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Latitudinal comparison of spawning season and growth of 0-group sole, *Solea solea* (L.)

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Received 14 October 2007; accepted 23 January 2008

Available online 2 February 2008

Abstract

0-Group sole, *Solea solea* (Linnaeus, 1758) were sampled in four nursery grounds: two on the Northern French coast and two on the Portuguese coast. Juvenile sole were collected at the Vilaine estuary (Northern Bay of Biscay) in 1992, in the Authie estuary (Eastern English Channel) in 1997, and in the Douro and Tagus estuary (Northern and central Portugal, respectively) in 2005. Left lapilli otoliths were used to estimate age and investigate variability in growth rates and hatch dates. In the French study areas nursery colonisation ended in early June in the Vilaine estuary and in late June in the Authie estuary. In the Portuguese estuaries nursery colonisation ended in May in the Douro estuary and in late June in the Tagus estuary. Growth rates were higher in the Portuguese estuaries, 0.767 mm d^{-1} in the Tagus estuary and 0.903 mm d^{-1} in the Douro estuary. In the French nurseries, growth rates were estimated to be 0.473 mm d^{-1} in the Villaine estuary and 0.460 mm d^{-1} in the Authie estuary. Data on growth rates from other studies shows that growth rates are higher at lower latitudes, probably due to higher water temperature. Spawning took place between early January and early April in the Villaine estuary's coastal area in 1992. In 1997, in the Authie estuary spawning started in late January and ended in early April. On the Douro estuary's adjacent coast spawning started in mid-January and ended in late March, in 2005, while on the Tagus estuary's adjacent coast spawning started in mid-February and ended in mid-April, in the same year. Literature analysis of the spawning period of sole along a latitudinal gradient ranging from 38°N to 55°N in the Northeast Atlantic indicated that there is a latitudinal trend, in that spawning starts sooner at lower latitudes. Results support that local conditions, particularly hydrodynamics, may overrule general latitudinal trends.

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Keywords: latitudinal variations; growth; spawning; *Solea solea*; nursery grounds; northeast Atlantic

1. Introduction

Determination of spawning period and 0-group juveniles' growth in fish is very important for the study of fish recruitment. Temporal changes in spawning can contribute to variations in year-class strength by influencing the spatial and temporal coexistence of larvae, prey availability, predator abundance, and favourable environmental conditions (Houde, 1987). Growth during the first months of life is also crucial for fish survival, since faster growth implies improved predator

avoidance and a wider choice in prey (Van der Veer and Bergman, 1987; Ellis and Gibson, 1995; Sogard, 1992, 1997).

However, the study of spawning in fish is generally difficult and time consuming, since it requires previous knowledge of the main spawning areas and several successive egg sampling surveys throughout the spawning period which generally extends over several months. The discovery of daily increments in the otoliths of marine fish (Pannella, 1971) provided a powerful tool to study the early life history of fish. Counts of such increments have been used to examine temporal and spatial variability in spawning and growth rates (Method, 1983; Yakovlich and Bailey, 1990). Hatch-dates of the young juveniles collected in coastal nursery grounds at the end of the settlement period can thus be back-calculated,

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overcoming the difficulties of traditional successive egg sampling.

The study of fish recruitment requires not only the determination of spawning periods and 0-group juveniles' growth but also the identification of the factors which govern their dynamics. Several studies suggest that the factors controlling recruitment of a species vary over its geographic range, e.g. along a latitudinal gradient (Houde, 1989; Miller et al., 1991; Pauly, 1994).

Gaston (1990) and Miller et al. (1991) developed the latter, called "species range hypotheses" (Leggett and Frank, 1997) which assumes that species differ in their susceptibility to different controls on recruitment due to different life history traits, and that species life history traits vary over their distribution range. Looking at the latitudinal and inshore–offshore variation in food, predation and abiotic factors, these assumptions lead to the following implications: (1) abiotic factors are most important at the edges of the species range; (2) predation plus abiotic factors control recruitment at the polar edge of the range; (3) food plus abiotic factors control recruitment at the equatorial edge. Miller et al. (1991) also predicted that recruitment would be more variable at the polar edge of the species range, least near the centre of the range, and be intermediate near the equatorial edge. However, they pointed out that inshore–offshore environmental gradients may swamp latitudinal effects. Some studies considering a wide spatial scale have found this pattern (e.g. Brunel and Boucher, 2006).

Since then, several studies observed variation patterns that do not correspond to the "species range hypotheses" expectation (Walsh, 1994; Leggett and Frank, 1997; Phillipart et al., 1998). Van der Veer et al. (2000) concluded that the likely trends in food, predation and abiotic factors, on which Miller et al. (1991) based their hypotheses, will probably act only in the juvenile stage, while year-class strength appears to be established already in the pelagic phase (Leggett and Frank, 1997; Van der Veer et al., 2000). The dominance of density independent factors operating at a local scale on the eggs and larvae stresses the importance of hydrodynamic circulation as a key factor in determining recruitment in flatfish (Leggett and Frank, 1997).

The common sole, *Solea solea* (L.), is a flatfish of high commercial importance in Northwest Europe. This species is found in coastal waters of the eastern North Atlantic, from western Scotland and the western Baltic Sea to Southern Western Europe, including the Mediterranean and extending southwards along the African coast as far as Senegal (Whitehead et al., 1986). Sole spawns over winter and spring generally in coastal waters except in the western English Channel (Horwood, 1993) and in the northern Bay of Biscay (Koutsikopoulos and Lacroix, 1992) where the main spawning activity occurs offshore at depths around 50–90 m.

Several studies have assessed the factors affecting recruitment in sole and, although some conclusions may seem contradictory (e.g. Henderson and Holmes, 1991; Rijnsdorp et al., 1992; Henderson and Seaby, 1994), it is generally agreed that recruitment of sole is determined before the end of the first year of life and that water temperature plays an important role (e.g. Rijnsdorp et al., 1992; Van der Veer et al., 2000;

Wegner et al., 2003; Henderson and Seaby, 2005). However, all of these studies were carried out in temperate waters; in fact Van der Veer et al. (1994) concluded that most studies on flatfish recruitment were conducted in temperate systems which may have biased the conclusions. They also referred that recruitment variability increases towards lower latitudes. Due to more prolonged spawning and settlement periods, variability in juvenile size increases and therefore size-selective mortality becomes an important factor. More studies in subtropical and tropical areas are needed for a better understanding of the factors controlling recruitment in flatfish, and sole in particular (Pauly, 1994; Van der Veer et al., 1994). One of the interests of the present study is the comparison of sub-tropical populations with temperate ones.

The main objectives of the present work were to assess geographical differences in (1) timing of spawning and (2) growth rates of *Solea solea* juveniles during their first months following settlement, in the Northeast Atlantic.

2. Materials and methods

2.1. Study areas

Along the French coast the Villaine (in the Northern Bay of Biscay) and Authie (in the eastern English Channel) estuaries (Fig. 1) were chosen for this study because they are located at different latitudes and characterised by two distinct sole populations. In these two areas, sole population dynamics is well documented (e.g. Lagardère, 1987; Koutsikopoulos et al., 1989; Marchand, 1991; Amara et al., 1993, 1994). Climate in these areas is temperate.

Nursery areas studied in Portugal are located on the Portuguese West coast (Fig. 1). The Douro and Tagus estuaries were chosen for this study because they are two of the most important nursery areas for this species at its subtropical range (Cabral et al., 2007) and also because they are located at different latitudes and at a considerable distance (ca. 300 km) (Fig. 1). This is an important distance since this is a biogeographic transition region, so that the north of Portugal has a temperate climate while the centre and South has a subtropical climate. Cabral et al. (2007) have shown that while cold-water fish species are found in the northern estuaries, they are absent from the south and central coasts. While the Douro is a deep and narrow estuary, the Tagus is one of the largest estuaries in Europe (320 km²) and much of its upper area is composed of extensive intertidal mudflats. Climate in this area is Mediterranean with mild winters and warm, dry summers (Aschmann, 1973).

Water temperatures in the adjacent coast of the study areas during a broad period that encompasses the spawning period (in the area between the 50 m and the 100 m bathymetric) were gathered at the World Data Centre for Remote Sensing of the Atmosphere (WDC-RSAT) and consist in Sea Surface Temperature derived from NOAA-AVHRR data. The range of SST values in this database is scaled between 0.125 °C and 31.75 °C (maximum temperature). The radiometric resolution is 0.125 °C. Data from all six of the passes that

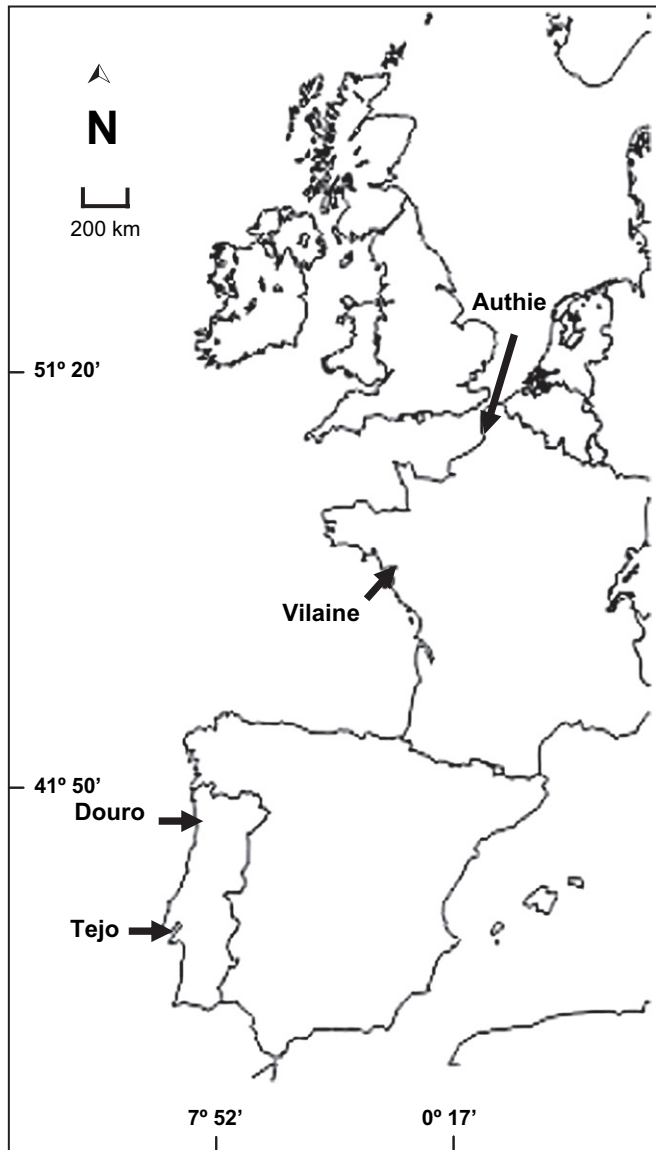


Fig. 1. Map of the western European coast (arrows indicate the study areas).

the satellite makes over Europe in each 24 h period are used. The SST maps are composed according the maximum temperature value given at every pixel's position to minimise cloud coverage. Weekly values were derived from the daily maximum images using the average at every pixel's position.

2.2. Juvenile collections

0-Group sole were collected at the end of the settlement period on four important and geographically distant nursery grounds of the French and Portuguese coasts. Juvenile sole were collected throughout the immigration period (from March to July in the French estuaries and March to September in the Portuguese estuaries) and length frequency distributions were analysed in order to determine the end of estuarine colonisation (which is detected when a normal distribution of length is observed and no new recruits are arriving). The

sampling was carried out in 1992 (Vilaine estuary), 1997 (Authie estuary), while both Portuguese estuaries were surveyed in 2005. 0-Group juveniles collected at the end of the colonisation period was analysed for each study area.

In the Vilaine estuary, estuarine colonisation ended in early June. 0-Group sole were collected from 13 stations on 2 June 1992, with a small sledge (1 m wide by 0.3 m high, 4.1 m length) without tickler chains, fitted with a 5 mm mesh mouth and a 1.5 mm cod end (all stretched) (Marchand and Masson, 1989). The average depth in this area is 6 m at mean tide. In the Authie, estuarine colonisation ended in late June. 0-Group sole were collected from eight stations parallel to the coast (the average depth is 5 m at mean tide) on 24 June. Juveniles were collected with a 3 m beam trawl with one tickler chain and fitted with 14 mm mesh mouth and 6 mm cod end (all stretched). In the Douro estuary, estuarine colonisation ended in May. 0-Group sole were collected at 10 stations on 7 May 2005. Trawls were conducted with a 12 m otter-trawl with 10 mm mesh size (stretched mesh) and a 5 mm cod end (beam-trawling is not possible in the Douro estuary due to its bottom morphology). To ensure that the trawl would not lose contact with the bottom, and thereby maintain a high catching efficiency for flatfish, the ground rope of the trawl was equipped with a heavy metal chain. In the Tagus estuary colonisation ended in late June. 0-Group sole were collected at 10 stations on 27 June 2005. Trawls were conducted with a 2.5 m beam trawl with 10 mm mesh size (stretched mesh) and a 5 mm cod end. Differences in fishing methods are not important, since the aim of the present study was to analyse the populations' structure in terms of age and length and not to directly compare densities.

All samples were preserved in 95% ethanol (in France) or immediately frozen (in Portugal). In the laboratory all sole were counted and total length (TL) measured to the nearest 1 mm.

2.3. Growth and spawning dates estimates

Otoliths of a sub sample of juveniles chosen randomly from each length category (5 mm) were examined. The left lapillus, which has the longest axis due to the bilateral asymmetry between the right and left lapillus, was used for all age estimates. Lapilli otoliths were used because they are relatively thin and have well-defined increments spatially more uniform than in sagittae otoliths, which have accessory primordia (Amara et al., 1994). The lapilli were removed from the cranium, cleaned and mounted with cyanoacrylate glue on microscope slides. They were polished in the sagittal plane to the central primordia, with a polishing bar (aluminium oxide). All increment counts were made using a light microscope at $\times 400$ or $\times 1000$ magnification. Otolith increments were counted three times, and the age was regarded as the mean of the three counts. Age was determined as described by Amara et al. (1994).

Growth was described by a linear model. An analysis of covariance (ANCOVA) was done to test among geographic area differences in growth (slope of age against length) over the first months of the juvenile life.

Spawning dates were estimated from age and date of capture. Duration of the embryonic period was calculated based on Fonds (1979) equation, according to the water temperature. Length–frequency distributions were converted to age using separate age–length keys developed from sub-samples of fish for each of the four areas. Spawning periods along a latitudinal gradient in the Northeast Atlantic were compared based on the present work and published literature.

3. Results

On the French coast, coastal waters were warmer in the Vilaine than in waters adjacent to the Authie estuary (Fig. 2). However, the temperatures were lower and less stable compared to those recorded on the Portuguese coast, particularly in the winter months. Waters adjacent to the Tagus estuary were always warmer than those adjacent to the Douro estuary (Fig. 3). The mean water temperature from September to July is 9.59 °C in the Authie estuary, 10.33 °C in the Vilaine estuary, 14.73 °C in the Douro estuary and 15.72 °C in the Tagus estuary.

Length–frequency distribution of 0-group sole at the end of the colonisation period showed a normal distribution fit in all nurseries studied (Fig. 4), although in Fig 4c a lack of normality related to the absence of individuals from the larger classes was observed (this was probably due to mortality caused by adverse environmental conditions that affected this size classes). Growth during the first months following settlement was best described by a linear model (Fig. 5). In the Vilaine estuary, growth rates of 0-group juveniles were estimated to be 0.473 mm d⁻¹ (range of total length of individuals analysed, TL: 20–66 mm; $n = 198$) in 1992, while in the Authie estuary growth rate was estimated to be 0.460 mm d⁻¹ (TL: 19–65 mm; $n = 226$) in 1997. In the Douro estuary, 0-group juveniles growth rate was estimated to be 0.903 mm d⁻¹ (range of total length of individuals analysed, TL: 31–91 mm; $n = 60$) in 2005, while in the Tagus estuary 0-group

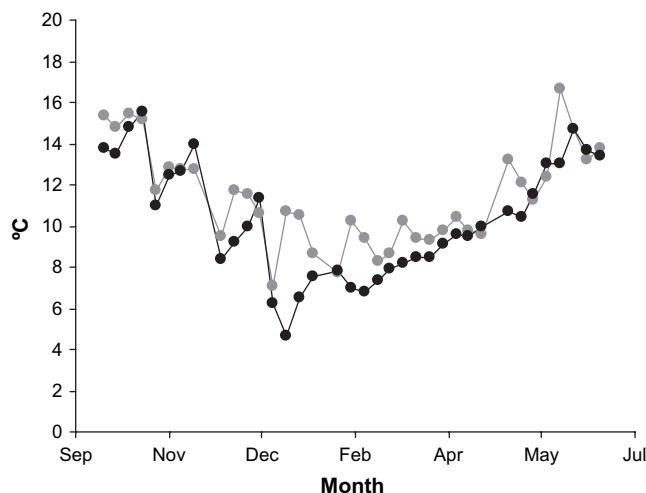


Fig. 2. Surface sea water temperatures in the study areas of France. Authie estuary data (1996–1997) presented in black, Vilaine coastal area data (1991–1992) presented in grey.

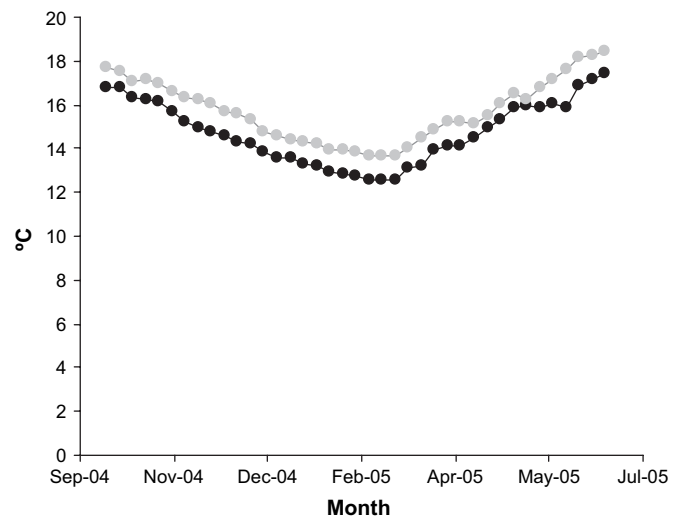


Fig. 3. Surface sea water temperatures in the study areas of Portugal. Douro estuary's adjacent coastal area data presented in black, Tagus estuary's adjacent coastal area data presented in grey.

juveniles growth rate was estimated to be 0.767 mm d⁻¹ (range of total length of individuals analysed, TL: 57–109 mm; $n = 215$) in 2005. Significant differences were found in the growth rates between all sites analysed ($P < 0.05$).

The analysis of *Solea solea* spawning period at different latitudes based on the present study and published literature shows a latitudinal trend in spawning dates, with spawning starting earlier at lower latitudes (Fig. 6). Both French estuaries followed this trend. In the Vilaine estuary hatch dates indicated earlier spawning, from December (3 December) to early April (5 April), than in the Authie, from late January (28 January) to mid-April (15 April). In the Douro estuary spawning started in mid-January (23 January) and ended in late March (30 March) in 2005, while in the Tagus estuary spawning started in mid-February (12 February) and ended in mid-April (21 April), in the same year. The Portuguese estuaries agree with the latitudinal trend when compared to the higher latitudes but not when compared to the French estuaries.

4. Discussion

4.1. Comparison of spawning periods

Results from the present study and literature analysis on the *Solea solea* spawning period at different latitudes indicates that there is a latitudinal trend, in that spawning starts sooner at lower latitudes (Fig 6).

Warmer water temperatures during the winter at lower latitudes are expected to have a strong influence on the onset of spawning in fish, leading to earlier colonisation of nursery grounds (Amara et al., 1994, 2000). Along with temperature, photoperiod can also be an important spawning triggering factor, as suggested by Devauchelle et al. (1987).

The French estuaries agree with this trend when compared to the higher latitudes, yet the Portuguese estuaries seem to

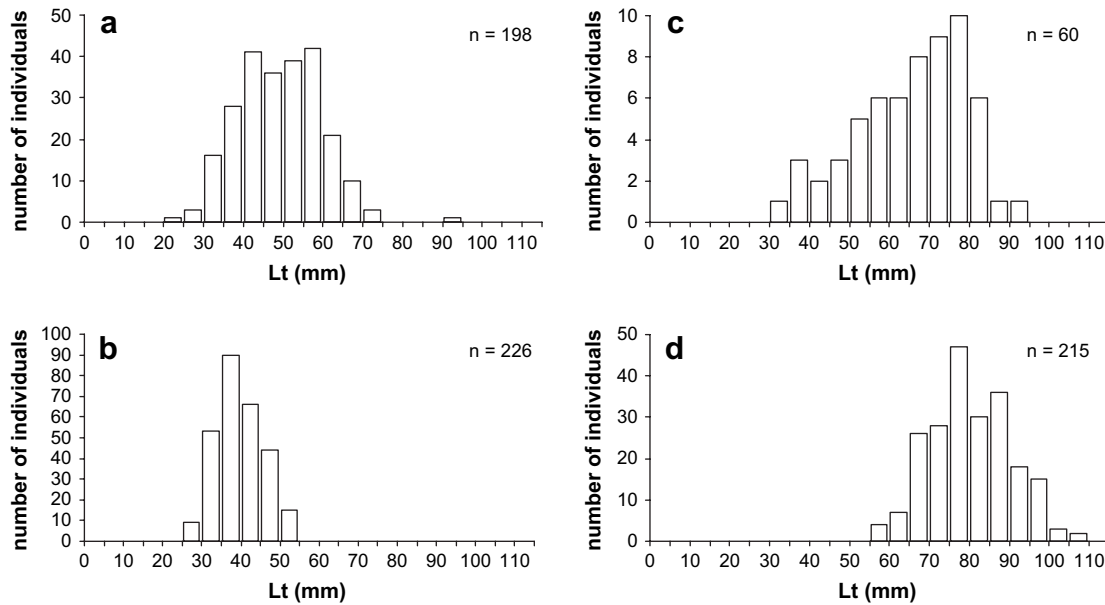


Fig. 4. Length frequency of 0-group juvenile *Solea solea* in each study area. (a) Vilaine estuary 1992; (b) Authie estuary 1997; (c) Douro estuary 2005; (d) Tagus estuary 2005.

be slightly out of trend. More information about the population dynamics of *Solea solea* at these latitudes would be needed in order to fully understand the observed results, yet some considerations may be done. In the case of the Portuguese coast special attention should be paid to the local hydrodynamics, due to the occurrence of coastal upwelling of cold water.

Northerly trade winds created by a latitudinal displacement of the Azores anticyclone favour offshore Ekman transport of surface water (Wooster et al., 1976; Peliz et al., 2002). Although upwelling is more frequent between March and September, it is

generally considered that winds that favour this phenomena are a recurrent feature of the Portuguese coast (Huthnance et al., 2002). Offshore Ekman transport of surface water will likely direct the eggs and larvae of flatfish away from the coastal nurseries, resulting in high mortality rates that will confound analysis and spawning season estimation based on otolith readings from the survivors.

Results from the Portuguese nurseries support that local conditions, particularly hydrodynamics, may overrule general latitudinal trends, as suggested by Leggett and Frank (1997) and Van der Veer et al. (2000).

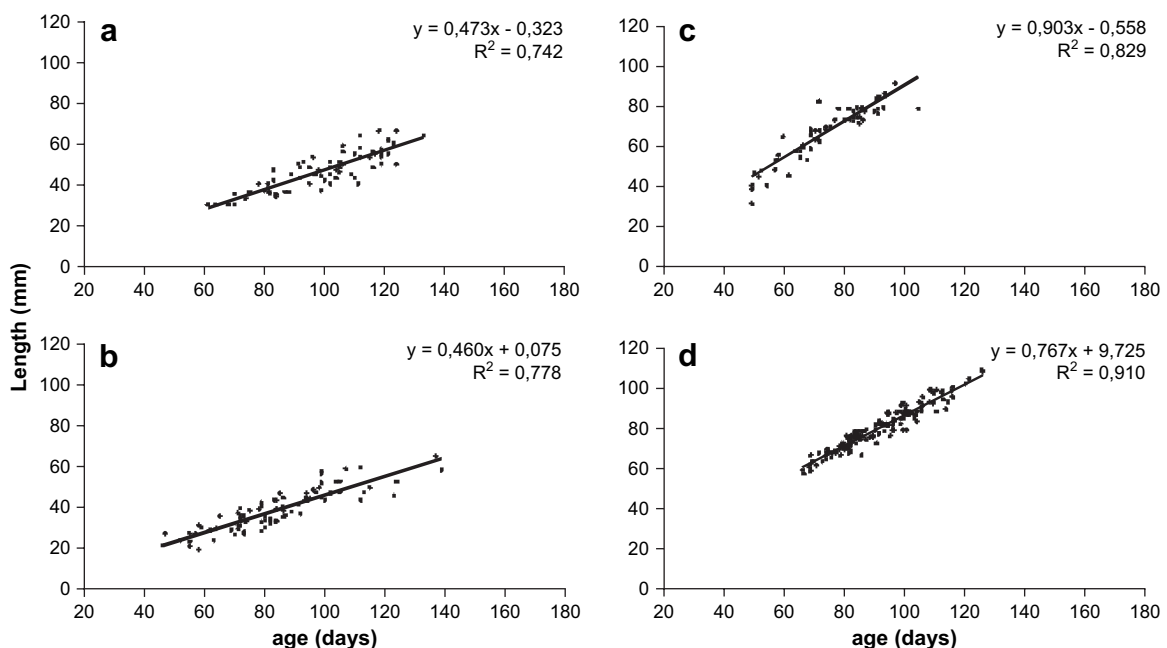


Fig. 5. Linear regression of size versus age in each study area. (a) Vilaine estuary 1992; (b) Authie estuary 1997; (c) Douro estuary 2005; (d) Tagus estuary 2005.

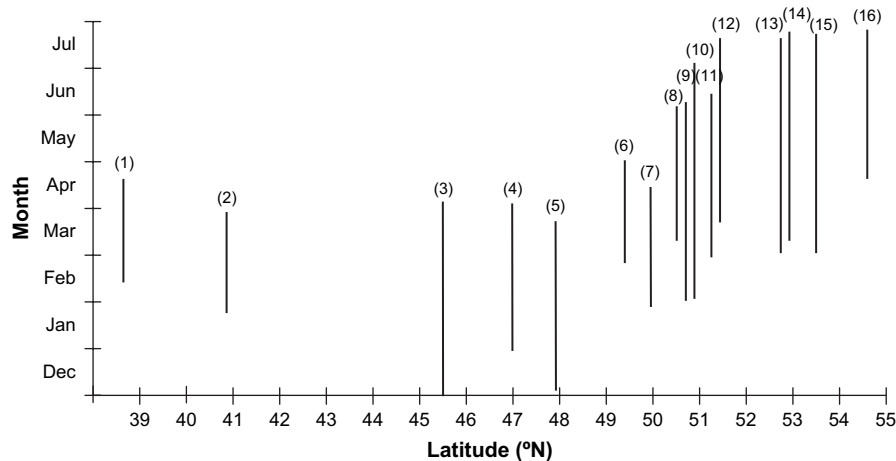


Fig. 6. *Solea solea* spawning period at different latitudes based on the present study (1, Tagus estuary; 2, Douro estuary; 4, Vilaine estuary; 7, Authie estuary) and published literature [Le Bec, 1983 (3), Deniel, 1984 (5), ICES, 1992 (6, 8, 11, 12, 13, 14, 15, 16), Horwood, 1993 (9), Woerling and Le Fevre Lehoerff, 1993 (10)].

4.2. Comparison of growth rates

Significant growth variations were observed between the two French nursery grounds studied due probably to the different temperature exposure histories (Fig. 2). In the Vilaine and Authie estuaries growth rate estimates were in the range of those recorded for other northern European juvenile sole populations (e.g. Rogers, 1994; Pihl, 1989; Amara et al., 2001). When fed ad libitum in hatchery on-growing systems, reared juvenile sole growth rates may vary from 0.5 to 1.5 mm d⁻¹ (Van der Veer et al., 2001) to 0.66 mm d⁻¹ (Ramos and Rouros, 1985). *Solea solea* growth rates were significantly higher in both Portuguese estuaries studied, when compared to the French nurseries. This was expected since temperature is generally considered the most important factor affecting growth and ocean water temperatures are higher at this latitude, throughout the year (despite cold water upwelling) and temperatures inside the estuarine nurseries are considerably higher than in the coast during the nursery period. The longer photoperiod may also contribute to this result. The Tagus estuary did not fully comply with the latitudinal trend. Although growth rate in this estuary was considerably higher than in France, it was also lower than that found in the Douro, a more northerly estuary. As already mentioned, more information on the population dynamics of *S. solea* at this latitude would be needed in order to fully understand the observed results, yet some considerations may be put forward.

Solea solea may be facing thermal stress in the Tagus estuary, since water temperature in the nursery grounds largely exceeds its metabolic optimum temperature, which is estimated to be 18.8 °C (LeFrançois and Claireaux, 2003). Energy spent on facing adverse conditions will be diverted from growth, thus hindering growth rates. Another important aspect that may affect fish growth is pollution. Heavy metal contamination is much higher in the Tagus than in the Douro, due to higher concentration of polluting industries and human pressure (Vinagre et al., 2004; França et al., 2005). Since the *S. solea* nursery in the Tagus is located in one of the most polluted areas of the estuary, pollution may be hindering sole juveniles' growth.

Solea solea growth has already been estimated for the Tagus estuaries by Cabral (2003) in 1995 and 1996 and by Fonseca et al. (2006) in 2003 and 2004, both using length progression analysis. In 1995 estimated growth rate at the first month of nursery residency was 0.70 mm d⁻¹, in 1996 it was 1.51 mm d⁻¹, in 2003 it was 0.80 mm d⁻¹ and in 2004 it was 1.19 mm d⁻¹ (Cabral, 2003; Fonseca et al., 2006). The growth rate determined for 2005 in the present study (0.767 mm d⁻¹) is within the range of estimations obtained in previous years and thus it may be concluded that growth rates are quite variable in this estuarine system.

5. Conclusions

This study shows that although major gradients affect spawning and growth of sole, local conditions may overrule the latitudinal trend. The development of longer data time-series in the southern distribution range of sole is needed in order to fully understand recruitment dynamics of this species.

Further investigation on the role of hydrodynamics in the pelagic stage of flatfish and on the metabolic scope and genetic variation within the *Solea solea* distribution range will certainly provide new insights into the factors controlling recruitment in sole.

Acknowledgements

This study had the support of Fundação para a Ciência e a Tecnologia (FCT) that financed several of the research projects related to this work and the Ph.D grant given to C.V. The authors would like to thank everyone involved in the sampling surveys and Nuno Serra for the help with the SST data.

References

- Amara, R., Lagardère, F., Desaunay, Y., 1993. Seasonal distribution and duration of the planctonic stage of Dover sole, *Solea solea*, larvae in the Bay of Biscay: an hypothesis. *Journal of Fish Biology* 43, 17–30.

- Amara, R., Desaunay, Y., Lagardère, F., 1994. Seasonal variation in growth of larval sole *Solea solea* (L.) and consequences on the success of larval immigration. *Netherlands Journal of Sea Research* 32, 287–298.
- Amara, R., Lagardère, F., Desaunay, Y., Marchand, J., 2000. Metamorphosis and estuarine colonisation in the common sole, *Solea solea* (L.): implications for recruitment regulation. *Oceanologica Acta* 23, 469–484.
- Amara, R., Laffargue, P., Dewarumez, J.M., Maryniak, C., Lagardère, F., Luczac, C., 2001. Feeding ecology and growth of 0-group flatfish (sole, dab and plaice) on a nursery ground (Southern Bight of the North Sea). *Journal of Fish Biology* 58, 788–803.
- Aschmann, H., 1973. Distribution and peculiarity of Mediterranean ecosystems. Origins and structure. In: Castri, F., Mooney, H.A. (Eds.), *Ecological Studies* 7. Springer, Berlin, pp. 11–19.
- Brunel, T., Boucher, J., 2006. Pattern of recruitment variability in the geographical range of the exploited northeast Atlantic fish species. *Journal of Sea Research* 55, 156–168.
- Cabral, H.N., 2003. Differences in growth rates of juvenile *Solea solea* and *Solea senegalensis* in the Tagus estuary, Portugal. *Journal of the Marine Biological Association of the United Kingdom* 83, 861–868.
- Cabral, H., Vasconcelos, R., Vinagre, C., França, S., Fonseca, V., Maia, A., Reis-Santos, P., Lopes, M., Ruano, M., Campos, J., Freitas, V., Santos, P.T., Costa, M.J., 2007. Relative importance of estuarine flatfish nurseries along the Portuguese coast. *Journal of Sea Research* 57, 209–217. doi:10.1016/j.seares.2006.08.007.
- Deniel, C., 1984. La reproduction des poissons plats (Téléostéens-Pleuronectiformes) en Baie de Douarnenez II. Cycles sexuels et fécondité des Soleides: *Solea vulgaris vulgaris*, *Solea lascaris*, *Buglossidium luteum* et *Microchirus variegatus*. *Cahiers de Biologie Marine* 25, 257–285.
- Devauchelle, N., Alexandre, J.C., Le Corre, N., Letty, Y., 1987. Spawning of sole (*Solea solea*) in captivity. *Aquaculture* 66, 125–147.
- Ellis, T., Gibson, R.N., 1995. Size selective predation of 0-group flatfishes on a Scottish coastal nursery ground. *Marine Ecology Progress Series* 127, 27–37.
- 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). *Marine Ecology Progress Series* 1, 91–99.
- Fonseca, V.F., Vinagre, C., Cabral, H., 2006. Growth variability of juvenile sole *Solea solea* (Linnaeus, 1758) and *Solea senegalensis* Kaup, 1858, and comparison with RNA-DNA ratios in the Tagus estuary, Portugal. *Journal of Fish Biology* 68, 1551–1562. doi:10.1111/j.0022-1112.2006.001042.x.
- França, S., Vinagre, C., Caçador, I., Cabral, H.N., 2005. Heavy metal concentrations in sediment, benthic invertebrates and fish in three salt-marsh areas subjected to different pollution loads in the Tagus estuary (Portugal). *Marine Pollution Bulletin* 50, 993–1018.
- Gaston, K.J., 1990. Patterns in the geographical ranges of species. *Biological Reviews of the Cambridge Philosophical Society* 65, 105–129.
- Henderson, P.A., Holmes, R.H.A., 1991. On the population dynamics of dab, sole and flounder in the lower Severn estuary. England. *Netherlands Journal of Sea Research* 27, 337–344.
- Henderson, P.A., Seaby, R.M.H., 1994. On the factors influencing juvenile flatfish abundance in the lower Severn estuary, England. *Netherlands Journal of Sea Research* 32, 321–330.
- Henderson, P.A., Seaby, R.M., 2005. The role of climate in determining the temporal variation in abundance, recruitment and growth of sole *Solea solea* in the Bristol Channel. *Journal of the Marine Biological Association of the United Kingdom* 85, 197–204.
- Horwood, J., 1993. The Bristol Channel sole (*Solea solea* (L.)): a fisheries case-study. *Advances in Marine Biology* 29, 216–367.
- Houde, E.D., 1987. Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium* 2, 17–29.
- Houde, E.D., 1989. Comparative growth, mortality, and energetics of marine fish larvae: Temperature and implied latitudinal effects. *Fisheries Bulletin* 87, 471–495.
- Huthnance, J.M., Aken, H.M.V., White, M., Barton, E.D., et al., 2002. Ocean margin exchange—water flux estimates. *Journal of Marine Systems* 32, 107–137.
- ICES, 1992. Report on the study group on the fecundity of sole and plaice in sub-areas IV, VII and VIII. Lowestoft, 6–10. July 1992. ICES C.M. 1992/G:16, 1–73.
- Koutsikopoulos, C., Desaunay, Y., Dorel, D., Marchand, J., 1989. The role of coastal areas in the life history of sole (*Solea solea* L.) in the Bay of Biscay. *Scientia Marina* 53, 567–575.
- Koutsikopoulos, C., Lacroix, N., 1992. Distribution and abundance of sole (*Solea solea*) eggs and larvae in the bay of Biscay between 1986 and 1989. *Netherlands Journal of Sea Research* 29, 81–97.
- Lagardère, J.P., 1987. Feeding ecology and daily food consumption of common sole, *Solea vulgaris* Quensel, juveniles of the French Atlantic coast. *Journal of Fish Biology* 30, 91–104.
- Le Bec, C., 1983. Fécondité de la sole *Solea solea* (Quensel, 1806) du golfe de Gascogne. *International Council for the Exploration of the Sea G53*, 16 pp.
- LeFrançois, C., Claireaux, G., 2003. Influence of ambient oxygenation and temperature on metabolic scope and scope for heart rate in the common sole, *Solea solea*. *Marine Ecology Progress Series* 259, 273–284.
- Leggett, W.C., Frank, K.T., 1997. A comparative analysis of recruitment variability in North Atlantic flatfishes—testing the species range hypothesis. *Journal of Sea Research* 37, 281–299.
- Marchand, J., 1991. The influence of environmental conditions on the settlement, distribution and growth of 0-group sole (*Solea solea* (L.)) in a macrotidal estuary (Vilaine, France). *Netherlands Journal of Sea Research* 27, 307–316.
- Marchand, J., Masson, G., 1989. Process of estuarine colonization by 0-group (*Solea solea*): hydrological conditions, behaviour, and feeding activity in the Vilaine estuary. *Rapport P.-v. Réunion Conseil international pour l'Exploration de la Mer* 191, 287–295.
- Method Jr., R.D., 1983. Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. *Fisheries Bulletin U.S.* 81, 741–750.
- Miller, J.M., Burke, J.S., Fitzhugh, G.R., 1991. Early life history patterns of Atlantic North American flatfish: likely (and unlikely) factors controlling recruitment. *Netherlands Journal of Sea Research* 27, 261–275.
- Pannella, G., 1971. Fish Otoliths: daily growth rates and periodical patterns. *Science* 173, 1124–1127.
- Pauly, D., 1994. A framework for latitudinal comparisons of flatfish recruitment. *Netherlands Journal of Sea Research* 32, 107–118.
- Peliz, Á., Rosa, T.L., Santos, A.M.P., Pissarra, J.L., 2002. Fronts, jets and counter-flows in the Western Iberian upwelling system. *Journal of Marine Systems* 35, 61–77.
- Phillipart, C.J.M., Henderson, P.A., Joahnnessen, T., Rijnsdorp, A.D., Rogers, S.I., 1998. Latitudinal variation in fish recruits in Northwest Europe. *Journal of Sea Research* 39, 69–77.
- Pihl, L., 1989. Abundance, biomass and production of juvenile flatfish in southeastern Kattegat. *Netherlands Journal of Sea Research* 24, 69–81.
- Ramos, J., Rouros, S., 1985. Growth of sole, *Solea solea* (Linnaeus, 1758) under intensive conditions. *Informes Técnicos del Instituto de Investigaciones Pesqueras* 121, 1–12.
- Rijnsdorp, A.D., Van Beek, F.A., Flatman, S., Millner, R.M., Riley, J.D., Giret, M., De Clerck, R., 1992. Recruitment in sole stocks, *Solea solea* (L.) in the northeast Atlantic. *Netherlands Journal of Sea Research* 29, 173–192.
- Rogers, S.I., 1994. Population density and growth rate of juvenile sole *Solea solea* (L.). *Netherlands Journal of Sea Research* 32, 353–360.
- Sogard, S.M., 1992. Variability in growth rates of juvenile fishes in different estuarine habitats. *Marine Ecology Progress Series* 85, 35–53.
- Sogard, S.M., 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* 60, 1129–1157.
- Van der Veer, H.W., Bergman, M.J.N., 1987. Predation by crustaceans on a newly settled 0-group plaice, *Pleuronectes platessa*, population in the Western Wadden Sea. *Marine Ecology Progress Series* 35, 203–215.
- Van der Veer, H.W., Berghahn, R., Rijnsdorp, A.D., 1994. Impact of juvenile growth on recruitment in flatfish. *Netherlands Journal of Sea Research* 32, 153–173.
- 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 Journal of Marine Science* 57, 202–215.

- Van der Veer, H.W., Dapper, R., Witte, J.I.J., 2001. The nursery function of the intertidal areas in the western Wadden Sea for 0-group sole *Solea solea* (L.). Netherlands Journal of Sea Research 45, 271–279.
- Vinagre, C., França, S., Costa, M.J., Cabral, H.N., 2004. Accumulation of heavy metals by flounder, *Platichthys flesus* (L. 1758) in a heterogeneously contaminated nursery area. Marine Pollution Bulletin 49, 1109–1126.
- Walsh, S.J., 1994. Recruitment variability in populations of lough rough dab (American plaice) *Hippoglossoides platessoides* (Fabricius) in the North Atlantic. Netherlands Journal of Sea Research 32, 421–431.
- Wegner, G., Damm, U., Purps, M., 2003. Physical influences on the stock dynamics of plaice and sole in the North Sea. Scientia Marina 67, 219–234.
- Whitehead, P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., Tortonese, E., 1986. Fishes of the North-Eastern Atlantic and Mediterranean, Vol. III. UNESCO, Paris.
- Woerling, D., Le Fevre Lehoerff, G., 1993. Fluctuations pluriannuelles de la ponte de la sole *Solea solea* (L.) sur le littoral du sud de la mer du Nord. Journal de Recherche Océanographique 18, 74–79.
- Wooster, W.S., Bakun, A., McLain, D.R., 1976. The seasonal upwelling cycle along the eastern boundary of the North Atlantic. Journal of Marine Research 34, 131–141.
- Yakovlich, M.M., Bailey, K.M., 1990. Hatching period, growth and survival of young walleye Pollock *Theragra chalcogramma* as determined from otolith analysis. Marine Ecology Progress Series 64, 13–23.