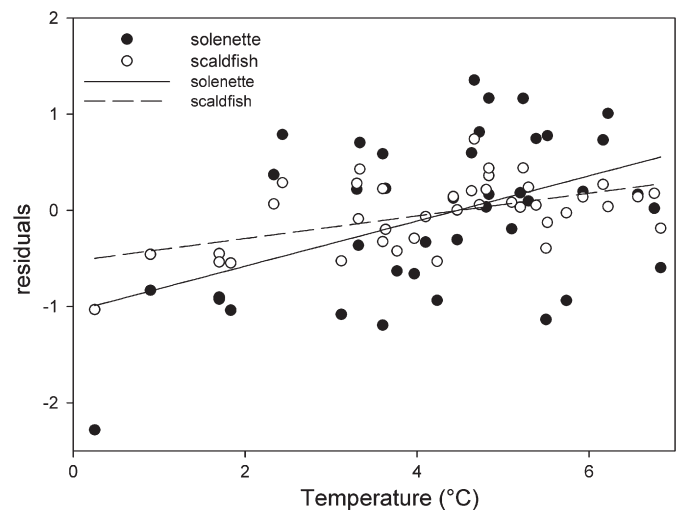


Fig. 5. Relationship between temperature and the relative abundance of solenette and scaldfish. On the y-axis are the residuals of a linear model in which autocorrelation explains a part of the variation in relative abundance.

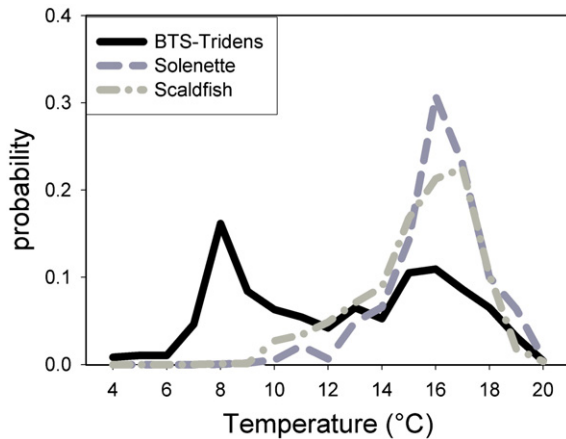


Fig. 6. The probability of occurrence at a specific temperature bin (1 °C) for both species in the BTS-Tridens, compared to the probability of a BTS-Tridens haul occurring in the same temperature bin.

species differs slightly: scadfish abundance increased following the winter of 1988 while solenette increased following the winter of 1989. The abundance of both species decreased in both areas in 1996. After the decrease, a recovery in abundance took place in both areas. The recovery of solenette was, however, again delayed in the northern area.

The recruitment of both species follows the overall pattern of the abundance and is higher in the second part of the time series (Fig. 7). The increase in recruitment occurred after the increase in abundance of the adults. Scadfish had an increased recruitment in 1989 (year class 1988) in both areas, while solenette had high recruitment in

1990 (year class 1989). These higher recruitments further increased the abundance of the adult stock the following year. The recruitment at age 1 was significantly related to the adult stock (Table 2). In the southern area, scadfish recruitment was positively correlated to the spawning temperature. In the northern area, solenette recruitment was positively correlated to both the winter temperature, January–March and to the spawning temperature.

The collected otoliths give an idea of the age composition of both species (Table 1). They show that while the species are of similar size and show similar patterns in the North Sea, they differ in lifespan. Scadfish can reach an age of 8 years, while solenette reach an age of 14 years. The lifespan found here (8 years for scadfish and 14 years for solenette) corresponds with the data from a more southern area, Bay of Douarnenez (Deniel, 1990). Changes between years in age composition were difficult to see, owing to the low number of otoliths collected in some years. However, even in the years following the cold winter of 1996, individuals that survived the cold winter were found: the year classes 1995 and earlier. For solenette, individuals born before 1996 were even caught in 2007.

4. Discussion

Abundance of both small Lusitanian flatfish species has increased in the North Sea since 1970, indicating both a northward expansion and an increase in local density. Only relative abundance is shown by this data, because the survey trawls have a mesh size of 40 mm and a rather coarse ground rope, which means that especially the smaller individuals are underrepresented. This is clear from our gear's much lower catch rates for both species in comparison with a smaller beam trawl fitted with a 20 mm stretched mesh and a cod-end liner of 4 mm knotless, employed at the same location during the BTS-Tridens

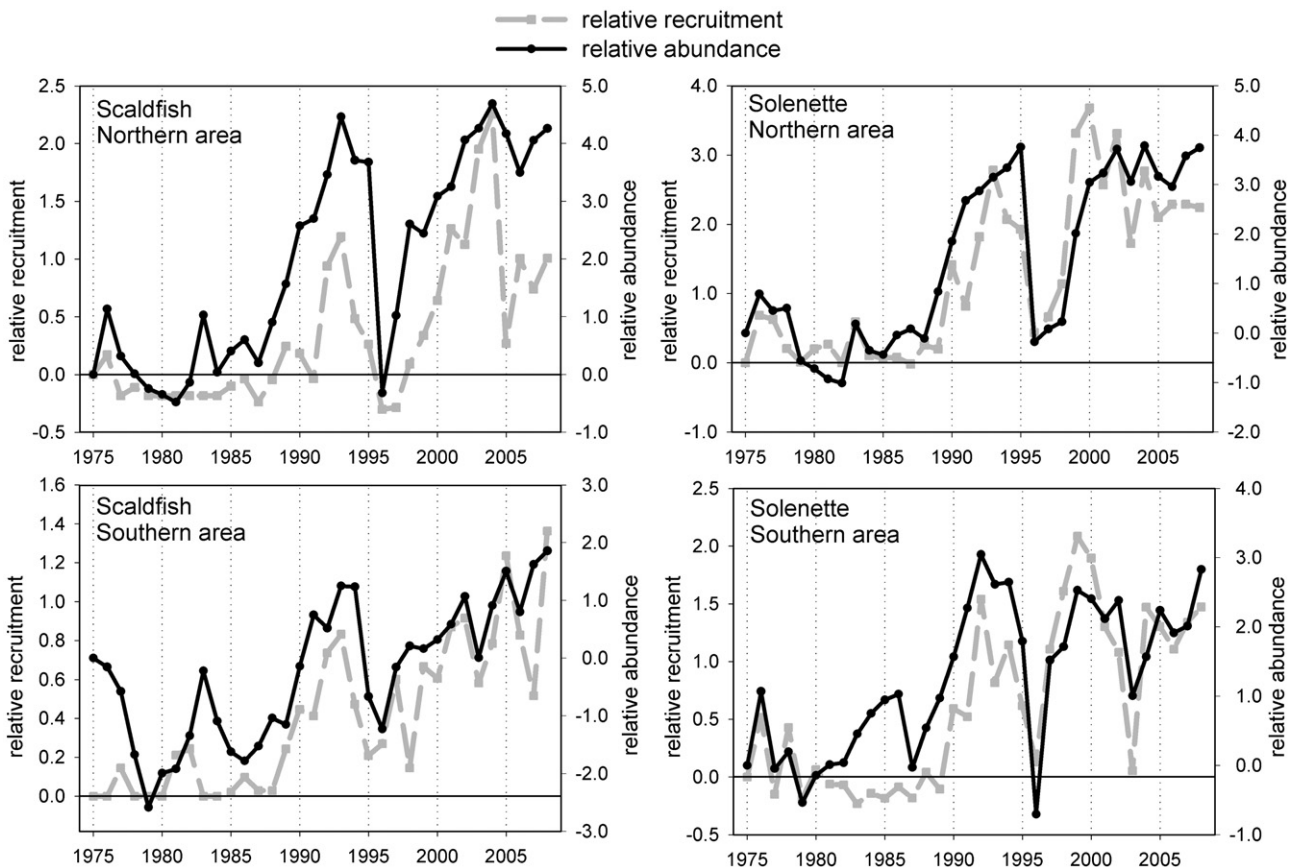


Fig. 7. The relative recruitment at age 1 (dashed grey) and relative adult abundance (solid black) for scadfish (left) and solenette (right) in the northern area (upper) and southern area (lower).

Table 2

Statistical results of the explanatory variables explaining a part of the variability in the recruitment at age 1 by species and area.

Species	Area	Adult stock	T_{Q1}	T_{Q2}	F	df	R^2
Scadfish	Northern	0.0000	0.1780	0.6093	31.72	31	0.51
Scadfish	Southern	0.0082	0.8530	0.0008	26.36	30	0.64
Solenette	Northern	0.0012	0.0061	0.0424	23.74	29	0.71
Solenette	Southern	0.0054	0.0107	0.3201	11.9	30	0.55

T_{Q1} : average temperature during the winter (Jan–March) following spawning; T_{Q2} : temperature during spawning (April–June). Non-significant P -values from the full model, while the significant values ($\alpha=0.05$, bold) are from the model after removal of non-significant terms. Degrees of freedom and F -statistic are from the final model.

(IMARES unpub.). Multiple small meshed beam trawls deployed behind each other demonstrate only efficiency for the first beam of maximal 27% for solenette and 35% for scadfish (Reiss et al., 2006). Our beam trawl, with a larger mesh size, is even less efficient and thus catches even a lower percentage of the present solenette and scadfish.

There is a clear connection between the observed changes in both species and the winter temperature: the increase in abundance at the end of the 1980s coincided with a series of mild winters that probably created the right conditions for both species to survive in the study area. Both species prefer warmer waters, even during summer, at the time of the surveys. This corresponds to the preference shown in the English groundfish survey (Dulvy et al., 2008). Their lack of preference for the warmest waters is probably because these are coastal waters that have less salinity owing to river inflow. Both species avoid lower salinity waters (Amara et al., 2004).

The decrease in abundance in 1996 is related to the low temperature during the winter of 1996. Most likely, the species moved to deeper waters in the western and central North Sea, which are warmer during the winter. This offshore movement would explain the higher catches in this area by the BTS-Tridens (west of 3° E and south of 55° N) compared to later years. This area has unfortunately only been sampled since 1996, making comparison with earlier periods impossible. Offshore movement of solenette during winter was reported before (Nottage and Perkins, 1983), and similar migrations are known of sole (*Solea solea*), another Lusitanian species (Horwood and Milner, 1998). Such a temperature induced re-distribution would also explain the fast recovery in abundance, which did not coincide with above average recruitment. The alternative explanation that the decreased abundance may be due to an increased mortality during the cold winter of 1996 would be consistent with high winter mortalities reported for other fish species, e.g. sole (Woodhead, 1964) which, following the severe winter of 1963, showed a decrease in the proportion of age groups born before that winter (ICES, 2007). No such clear change in age composition is visible in our otolith collection of solenette and scadfish. Instead, year classes born before 1996 were still present in later years (Table 1). It is however unclear of these survived the winter in the southern area of the North Sea or immigrated into the North Sea in later years. This is due to the randomness in otolith collection, making conclusions on possible explanations difficult.

The bottom temperature is closely related to depth, as deeper North Sea waters are on average colder in summer. Thus, the northward movement of both species as shown here results automatically in a movement into deeper waters of the northern North Sea. The species usually occur to 40 m (solenette) and 100 m (scadfish); however it is unlikely that depth is the limiting factor for the northward movement. Both species were reported in deeper waters, for scadfish to a depth of 200 m (Bauchol 1987) and solenette to 450 m (Muus and Nielsen, 1999).

Changes in the fish assemblage owing to fishing are another potential explanation for the increase in small fish species (Heessen and Daan, 1996; Daan et al., 2005). Changes linked to fishing result in less predation pressure by large fish on smaller fish. As shown by stomach samples collected during the “ICES year of the stomach”,

scadfish and solenette predators include whiting (*Merlangius merlangus*), red gurnard (*Aspitrigla cuculus*), grey gurnard (*Eutrigla gurnardus*) and turbot (*Psetta maxima*), all of which are fished. Fishing, by removing larger predatory fish, could thus result in a lower predation pressure. The lower predation pressure may have thus facilitated the increase of solenette and scadfish, but cannot explain the sudden increase in the late 1980s, as fishing pressure has shown a gradual development in time (ICES, 2007).

Another fishing-related explanation would be changes in trawling. Scadfish and solenette are non-target species, but they are caught and discarded by the commercial beam-trawl fleet (Van Beek 1998). The beam-trawl effort changed in 1989 with the partial closure of the shallow coastal nursery area of plaice (*Pleuronectes platessa*), the so called “plaice box”; fishing was relocated outside of this box (Pastoors et al., 2000). However, since scadfish and solenette increased both within and outside the “plaice box”, the change in fishing effort distribution seems an unlikely explanation for the observed changes in both species.

Winter temperature thus seems to be the main driving factor behind the observed changes. The mechanism by which temperature affected the distribution is shown by the development in recruitment. The increase in recruitment did not precede, but followed the increase in adult stock. Adults have moved into the new area and subsequently spawned there. That the movement of adults into the northern area and the improved conditions resulted in spawning is corroborated by an egg survey in 1989, which showed egg production by both species above the Dutch and German Wadden Isles, a large part of the northern area (Van der Land, 1991). Adults moving into a new area and successfully spawning there is opposite to what was found for blue mouth (*Helicolenus dactylopterus*) in the North Sea, which invaded almost only as a single year class (Heessen et al., 1996) but was unable to reproduce and thus establish itself in the new habitat.

In both sub-areas and for both species, statistical analyses of recruitment showed a significant relationship between adult stock and recruitment. Analyses also indicated that spawning temperature and winter temperature can explain a part of the variation in recruitment. Recruitment estimates are, however, based on the catch of the smallest individuals for which the catchability of the used gears is very low creating a large measurement error. Further, because we used a fixed cut-off length for recruitment for the whole period, variation in growth has been considered negligible. This is not a valid assumption, given the changes in growth rates of juveniles of other species (Teal et al. 2008), but since we do not have otolith samples throughout the observation period, this problem cannot be overcome. The inter-annual variability in the recruitment estimates should be considered taking account of the variation introduced by these assumptions.

That the new habitat is suitable for both species even for spawning makes it likely that they will persist there; a single cold year might force them out, but they can recover within a few years. The food web will be affected by the increased abundance of these species, owing to the high energy demand of the small flatfish species, as is shown for solenette (Jennings et al., 2008). This will almost certainly affect the competition among benthivorous fish such as the commercial flatfish: plaice and sole, which have an overlap in diet with solenette (Piet et al., 1998; Amara et al., 2004). Along with predation by scadfish on

the early juveniles of the commercial species (Rogers, 1991), it may also affect the commercial flatfish species and the fisheries. For example, predation on and competition with commercial species could already have played a role in the “plaice box”, given that after its closure in 1989, the expected positive effect on plaice did not occur (Pastoors et al., 2000). The closure coincided with the increase in abundance of the small flatfish species in that same area. A more thorough analysis of the increase in abundance of the small flatfish species and the failure of the recovery of plaice is needed.

Climate predictions are that the number of severe winters will decrease and the temperature will rise gradually (IPCC, 2007). This makes it likely that the abundance of these two species will increase and expand further northwards, affecting the interaction with commercial species.

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