Journal of Sea Research
July-August 2010, Volume 64, Issues 1-2, Pages 45-53
Proceedings of the Seventh International Symposium on Flatfish Ecology, Part I
http://dx.doi.org/10.1016/j.seares.2009.07.001

Impact of warming on abundance and occurrence of flatfish populations in the Bay of Biscay (France)

Marie Hermant[a], Jeremy Lobry[b], Sylvain Bonhommeau[c], Jean-Charles Poulard[b] and Olivier Le Pape[c, *]

[a] Ecologie de la diversification, UMR CNRS 6553, Université de Rennes 1, Campus de Beaulieu, F-35042 Rennes cedex, France
[b] Département Ecologie et modèles pour l'halieutique, IFREMER, rue de l'ile d'Yeu, B.P. 21102, 44311 Nantes, France
[c] Université Européenne de Bretagne, UMR 985 Agrocampus Ouest, Inra «Ecologie & Santé des Ecosystèmes», Ecologie halieutique, Agrocampus Rennes, 65 rue de St Brieuc, CS 84215, 35042 Rennes, France

*: Corresponding author : O. Le Pape, email address : Olivier.le_pape@agrocampus-ouest.fr

Abstract:

The aim of the present study was to analyse the influence of warming on flatfish populations in the Bay of Biscay. 17 autumn cruises conducted from 1987 to 2006 over the whole shelf of the Bay of Biscay provided data for the abundance and occurrence of adults for twenty flatfish species. Trends in flatfish abundance were analysed with regard to geographic range of populations and interannual fluctuations in abundance were related to seawater temperature.

Results showed significant trends in abundance and occurrence for 55% of the flatfish species in the Bay of Biscay. The response to warming of seawater was correlated to geographic ranges of species. While the abundance of the northern temperate species decreased, that of southern ones increased. Moreover, for 40% of the species which densities have significantly changed, abundances were correlated to temperatures in their year of birth, positively for southern species and negatively for northern ones. Last, the abundance of flatfish adults over the Bay of Biscay was compared to previous data on juveniles in the Bay of Vilaine, one of the estuarine nursery ground in this area. For the northern species which have disappeared, the decline in juvenile abundances preceded that of adults by several years, indicating that the recruitment is the process affected.

We concluded on a major impact of warming to explain changes in flatfish species abundances. Nevertheless, the impact of fishing interacts with that of climate change because the exploited species appeared to be the most negatively affected.

Keywords: Flatfish; Temporal Trends; Interannual Variability; Climate Change; Geographic Distribution; Bay of Biscay

1. Introduction

The temperature of the upper 300 m of the North Atlantic increased by about 0.6°C between 1984 and 1999, with substantial interannual variability (Brander *et al*., 2003). In the same way, long-term trends and interannual variations in abundances and distribution of fish have been observed over the past few years. Perry *et al.* (2005) showed a northward shift of fish species in the North Sea over the last 25 years, related to changes in seawater temperature. Other studies have related successive northward and southward migrations of fish species to alternating warming and cooling events of the North Atlantic seawater (Drinkwater, 2005). Rose (2005) found that these changes in fish distribution linked to climate change in the North Atlantic depend on the physiological limits of species.

In addition to sea temperature, other factors, and especially exploitation, have to be taken into account when trying to explain changes in distribution and abundance of fishes: in their study on the commercial gadoid and flatfish species of the North Atlantic, Brander *et al.* (2003) demonstrated that the abundance of warm water species in capture increased in comparison to colder water species and suggested that consequences of fishing overlay those of the seawater warming. On the other hand, Pauly (1994) and van der Veer *et al.* (2003) suggested that the replacement of sub-polar species by tropical ones will result in higher occurrences of small flatfish species of less commercial interest.

The Bay of Biscay is an arm of the North Atlantic extending along the west coast of France down to the north coast of Spain (ICES Area VIIIa/c), located at the interface between the North Atlantic sub-polar and sub-tropical gyres. In this area, the seawater temperature in winter has significantly increased over the last century, with the fastest rate of prolonged change occurring in the last two decades. Moreover, this general trend does not appear to be slowing down (Koutsikopoulos *et al*., 1998; Garcia Soto *et al*., 2002).

Poulard and Blanchard (2005) have investigated the relationship between seawater warming and species composition of the fish communities in the Bay of Biscay. They showed a change in species composition of fish communities, with an expansion of the sub-tropical and tolerant species and a decline of the temperate and boreal species. Désaunay *et al.* (2006) investigated changes in abundance of 4 selected commercial flatfishes with regard to their biogeographic distribution. They noted a regression of northern winter spawners such as plaice and dab, and an expansion of a southern summer spawner, the wedge sole. However, our understanding of the effects of climate change on fish populations is still hampered by the lack of long-term and in-depth analyses at the level of populations.

The objective of the present study was to investigate the impact of climatic variability and warming trend on all of the flatfish populations in the Bay of Biscay. The aim was here to complete the previous approaches by a global study on the entire flatfish community, linked to analyses on the process involved in the observed changes. Groundfish surveys provided data for twenty flatfish species caught in this area over the two last decades. Here we addressed the following questions: Do flatfish populations show long-term trends in abundance and occurrence? Is the interannual variability of abundance related to seawater temperature? What are the involved processes? We finally discussed the relative roles of climate warming and fishing pressure on flatfish populations.

2. Material and methods

2.1. Sea surface temperature (SST) in the Bay of Biscay for the two last decades

Sea surface temperatures were extracted from a database provided by the Hadley centre, Met Office (http://badc.nerc.ac.uk). These data were measured *in situ* from 1870 to present, each month, and satellite observations were included in the modern period. The data were interpolated on a 1° latitude-longitude spatial grid (Rayner *et al*., 2003). SST values were extracted from this database from 1960 to 2006 from nodes of the grid located between 43.5°N and 47.5°N, and 1.5°W and 4.5°W (9 nodes located in the Bay of Biscay). Annual, summer (June-August) and winter (January-Mars) mean SST were calculated over this area.

Bottom temperature were not available on such a complete series but only on a restricted data set (Ifremer, unpub. data), consisting in summer mean temperatures (from June to August) at 100m in depth in the Bay of Biscay from 1967 to 2002. A comparison between the common parts of the two data sets (mean temperatures from June to August between 1967 and 2002) was performed and a significant correlation was found (Pearson correlation coefficient r = 0,68 ; n = 36 ; $p = 10^{-5}$). This relation was obtained on summer data, when the maximum stratification of the water column occurs. The SST was thus assumed to represent interannual variations of temperatures in the water column on the continental shelf. We used the exhaustive SST time series to study trends in water temperature in the Bay of Biscay and relations with flatfish densities.

2.2. Data from groundfish surveys over the Bay of Biscay shelf

17 groundfish surveys have been carried out annually since 1987 by Ifremer in the Bay of Biscay (Fig. 1) from September to December (Souissi *et al.*, 2001; Poulard and Trenkel, 2007). The survey area was located between 48°30' N in the North and 43°15' N in the South. The sampling scheme was stratified according to latitude and depth (Fig. 1). A 36/47 otter trawl with a 20 mm mesh codend liner was used. Hauls were run for 30 min, with a towing speed of 4 knots. Fishing was mainly limited to daylight hours. Catch numbers were recorded for all species, all finfish were measured. From 56 to 113 hauls were carried out per year (Fig. 1) and provided data on the occurrence and abundance of twenty flatfish species.

Abundances (number of individuals per trawled surface, in hectare, for each species) were estimated on the stratified sampling scheme, with relation to mean density in each depth×latitude area and to the surface of these areas, as described in Pennington and Grosslein (1977). As age composition was not available for the studied species from these surveys, all year classes were pooled to estimate abundance. The occurrence of each species was expressed as the relative number (in %) of positive hauls in a survey.

2.3. Flatfish species in the Bay of Biscay

Data were collected for the 20 flatfish species caught in the Bay of Biscay during this series of annual surveys (Table 1). Mean latitudinal range of each species was estimated from the northern and southern limits of their geographic distribution according to the general description by Wheeler (1978), who provided a reference previous to the beginning of our time series, where geographic range were estimated at the same time for all the studied species. Moreover, thank to this mean latitudinal range, the 20 species were classed in three class of biogeography related to their mean latitudinal range (Table 1) and to the location of the study site (Fig. 1): southern species (<43.5°N), species centered in the Bay of Biscay (midrange species, [43.5-48 °N]), northern species (>48°N).

Fishing effort was little known for most of species in the Bay of Biscay. Exploitation level was described according to expert knowledge as a qualitative variable classified in 3 categories: (i) Commercial targeted species; (ii) Occasional commercial species, involuntarily caught in limited number with target species; (iii) Non-commercial species, rarely captured because they live in inaccessible environments for fishing gears and/or their size makes them unfit for commercialization.

2.4. Mean age of the catches by flatfish species

Mean age of the catches by flatfish species was determined according to the Von Bertalanffy growth equation:

$$(1) \qquad \bar{t} = t_0 - \frac{1}{K} \times \ln\left(\frac{L\infty - \overline{L_t}}{L\infty}\right)$$

where K is the growth rate (year^{-1}), L_∞ is the ultimate length of the catches (cm), $\overline{L_t}$ is the mean length of the catches for the considered species over all the years of the study (cm) and t_0 is the theoretical age for a length of 0 cm (years). K, L_∞ and t_0 were obtained from Fishbase database (www.fishbase.org).

2.5. Statistical analysis

2.5.1. - Temporal trends in biological and environmental time series

We first analyzed the temporal trends in seawater temperature and in flatfish abundances and occurrences. A Kendall correlation test was used to check for correlation between the year and 3 SST indices (annual, summer and winter temperatures) and for correlation between the year and the annual abundances of each species. This non-parametric method was chosen because of the non-linear trends between the year and the studied responses variables (Fisher, 2003). Temporal trends in SST were analysed over the whole time series (1960-2006) and over the period covering the study (1987-2006).

Some species were caught in low numbers (< 10 ind. $ha^{-1}.year^{-1}$) that may break up the trends in abundances. To complete the results on the abundances, we also checked the trends in occurrences. We used a logistic model to test correlation between the year and the annual occurrences of each species, given the binary nature of this variable (probability of presence).

2.5.2. - Metaanalysis of these population trends

To synthetize the results, we realized a global analysis by pooling all the population trends in the same analysis (Planque and Fredou, 1999). In that aim, we plotted the temporal slope obtained from the Kendall correlation test for each of the 20 species on their mean latitude. In such a meta-analysis, significant and unsignificant slope obtained for each population were compiled (Richardson and Shoeman, 2004) to analyse the global response of flatfish populations with relation to their biogeographic distribution. Furthermore, we grouped populations with regards to their mean latitudinal range (Southern Biscay, Bay of Biscay, Northern Biscay, Table 1) and we tested with an analysis of variance (AOV) if temporal trends differ among these categories. For each of these groups, we also tested with a student t-test, if the distribution of the temporal slopes differed from 0.

2.5.3. - Correlations between SST and abundances time series

Interannual variability in the abundances of each species was related to annual mean SST. This comparison was performed with a time lag from 0 to 6 years between the two time series. Abundance of a given year was related to SST of the same year and to those of the 6 previous years.

Time series of annual mean SST and abundances were first compared using raw data. The correlations were then checked after removing trends and autocorrelation from the time series. Indeed, procedures for statistical testing of the correlation between the abundances and SST series must account for the autocorrelation (low-frequency variability) and trends in the time series because they may result in an artificial increase in the statistical significance of the correlation test (Pyper and Peterman, 1998). The aim was to transform the original data to eliminate statistically significant trends and to account for autocorrelation whilst retaining the high frequency signal (Fox *et al*., 2000). To assess correlations between SST and interannual variations in abundances time series, we first removed the trends by prewhitening the data series prior to statistical testing. Prewhitening of the abundances and SST time series was performed by applying a linear model to times series and using residuals (calculated by the least squares method) in the correlations. We then adjusted the d.f. in the statistical tests to compensate for autocorrelation (Pyper and Peterman, 1998). To adjust d.f., we applied the equation proposed by Chelton (1984) and modified by Pyper and Peterman (1998):

$$\frac{1}{N*} = \frac{1}{N} + \frac{2}{N}\sum_{j} r_{xx}(j) r_{yy}(j) \qquad (2)$$

where N* is the corrected sample size, considered as the number of independent joint observations on the two time series, X (abundance data) and Y (SST data), N is the length of the initial time series and $r_{xx}(j)$, and $r_{yy}(j)$ are the autocorrelation of X and Y at lag j. Estimators of autocorrelation r are obtained using the Box–Jenkins' equation (Box and Jenkins, 1976) modified by Chatfield (1989):

$$r_{xx}(j) = \frac{N}{N-j} \times \frac{\sum_{t=1}^{N-j}\left(X_t - \overline{X}\right)\left(X_{t+j} - \overline{X}\right)}{\sum_{t=1}^{N}\left(X_t - \overline{X}\right)^2} \qquad (3)$$

where $\overline{X}$ is the overall mean.

Pyper and Peterman (1998) tested a variety of d.f. adjustment methods and found Eq. (2) to be robust and unbiased compared with other methods. This method is also robust to the number of lags applied in the d.f.-reduction (Eq. 2). In the present analysis, we calculated autocorrelations until the fourth lag approximately equal to N/5, following Pyper and Peterman (1998). The correlation was then assessed using Pearson coefficients with d.f. correction for autocorrelation as described above (Eq. 2). The p-value was assessed by comparing the Pearson coefficient against its theoretical distribution with N* – 2 d.f.

3. Results

3.1. SST increase in the Bay of Biscay

Kendall correlation tests showed an increase in annual, winter and summer mean SST over the period 1960-2006 (Table 2). Similar trends were found for annual and summer mean SST in the recent period when fish data are available, between 1987 and 2006 (Fig. 2; Table 2).

3.2. Changes in abundance/occurrence of flatfish populations with respect to latitudinal distribution

Over the 20 flatfish species caught during the study, 8 (40%) showed a significant change in their abundances and 9 (45%) in their occurrences (Table 3). These two variables increased for the imperial scaldfish, the wedge sole and the thickback sole, whereas they decreased for the dab, the flounder and the plaice. The number of catches has dropped dramatically for the last 3 species since 1995 (1 dab, no flounder and 3 plaices). While the Norwegian topknot and the turbot showed a decrease only in their abundances, a clear increase in occurrence was found for the scaldfish, the deepwater sole and the solenette. On the whole, among the 20 flatfish species studied in the Bay of Biscay, 5 species were in decline (in abundance and/or occurrence) and 6 in expansion.

When these results were considered with regards to species latitudinal range, they provided a general signal (Table 3): the mean latitudinal ranges of 5 of the 6 increasing species were southern from the Bay of Biscay, the last one being centred in this Bay, while the mean distributions of the 5 declining species were located at higher latitude (Table 1). The metanalysis on the 20 species reinforced this general pattern (Fig. 3): the slope of the temporal trend declined with increasing mean latitudinal range. If this linear relation between mean latitude and temporal slope was not significant, slope were different (AOV, p<1%) between southern, midrange and Northern species (Fig. 4). Moreover t-test demonstrated that slopes were positive (p < 1 %) for southern species, not significantly different from 0 for species centred in the Bay of Biscay and negative for northern species (p<1%). These patterns were confirmed from species occurrence; even if levels of significance were different, both probability of catch and densities provided comparable results and the sign of the slope of the time trends were similar for the 20 species (Table 3).

Regarding the level of exploitation of these species, non commercial, occasional and target species were all distributed on the whole latitudinal range but the proportion of targeted species increased with latitude (Fig. 3). 3 of the 5 northern significantly declining species appeared to be targeted but 4 of the 6 southern species in expansion were non-commercial species (Table 1). When all the species were taken into account (Fig. 3), there was no discrepancies in the relation between latitudinal range and temporal trends with regards to level of exploitation.

3.3. Influence of annual mean SST on abundance of flatfish species

Relation between time series of annual mean SST and abundances were first analysed without removing trends and significant relations were obtained for 5 species (Fig. 5A). For 4 species, the highest correlation between annual mean SST and abundances was found for a lag equal to the mean age of the population, as calculated with the mean size of the catches and the von Bertalanffy growth equation (Fig. 5A). A different pattern was found for the plaice. This population with a mean age of 3 years showed a maximum correlation coefficient for a lag of one year (r = -0.76), but correlation coefficients for lags of 2 and 3 years remain close to the maximum value (r = -0.71 and r = -0.75 respectively).

The correlations were then checked after removing trends and autocorrelation in the time series (Fig. 5B). Correlations between annual mean SST and abundances were significant for the imperial scaldfish and the turbot for a lag equal to the mean age of the populations.

Systematically, correlations between temperatures and abundances were negative for the declining species distributed in the north of the Bay of Biscay and positive for the expanding species distributed in the south of the bay (Fig. 5).

4. Discussion

4.1. Seawater warming in the Bay of Biscay

The present study indicated a significant increase in annual, summer and winter SST over the whole continental shelf of the Bay of Biscay since 1960. These results were consistent with those obtained at a global scale on the consequences of warming in the coastal zone (Sundermann *et al.*, 2001) and with the previous studies which described a seawater warming in the southern part of the Bay of Biscay since the 70s (Koutsikopoulos *et al.*, 1998; Planque *et al.*, 2003), then in the northern part since the 80s (Désaunay *et al.*, 2006). In a study outside the continental shelf of the Bay of Biscay, Blanchard and Vandermeirsch (2005) specified that warming affects the entire water column, with an increase in sea temperature of 0.8°C between 50 and 200 m over the period 1970-2000. The preliminary analysis realized here on available bottom temperature on the continental shelf also demonstrated that variations in surface temperature also affect the bottom layer. Therefore, this warming impacts the habitat of flatfishes which live in the bottom waters of the continental shelf.

4.2. Impact of warming on flatfish populations

4.2.1. - Trends in abundance and occurrence with regards to geographical distribution

The impact of warming on flatfish populations in the Bay of Biscay was demonstrated through the latitudinal distribution of the affected species. It is important to notice that the approximates of the latitudinal range taken from Wheeler (1978) could be cautious for some species. Nevertheless, these data were used to estimate a mean latitudinal range for a metaanalysis and they provided imprecise but standardized and simultaneous approximates. The mean latitudinal ranges of the 5 declining species were between 47.5°N and 58.5°N, those of the 6 expanding species between 7.5°N and 46°N. This clearly indicated a rarefaction of the northern species and an expansion of the southern ones with a limit in the Bay of Biscay (43.5-48° N). More precisely, the mean latitudinal range of 4 over the 5 declining species was northern than the Bay of Biscay. For the last one, it was located at the North of this Bay. These northern species have a preference for cold waters. For instance, the plaice favours temperatures between 2 and 15°C (Fox *et al.*, 2000). By contrast, among the 6 expanding species, the mean latitudinal distribution of the scaldfish was located in the Bay of Biscay but, for the 5 other species, it was largely more southern. Some of them, such as the imperial scaldfish and the wedge sole, could be described as subtropical species, as their distribution extends until southern hemisphere. Southern species are thus adapted to cope with higher temperatures. Moreover, this conclusion appeared consistent when all the species were taken into account; the trends demonstrated on species for which significant results were obtained were reinforced by metaanalysis. The pattern of increasing southern species and decreasing northern species appeared general with this method previously validated to analyse trends in primary production with regards to climate change worldwide (Richardson and Shoeman, 2004).

While the northern temperate species distribution retreated northwards to avoid the temperature increase, the southern temperate species took advantage of seawater warming to spread over the Bay of Biscay. These processes have already been highlighted in the North Atlantic. Quéro *et al.* (1998) have first noted an increase in abundance of tropical species in the south of the Bay of Biscay and a northward shift of these species from 16° to 30°N since 1965, some of them until the Irish Sea. Perry *et al.* (2005) showed a significant change in mean latitudes in relation to warming for 15 fish species in the North Sea. Their center of distribution moved from 48 to 403 km over the last 25 years and most of these shifts were northward. They notably indicated polar shifts for the scaldfish, the dab and the common sole. In the same way, several studies have reported successive northward and southwards migrations in cod (*Gadus mordhua*) caused by alternating events of warming and cooling of North Atlantic seawater since the beginning of the 20th century (Drinkwater, 2005). Thus, northward redistribution, or polar drift, appeared as a response to climate change of flatfish species according to their temperature requirements (Stebbing *et al.*, 2002; Perry *et al.*, 2005; Drinkwater, 2005). Because most of fish species tend to prefer a specific range of temperature, changes of geographical distribution of species often matches with long term changes in temperature. In the northern hemisphere, seawater warming induced a northward shift of fish distributions (Rose, 2005).

4.2.2. - Relationships between temperature and abundance

To estimate the short-term impact of warming on flatfish populations in the Bay of Biscay, we performed comparisons between temperature and abundance time series. Then, we compared the time lags (in years) in correlation with the mean age in the population. Without age determinations from otoliths, this mean age was roughly estimated from growth parameters taken from fishbase and this method only provided an uncertain qualitative estimate. With transformed data (removed trend and autocorrelation), few (2 species) significant correlations were obtained, as the short term effect could be hidden by (i) the pool of several cohorts in abundance indices, and subsequent autocorrelation in abundance time series and (ii) variability unexplained by temperature and uncertainty in estimates related to surveys (Poulard and Trenkel, 2007). Moreover, variability in flatfish abundance is related to the long-term changes in temperature and a comparison between abundance and SST time series by smoothing the data would be appropriate to observe low-frequency variability (Fox *et al.*, 2000). However, such method was not appropriate here because of the shortness of the series. The solution was hence to compare the series while trends were preserved. Using this approach, correlation coefficients result from the combination of both long-term changes (low-frequency variability and, easily viewable here, trend) and short-term changes (high-frequency variability). Even if these correlations could be used to test the relation between temperature and abundance, because their significance was over-estimated by temporal autocorrelation, they provided an indication of the covariations. When trends were preserved, species showed the highest correlation for a time lag close or equal to the estimated mean age of the population. The same pattern was obtained with the transformed series for 2 of these 5 species, also with significant correlations for a lag equal to the mean age of the population. Furthermore, with regards to warming, these correlations were consistent to the results on temporal trends in abundance and occurrence: they were negative for the northern temperate species and positive for the southern ones. These results suggested that flatfish abundance is related to temperature in their year of birth.

4.2.3. - Response of flatfish population to temperature increase: a consequence of changes in recruitment

The northward redistribution of flatfish species in the Bay of Biscay could be explained by two processes. First, the individuals could migrate to follow their temperature range. However, such migrations are unlikely for flatfishes as they are quite sedentary, their movements being reduced and essentially seasonal. Adults migrate to deeper waters in winter to reproduce and come back inshore in summer to feed (Deniel, 1981; Quéro and Vayne, 1997). Secondly, the response of species to climate change could depend on the success of the different phase of their life cycle (Rose, 2005; Wood *et al.*, 2002). The recruitment is one of the key stages which could be affected by temperature (Henderson, 1998; Phillipart *et al.*, 1998; Fox *et al.*, 2000) and its variability strongly influences the population structure (Levin and Stunz, 2005). For a large proportion of flatfish species, the recruitment and the growth of juveniles occur in coastal nurseries (Gibson, 1994). A disturbance in recruitment impacts the adult abundance at the end of the time needed for the juveniles to join adult population over the continental shelf, i.e. several years after. In the present study, for 40% of species which densities have changed, noticeable correlation were found between abundances and temperatures and the highest correlations were obtained for a time lag equal to the mean age of the population. Moreover, these correlations were negative for southern species and positive for northern one. It indicated that abundances of adult flatfishes depend on temperatures in their year of birth and emphasized the impact of warming on recruitment.

This hypothesis of the effects of warming on the recruitment could also be highlighted for species of which abundance sharply decreased and quite disappeared from the catches before the end of the time series (plaice and dab). Désaunay *et al.* (2006) estimated the abundance of flatfish juveniles in the Bay of Vilaine nursery ground over the period 1981-2001. They indicated a drop in juvenile captures for the plaice and the dab since 1990 and 1993 respectively. As observed in the present study, adult abundance of both species decreased in the Bay of Biscay from 1995. This abundance drop could not arise from a northward migration of individuals, because the disappearance of juveniles and adults was not synchronous. For these 2 northern temperate species, the strong reduction of the adult abundance in the Bay of Biscay seems rather to be the consequence, with a time lag of several years, of a disruption of recruitment related to temperature rising. Brunel and Boucher (2007) led to the same conclusion about the major effect of warming on exploited fish population recruitment in the North Atlantic.

Therefore, in response to seawater warming, delayed trends in abundance time-series between juveniles nursery grounds and adults on the continental shelf, and correlations between abundances and temperature in the year of birth, indicated a northward redistribution of flatfishes in the Bay of Biscay induced by changes that subsequently affect the recruitment success.

4.2.4. - Ecological explanations of the effect of warming on flatfish recruitment

Seawater temperature affects metabolic and physiological rates, behaviour and hence population dynamics of fish (Brander *et al.,* 2003). Fish recruitment is especially affected by seawater warming (Philippart *et al.,* 1998; Fox *et al.*, 2000; Clark and Hare, 2002). Recruitment may be affected by sea temperature through (i) metabolic costs of spawners (Fisher, 2003; Gibson, 2005), (ii) eggs development (Van der Land, 1991; Dethlefsen et al., 1996), (iii) activity of predators that feed on fish eggs and larvae (Wood *et al*., 2002), (iv) natural mortality of eggs and larvae (van der Veer *et al*., 2000), (v) food availability (Cushing, 1990; Miller *et al*., 1991; Houde, 1997; Mountain, 2002; Clark and Hare, 2002) and, thus, growth (Fonds, 1979) and survival (Suthers, 1998) of larvae but also (vi) growth (Fonds 1975; Yamashita *et al.* 2001; Lekve *et al.* 2002; Le Pape *et al.*, 2003; Trescher *et al.*, 2007; Teal *et al.*, 2008) and mortality of juveniles (Miller *et al.*, 1988; Suthers, 1998). Thus, many behavioral and physiological processes during spawning and larval phase may be affected by seawater warming.

Thus, the early life history stages of flatfish species are sensitive to seawater temperature (Fonds, 1979). The list of temperature dependent factors influencing recruitment is extensive (see overview in Cushing, 1995) and it is very difficult to analyze the process involved in the consequences of sea warming. The relative importance of regulating factors on recruitment success differs according to species and region (see overview in Van der Veer *et al*., 2000), as fish populations respond to different predominant mechanisms (Nash and Geffen, 2000; Désaunay *et al*., 2006). In the Bay of Biscay, as in other temperate areas, the influence of warming on recruitment success probably differs for sub-tropical and cold-temperate species (Wood *et al*., 2002). One relevant hypothesis to explain patterns of changes in the Bay of Biscay refers to the differences in life cycle of flatfish with regard to their latitudinal range. While cold northern flatfishes spawn during the winter-spring season, warm southern species spawn during spring-summer. These features were verified for the flatfishes that exhibits significant trends in the Bay of Biscay; except for the deep water sole (spawning season unknown), all the southern species spawn in spring-summer and the northern species in winter-spring (Wheeler, 1969; Legett and Frank, 1997; Désaunay *et al.*, 2006). During winter, as metabolic costs of spawners are generally optimized for a temperature lower than the thermal optimum for the growth of young stages (Fisher, 2003; Munday *et al*., 2008), sea warming negatively influences the recruitment of winter-spring spawning northern species. Especially, Van der Veer (1986) and Fox *et al.* (2000) showed a negative relationship between winter sea temperature at the time of spawning and the year-class strength of the plaice around the British Isles and in the North Sea. A similar relationship has been demonstrated for the dab in the Bristol Channel by Henderson (1998). On the contrary, winter growth of benthic juveniles of southern spring-summer spawners could have been enhanced by winter warming and this faster growth would have increased their survival (Suthers, 1998). The pelagic larval phase of spring-summer spawning southern species was however not modified, because summer warming is below their (warm) maximal spawning thermal range. In the same time, increase in the summer growth of northern winter-spring spawning juveniles (Le Pape *et al.*, 2003) seemed not to compensate more consequent losses (van der Veer *et al*, 2000; Levin and Stunz, 2005) related to the previous phase of the life cycle (winter-spring spawning, hatching and pelagic larvae). Hence, a shift could have occurred between increase of southern warm species and decline of northern cold ones with relation to their different life cycle.

4.3. Impact of fishing on flatfish populations

The study of changes in abundance and occurrence of flatfish populations in the Bay of Biscay cannot ignore the effect of fishing. Quéro and Cendrero (1996) have collected large amount of data about catches of fishes in the Arcachon basin (south of the Bay of Biscay). They indicated that the turbot, the brill, the plaice, the common sole and the wedge sole are targeted commercial species and they specified that the Senegalese sole, the sand sole and the thickback sole are often caught and confused with the common sole. These indications confirmed the categories of exploitation level that have been established in this study, according to specialists (Table 1). This classification showed that among the 6 northern temperate species which have significantly dropped in abundance, 4 are target species for fishing and 2 are non-commercial. In contrast, among the 5 southern temperate species which have significantly increased, 3 are non-commercial and 2 undergo a targeted or occasional exploitation. The impact of fishing on flatfish populations tends therefore to combine with climate change (Gibson, 2005), with a reduction of abundance for 45% of the large northern exploited species and an increase for 50% of the small southern non-commercial species. However, as abundances decreased also for 25% of non-commercial species and increased for 11% of target species, a more general impact of warming could be pointed out; when all of the flatfish populations were considered in the metaanalysis, no difference in trends with regard to the level of exploitation appeared on the 20 species. Nonetheless, target species appeared in a larger proportion in Northern than in Southern species. This last result appeared related to previous conclusions of Pauly (1994) and Van der Veer *et al.*, (2003): the replacement of sub-polar species by tropical ones will result in higher occurrences of small flatfish species of less commercial interest. Thus climate changes can explain different trends between target and commercial flatfish. Nevertheless, fishing pressure can increase this pattern threw overexploitation of commercial species and also threw reduction of higher levels of the food webs (Pauly et al.,1998) and lower predation on small southern species.

5. Conclusion

Trawl survey data collected in the Bay of Biscay during the two last decades enabled us to show a significant variation in abundance for 55% of the flatfish species. The impact of climate change was evident with regard to the latitudinal range of population because the species in decline have their center of distribution northernmost than species in expansion, with a limit in the Bay of Biscay. This was a generalization of the previous results on 4 commercial flatfish species (Désaunay et al., 2006); it confirmed changes in species composition of fish communities (Poulard and Blanchard, 2005) and demonstrated a general pattern of increase of southern species and decrease of northern ones. The analysis of abundance time-series suggested an effect of seawater warming on recruitment. Indeed, for 3 northern temperate species, the recruitment reduction occurred several years before the adult abundance decrease. Moreover, the correlation between abundances of species and the temperature in their year of birth emphasized this assumption. Nevertheless, although the impact of seawater warming on flatfish populations in the Bay of Biscay was established, processes remain uncertain and are probably different between southern and northern species.

The impact of climate change on flatfish populations seemed to be amplified by fishing (Brander, 2005), with a stock reduction in exploited species and an expansion of non-commercial species.

Acknowledgements

We thank J.-C. Mahé (Ifremer, Lorient, France) who is in charge of the Ifremer groundfish surveys in the Bay of Biscay and Celtic sea and all our colleagues involved in the data collection. We would also like to thank Yves Désaunay for his fruitful help to plan this study, Benjamin Planque (IMR, Tromsoe, Norway) and the other reviewer for their helpful and precise suggestions and advice which have been essential to improve this paper.

References

Blanchard F., Vandermeirsch F., 2005. Warming and exponential abundance increase of the subtropical fish Capros aper in the Bay of Biscay (1973-2002). C.R. Acad. Sci. Biol. 328, 505-509.

Box G.E.P., Jenkins G.W., 1976. Time Series Analysis: Forecasting and Control. San Francisco, CA: Holden-Day, 575 pp.

Brander K., Blom G., Borges M. F., Erzini K., Henderson G., MacKenzie B. R., Mendes H., Ribeiro J., Santos A. M. P., Toresen R., 2003. Changes in fish distribution in the eastern North Atlantic: Are we seeing a coherent response to changing temperature? - ICES Mar. Sci. Symp. 219, 261-270.

Brander K.M.. 2005. Cod recruitment is strongly affected by climate when stock biomass is low. ICES J. Mar. Sci. 62, 339-343.

Brunel T., Boucher J., 2007. Long-term trends in fish recruitment in the North East Atlantic related to climate change. Fish. Oceanogr. 16, 336-350.

Chatfield C., 1989. The Analysis of Time Series: An Introduction. London: Chapman and Hall, 268 pp.

Chelton D.B., 1984. Commentary: short-term climatic variability in the Northeast Pacific Ocean. In: The influence of ocean conditions on the production of Salmonids in the North Pacific. W. Pearcy (ed.) Corvalis, Oregon: Oregon State University Press. pp. 87–99.

Clark W., Hare S., (2002). Effects of climate and stock size on recruitment and growth of pacific halibut. N. Am. J. Fish. Manage. 22, 852-862.

Cushing D.H., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. 26, 249-293.

Cushing D., 1995. Population Production and Regulation in the Sea: A Fishery Perspective. Cambridge: Cambridge University press, 354 pp.

Dethlefsen V., von Westernhagen H.,Cameron P., 1996. Malformations in North Sea pelagic fish embryos during the period 1984–1995. ICES J. Mar. Sci. 53(6),1024-1035

Deniel C., 1981. Les poisons plats (Téléostéens, Pleuronectiformes) en baie de Douarnenez : reproduction, croissance et migration des Bothidae, Scophthalmidae, Pleuronectidae et Soleidae. Thèse de doctorat de l'Université de Bretagne Occidentale, France. 476 pp.

Désaunay Y., Guérault D., Le Pape O., Poulard J.C., 2006. Changes in occurrence and abundance of northern/southern flatfishes over a 20-year period in a coastal nursery area (Bay of Vilaine) and on the eastern continental shelf of the Bay of Biscay. Sci. Mar. 70: 193-200.

Drinkwater K.F., 2005. The response of Atlantic cod (Gadus morhua) to future climate change. ICES J. Mar. Sci. 62, 1327-1337.

Fischer T., 2003. The effects of climate induced temperature changes on cod (Gadus morhua L.): Linking ecological and physiological investigations. Rep. Pol. Mar. Res. 454, 101 pp.

Fonds M., 1975. The influence of temperature and salinity on growth of young sole Solea solea L. 10th Europ. Symp. Mar. Biol., Ostend, Belgium, Sept. 17-23 1, 109-125.

Fonds M., 1979. Laboratory observations on the influence of temperature and salinity on development of the eggs and growth of the larvae of Solea solea (Pisces). Mar. Ecol. Progr. Ser. 1, 91-99.

Fox C.J., Planque B.P., Darby C.D., 2000. Synchrony in the recruitment time-series of plaice (Pleuronectes platessa L) around the United Kingdom and the influence of sea temperature. J. Sea Res. 44, 159-168.

Garcia-Soto, C., Pingree, R., Valdes, L., 2002. Navidad development in the southern bay of Biscay: Climate change and swoody structure from remote sensing and in situ measurements. J. Geophys. Res. 107, 1-29.

Gibson R.N., 1994. Impact of habitat quality and quantity on the recruitment of juveniles flatfishes. Neth. J. Sea Res. 32, 191-206.

Gibson R.N., 2005. Flatfishes. Biology and exploitation. Fish and aquatic resources series 9. Blackwell Pub. Oxford UK. 391 pp.

Henderson P.A., 1998. On the variation in dab Limanda limanda recruitment: a zoogeographic study. J. Sea Res. 40, 131-142.

Houde E.H., 1997. Patterns and consequences of selective processes in teleost early life histories. In : Early life history and recruitment in fish populations., Fish Fisher. Ser. 21 (eds. R. C. Chambers and E. A. Trippel), Chapman & Hall, London, pp. 173-196.

Koutsikopoulos C., Beillois P., Leroy N., Taillefer F., 1998. Temporal trends and spatial structures of the sea surface temperature in the Bay of Biscay. Oceanol. Acta 21, 335-344.

Legett W., Frank K., 1997. A comparative analysis of recruitment variability in North Atlantic flatfishes - testing the species range hypothesis. J. Sea Res. 37, 281-299.

Lekve K., Ottersen G., Stenseth N.C., Gjosaetter J., 2002. Length dynamics in juvenile coastal Skagerrak cod: effects of biotic and abiotic processes. Ecology 86, 1676-1688.

Le Pape O., Holley J.F., Guérault D., Désaunay Y., 2003. Coastal and estuarine essential fish habitat quality. Estimations based on the size of juvenile common sole (Solea solea L.). Estuar. Coast. Shelf Sci. 58, 793-803.

Levin P.S., Stunz G.W., 2005. Habitat triage for exploited fishes: can we identify essential fish habitat? Estuar. Coast. Shelf Sci. 64, 70-78.

Miller T.J., Crowder L. B., Rice J. A., Marshall E.A., 1988. Larval size and recruitment mechanisms in fishes: Toward a conceptual framework. Can. J. Fish. Aquat. Sci. 45, 1657-1667.

Miller J.M., Burke J. S. Fitzburgh, G. R., 1991. Early life history patterns of Atlantic North American flatfish: likely and unlikely factors controlling recruitment. Neth. J. Sea Res. 27, 261-275.

Mountain, D.G., 2002. Potential consequences of climate change for the fish resources in the Mid'Atlantic region. Amer. Fish. Soc. Symp. 32, 185-195.

Munday P., Jones G.P., Pratchett M.S., Williams A.J., 2008. Climate change and the future for coral reef fishes. Fish Fisher. 9, 261-285.

Nash R.D.M., Geffen A.J., 2000. The influence of nursery grounds processes in the determination of year-class strength in juvenile plaice Pleuronectes platessa L. in Port Erin Bay, Irish Sea. J. Sea Res. 44, 101-110.

Pauly D., 1994. A framework for latitudinal comparisons of flatfish recruitment. Neth. J. Sea Res. 32, 107-118.

Pauly D., Christensen V., Dalsgaard J., Froese R., Torres F., (1998). Fishing down marine fod webs. Science 279, 860-863.

Pennington M.R., Grosslein M.D., 1977. Accuracy of abundance indices based on stratified random trawl surveys. Internat. Comm.. North Atlant. Fisher. Res. Doc. 78/VI/77, 1-41.

Perry A.L., Paula J.L., Ellis J.R., Reynolds J.D., 2005. Climate change and distribution shifts in marine fishes. Science 308, 1912-1915.

Philippart C.J.M., Henderson P.A., Johannessen T., Rijnsdorp A.D., Rogers S.I., 1998. Latitudinal variation in fish recruits in Northwest Europe. J. Sea Res. 39, 69-77.

Planque B., Beillois P., Jégou A.M., Lazure P., Petitgas P., Puillat I., 2003. Large-scale hydroclimatic variability in the Bay of Biscay: the 1990s in the context of interdecadal changes. ICES Mar. Sci. Symp. 219, 61-70.

Planque B., Fredou T., 1999. Temperature and the recruitment of Atlantic cod (Gadus morhua). Can. J. Fisher. Aquat. Sci. 56, 2069-2077

Poulard J.C., Blanchard F., 2005. The impact of climate change on the fish community structure of the eastern continental shelf on the Bay of Biscay. ICES J. Mar. Sci. 62, 1436-1443.

Poulard J.C., Trenkel V., 2007. Do survey design and wind conditions influence survey indices ? Can. J. Fish. Aquat. Sci. 64, 1551-1562

Pyper B.J., Peterman R.M., 1998. Comparison of methods to account for autocorrelation analyses of fish data. Can. J. Fish. Aquat. Sci. 55, 2127-2140.

Quéro J.C., Cendrero O., 1996. Incidence de la pêche sur la biodiversité ichtyologique marine : le bassin d'Arcachon et le plateau continental sud Gascogne. Cybium 20, 323-356.

Quéro J.C., Vayne J.J., 1997. Les poissons de mer des pêches françaises : identification, inventaire et répartition de 209 espèces. 1ère édition, Delachaud et Niestlé SA, Lausanne – Paris, 304 pp.

Quéro J.C., Du Buit M.H., Vayne J.J., 1998. Les observations de poissons tropicaux et le réchauffement climatique des eaux dans l'Atlantique européen. Oceanol. Acta 21 (2), 345-351.

Rayner N.A., Parker D.E., Horton E.B., Folland C.K., Alexander L.V., Rowell D.P., Kent E.C., Kaplan A., 2003. Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. J Geophys. Res. 108, 4407, doi:10.1029/2002JD002670.

Richardson A.J., Schoeman D.S., 2004. Climate impact on plankton ecosystems in the North East Atlantic. Science 305, 1609-1612.

Rose G.A., 2005. On distributional responses of North Atlantic fish to climate change. ICES J. Mar. Sci. 62, 1360-1374.

Souissi S., Ibanez F., Ben Hamadou R., Boucher J., Cathelineau A. C., Blanchard F., Poulard J.C., 2001. A new multivariate mapping method for studying species assemblages and their habitats: example using bottom trawl surveys in the Bay of Biscay (France). Sarsia 86, 527-542.

Stebbing A.R.D., Turk S.M.T., Wheeler A, Clarke K.R., 2002. Immigration of southern fish species to south-west England linked to warming of the North Atlantic (1960-2001). J. Mar. Biol. Assoc. U.K. 82, 177-180.

Sundermann J., Beddig S., Huthnance J., Mooers C.N.K., 2001. Impact of climate change on the coastal zone: discussion and conclusions. Clim. Res. 18, 1-3.

Suthers I.M., 1998. Bigger? Fatter? Or is faster growth better? Considerations on condition in larval and juvenile coral-reef fish. Austr. J. Ecol. 23, 265-273.

Teal L.R., de Leeuw J.L., van der Veer H.W., Rijnsdorp A.D., 2008. Effects of climate change on growth of 0-group sole and plaice. Mar. Ecol. Progr. Ser. 358, 219-230.

Tresher R.E., Koslow J.A., Smith D.C., 2007. Depth mediated reversal of the effects of climate change on long term growth rates of exploited marine fish. Proc. Nat. Acad. Sci. U.S.A.. 104, 7461-7465.

Van der Land M.A., 1991. Distribution of flatfish eggs in the 1989 egg surveys in the southeastern North Sea, and mortality of plaice and sole eggs. Neth. J. Sea Res. 27, 277-286.

Van der Veer H.W., 1986. Immigration, settlement and density-dependent mortality of a larval and early post-larval 0-group plaice (Pleuronectes platessa) population in the western Dutch Wadden Sea. Mar. Ecol. Prog. Ser. 29, 223-236.

Van der Veer H.W., Berghahn R., Miller J.M., Rijnsdorp A.D., 2000. Recruitment in flatfish, with special emphasis on North Atlantic species: Progress made by the flatfish symposia. ICES J. Mar. Sci. 57, 202-215.

Van der Veer, H.W., Kooijman, S., van der Meer, J., 2003. Body size scaling relationships in flatfish as predicted by Dynamic Energy Budgets (DEB theory): implications for recruitment. J. Sea Res. 50, 255-270.

Wheeler A., 1969. The fishes of the British Isles and North-West Europe. MacMillan eds. 613 pp.

Wheeler A., 1978. Key to the fishes of northern Europe. Frederick Warne, London, 380 pp.

Wood R., Boesch D., Kennedy V., 2002. Future consequences of climate change for the Chesapeake bay ecosystem and its fisheries. Amer. Fish. Soc. Symp. 32, 171-184.

Yamashita, Y., Tanaka, M., Miller, J. M., 2001. Ecophysiology of juvenile flatfish in nursery grounds. J. Sea Res. 45, 205-218.

Figures

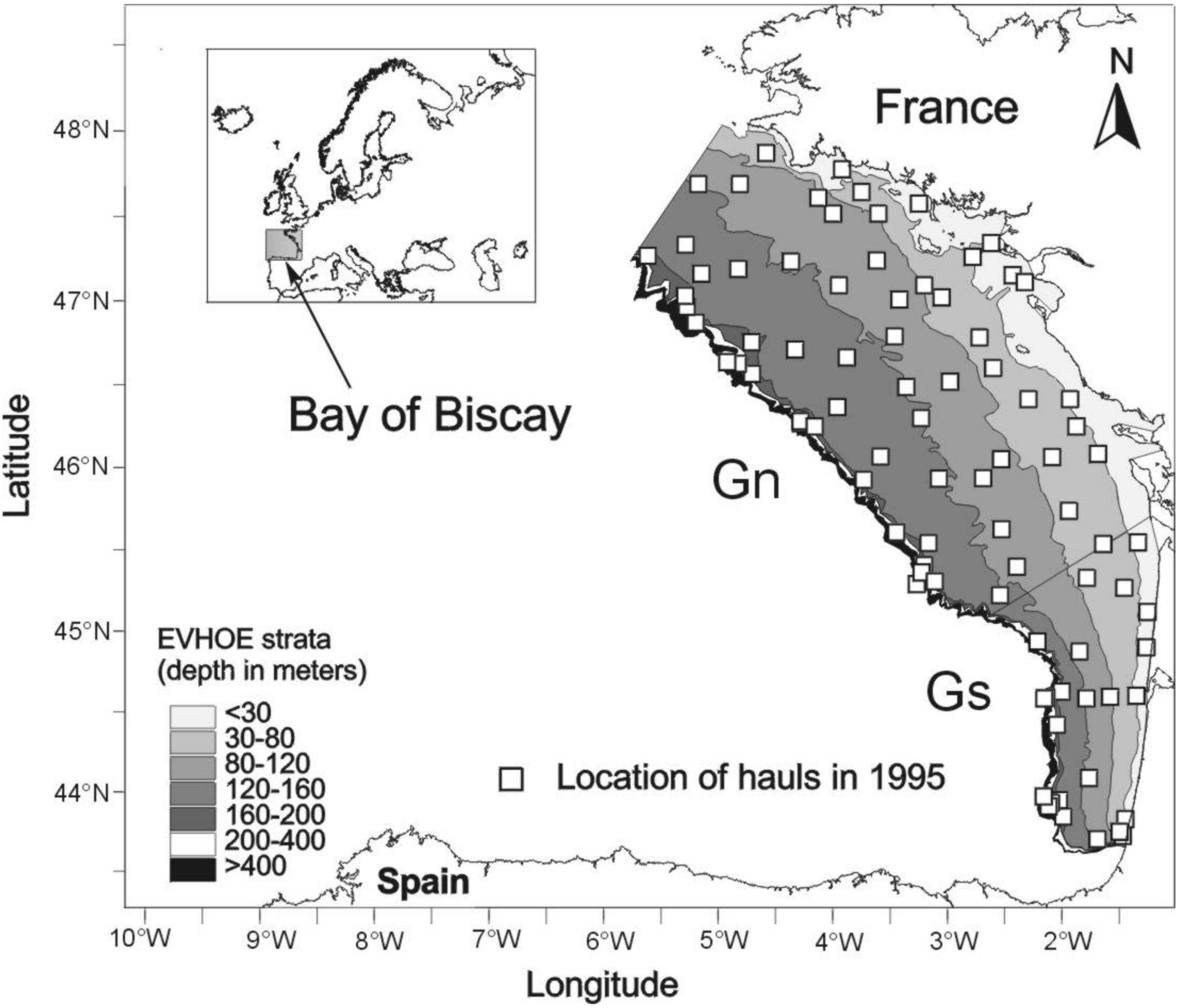

Figure 1: Map of the Bay of Biscay, with its location in Europe in the upper left corner, showing the area sampled during the 17 groundfish surveys carried out by Ifremer from September to December since 1987, with the sampling design of 1995, given as example. The sampling scheme was stratified according to latitude (Gn, for North, and Gs, for South) and depth.

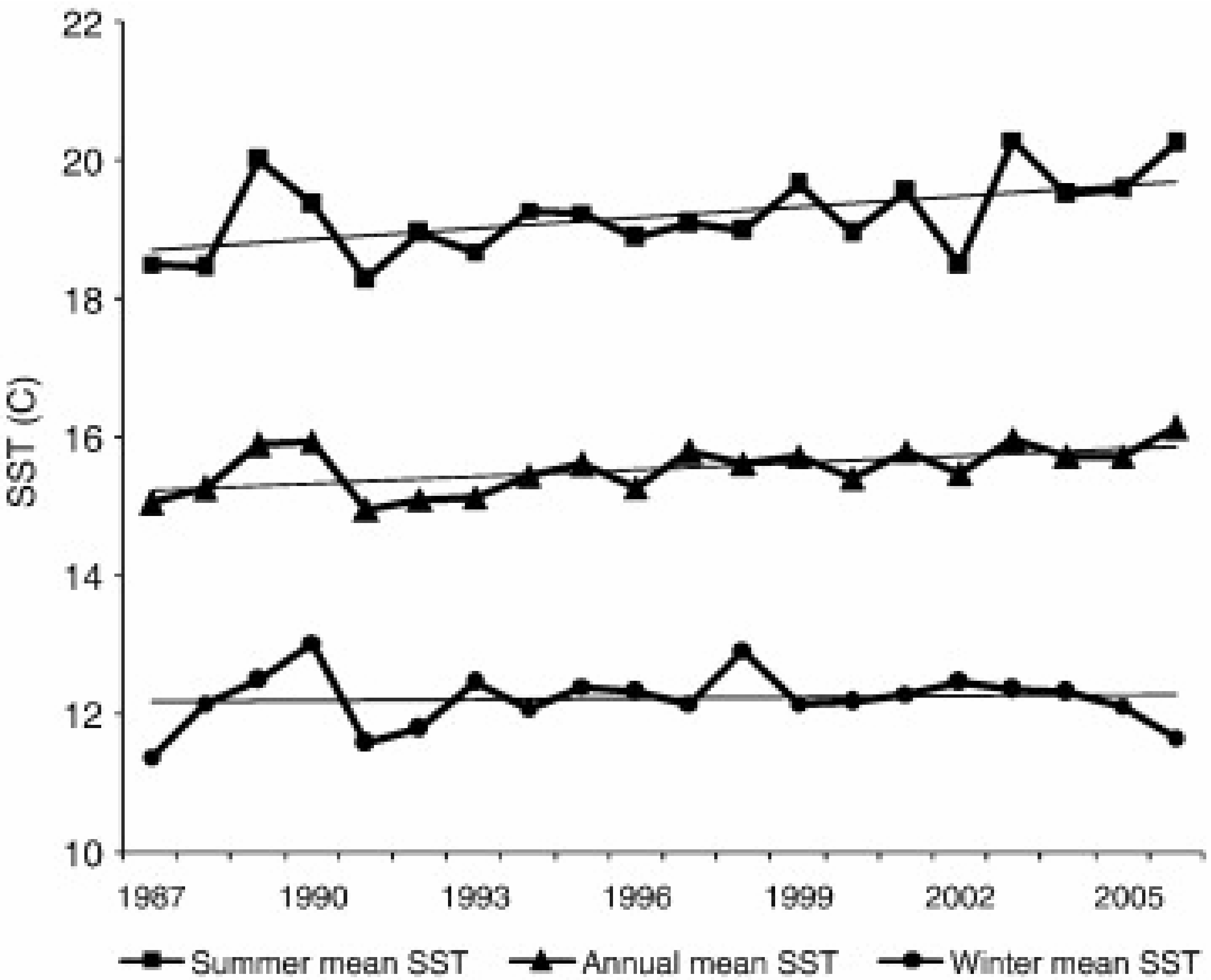

Figure 2: Time series of the see surface temperature in the Bay of Biscay for four flatfish species in the Bay of Biscay since 1987.

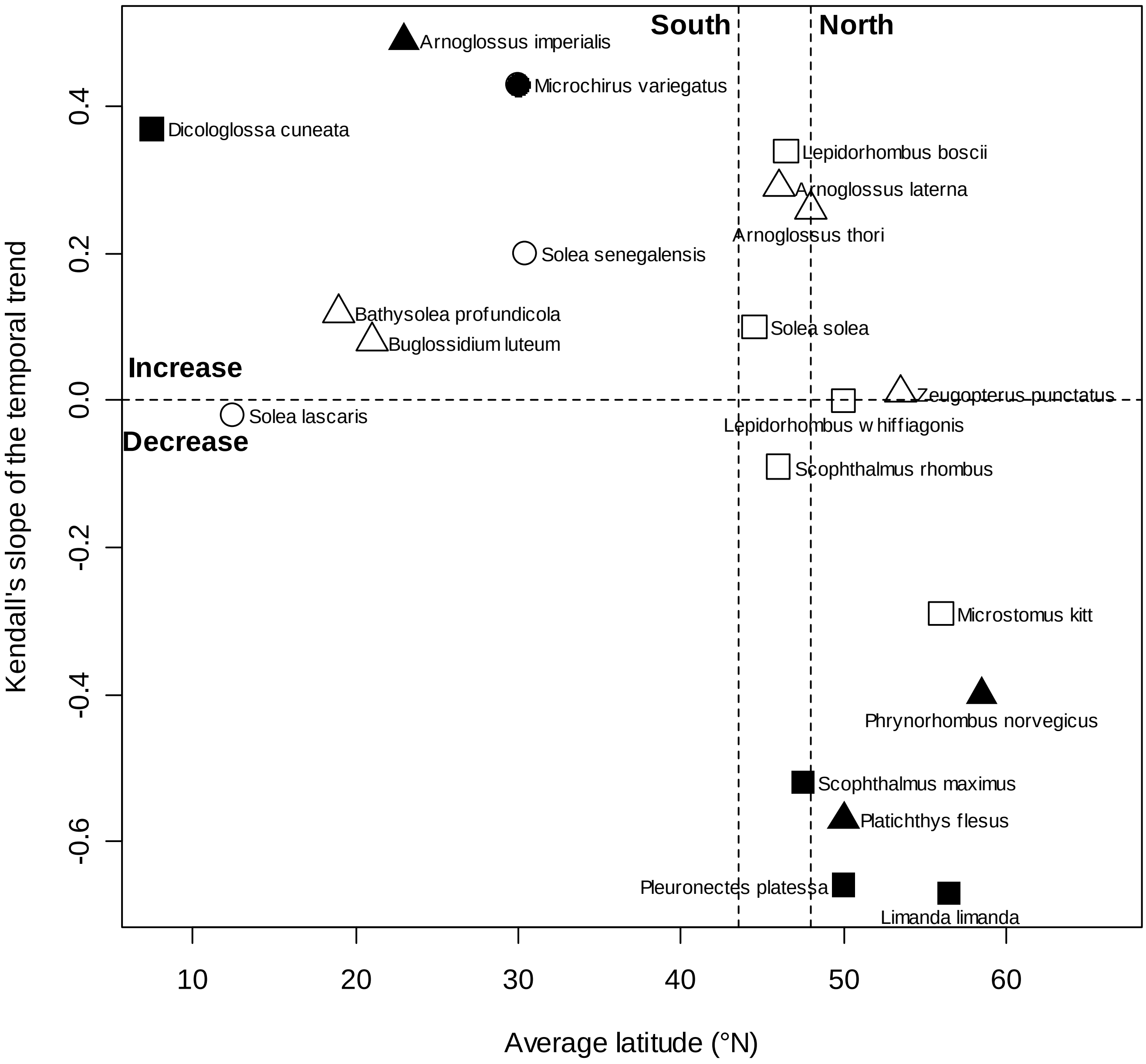

Figure 3: Relation between the Kendall's slope of the temporal trend in fish densities since 1987 and the mean latitudinal range for the 20 flatfish species caught in the Bay of Biscay. Horizontal dotted line: limit between negative and positive temporal trend; vertical lines: southern and northern limits of the Bay of Biscay. Species are identified with symbols related to their level of exploitation: triangle: not commercial, circle: occasional, square: targeted. Filled symbol correspond to significant slopes.

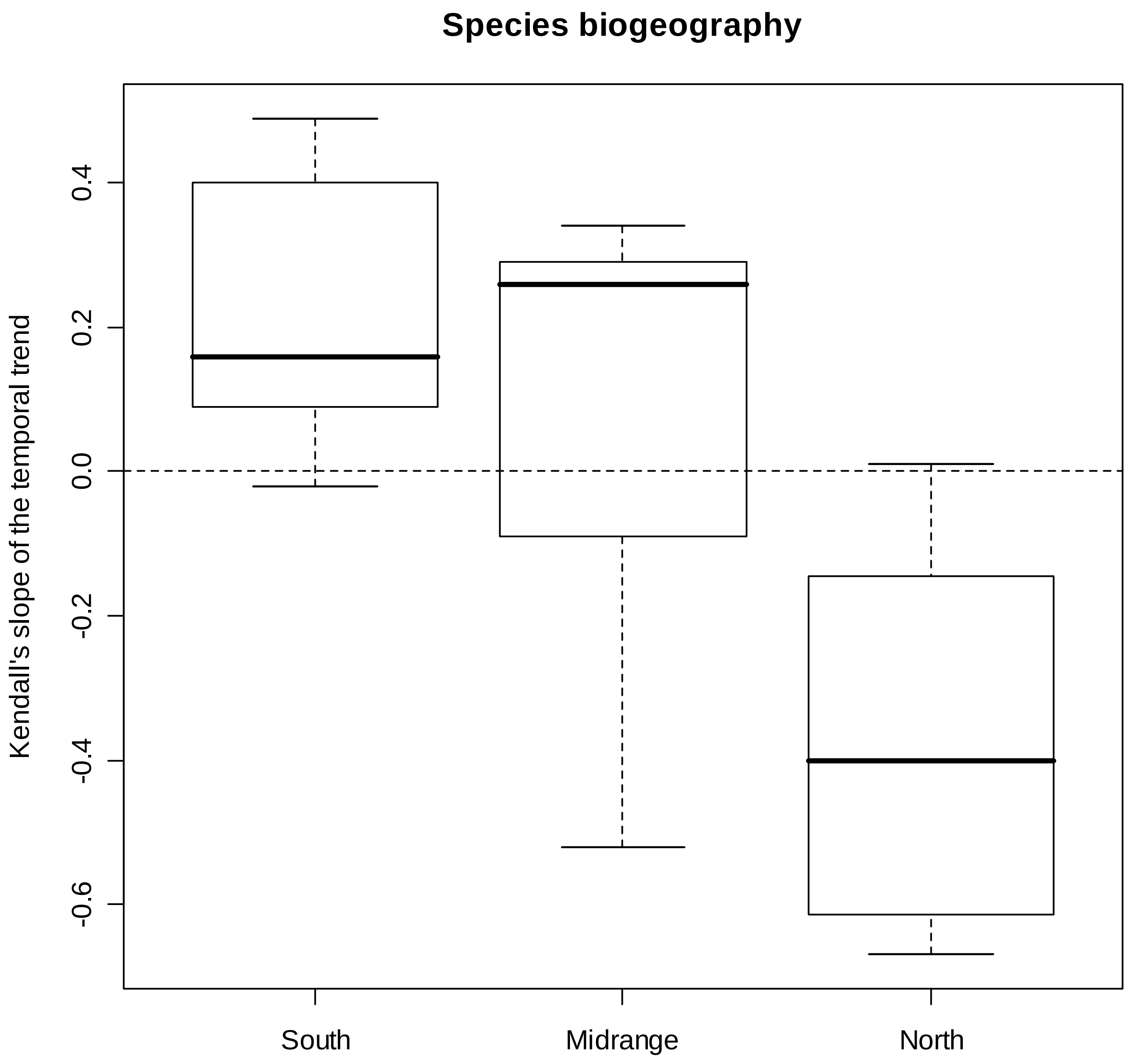

Figure 4: Boxplots of the distribution of the Kendall's slopes of the temporal trend in fish densities since 1987 for the three groups of flatfish species (southern, centred in the Bay of Biscay, northern).

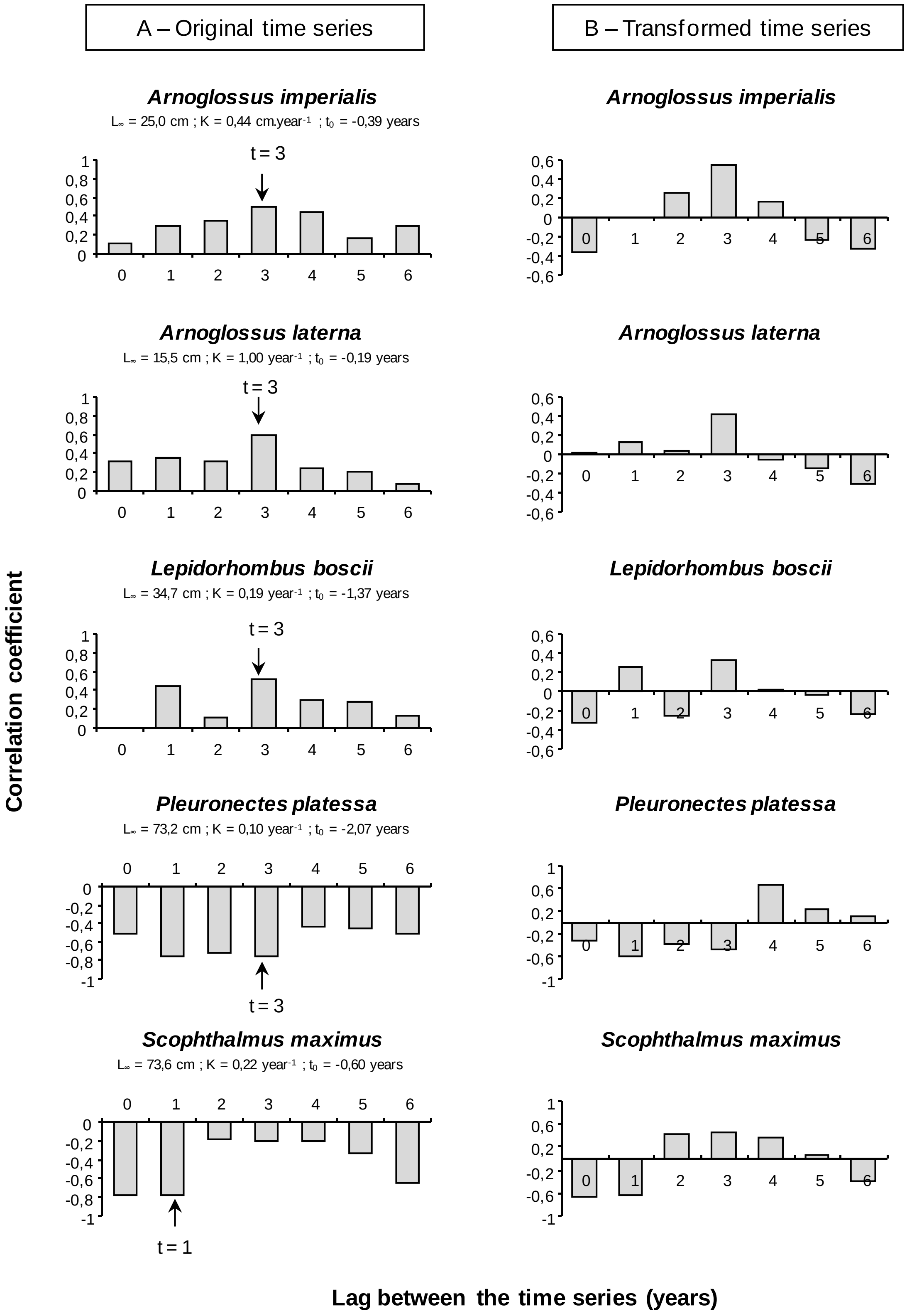

Figure 5: Coefficients of the linear correlation between mean annual SST and flatfish abundances with a lag from 0 to 6 years between the two time series, using (A) original data and (B) transformed data (after removing trends and autocorrelation). t is the mean age of the populations (expressed in years). Parameters of the Von Bertalanffy growth equation used to calculate this mean age are indicated for each species on part A.

Tables

Table 1: Northern and southern limits of geographic distribution, mean latitude, latitudinal position with regard to the Bay of Biscay and exploitation level of the 20 caught flatfish species

Species	Common name	Limits of distribution	Mean latitudinal range	Range classification for the Bay of Biscay	Exploitation level
Arnoglossus imperialis (Rafinesque, 1810)	Imperial scaldfish	58°N – 12°S	23°N	Southern species	Not commercial
Arnoglossus laterna (Walbaum, 1792)	Scaldfish	62°N – 30°N	46°N	Midrange species	Not commercial
Arnoglossus thori Kyle, 1913	Thor's scaldfish	54°N – 42°N	48°N	Midrange species	Not commercial
Bathysolea profundicola (Vaillant, 1888)	Deepwater sole	55°N – 17°S	19°N	Southern species	Not commercial
Buglossidium luteum (Risso, 1810)	Solenette	59°N – 17°S	21°N	Southern species	Not commercial
Dicologlossa cuneata (Moreau, 1881)	Wedge sole	47°N – 32°S	7.5°N	Southern species	Targeted
Lepidorhombus boscii (Risso, 1810)	Fourspot megrim	62°N – 31°N	46.5°N	Midrange species	Targeted
Lepidorhombus whiffiagonis (Walbaum, 1792)	Megrim	66°N – 34°N	50°N	Northern species	Targeted
Limanda limanda (Linnaeus, 1758)	Dab	71°N – 42°N	56.5°N	Northern species	Targeted
Microchirus variegatus (Donovan, 1808)	Thickback sole	58°N – 2°N	30°N	Southern species	Occasional
Microstomus kitt (Walbaum, 1792)	Lemon sole	70°N – 42°N	56°N	Northern species	Targeted
Phrynorhombus norvegicus (Günther, 1862)	Norwegian topknot	70°N – 47°N	58.5°N	Northern species	Not commercial
Platichthys flesus (Linnaeus, 1758)	Flounder	70°N – 30°N	50°N	Northern species	Not commercial
Pleuronectes platessa Linnaeus, 1758	Plaice	70°N – 30°N	50°N	Northern species	Targeted
Scophthalmus maximus (Linnaeus, 1758)	Turbot	65°N – 30°N	47.5°N	Midrange species	Targeted
Scophthalmus rhombus (Linnaeus, 1758)	Brill	62°N – 30°N	46°N	Midrange species	Targeted
Solea lascaris (Risso, 1810)	Sand sole	58°N – 33°S	12.5°N	Southern species	Occasional
Solea senegalensis Kaup, 1858	Senegalese sole	47°N – 14°N	30.5°N	Southern species	Occasional
Solea solea (Linnaeus, 1758)	Common sole	62°N – 27°N	44.5°N	Midrange species	Targeted
Zeugopterus punctatus (Bloch, 1787)	Topknot	64°N – 43°N	53.5°N	Northern species	Not commercial

Table 2: Coefficient and significance (ns: non significant; P > 5%) of the Kendall correlation between the year and the annual, winter and summer mean SST in the Bay of Biscay over the whole time series (1960-2006) and over the period covering the study (1987-2006).

	r	P (in %)
1960-2006		
Annual SST	0.38	< 0.1
Winter SST	0.22	2
Summer SST	0.42	< 0.1
1987-2006		
Annual SST	0.44	< 1
Winter SST	0.03	ns
Summer SST	0.51	2

Table 3: Trends in abundance and occurrence for the twenty flatfish species sampled over the continental shelf of the Bay of Biscay during the seventeen surveys conducted from 1987 to 2006. r: coefficient of the Kendall correlation between the year and the abundance, a: coefficient of the logistic regression between the year and the occurrence. P: significance in % (ns: unsignificant; P > 5%). Species are classified as northern, southern or midrange species for the Bay of Biscay according to their mean latitudinal range.

Species	**Abundance**		**Occurrence**	
	r	**P (in %)**	**a**	**P (in %)**
Northern species				
Phrynorhombus norvegicus	-0.40	3	-0.05	ns
Limanda limanda	-0.67	< 0.1	-0.25	< 0.1
Microstomus kitt	-0.29	ns	-0.01	ns
Zeugopterus punctatus	0.01	ns	0.03	ns
Lepidorhombus whiffiagonis	0.00	ns	-0.01	ns
Platichthys flesus	-0.57	< 1	-0.23	< 0.1
Pleuronectes platessa	-0.66	< 0.1	-0.17	< 0.1
Midrange species				
Arnoglossus thori	0.26	ns	0.11	ns
Scophthalmus maximus	-0.52	< 1	-0.06	ns
Lepidorhombus boscii	0.34	ns	0.02	ns
Arnoglossus laterna	0.29	ns	0.06	< 0.1
Scophthalmus rhombus	-0.09	ns	-0.07	ns
Solea solea	0.10	ns	0.01	ns
Southern species				
Solea senegalensis	0.20	ns	0.20	ns
Microchirus variegatus	0.43	2	0.09	< 0.1
Arnoglossus imperialis	0.49	< 1	0.08	< 0.1
Bathysolea profundicola	0.12	ns	0.09	< 1
Buglossidium luteum	0.08	ns	0.04	1
Solea lascaris	-0.02	ns	0.03	ns
Dicologlossa cuneata	0.37	4	0.04	< 1