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Davies, Julie Olivia; Hüssy, Karin

Publication date:
2012

Document Version
Publisher's PDF, also known as Version of record

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Citation (APA):
Coad, J. O., & Hüssy, K. (2012). Boom in boarfish abundance: insight from otolith analysis.

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Boom in boarfish abundance: Insight from otolith analysis

Julie Olivia Coad, Karin Hüsey

National Institute of Aquatic Resources, Technical University of Denmark, Jaegersborg Alle 1, 2920, Charlottenlund, Denmark

Corresponding author: tel: +45 3194 0600; e-mail address: joco@aqu.dtu.dk

Abstract

*The boarfish (*Capros aper*) is a pelagic shoaling species widely distributed along the Northeast Atlantic continental shelf. In recent years, this species has experienced a dramatic boom in abundance in the Bay of Biscay and Celtic Sea. This study aims at resolving the mechanisms responsible for this increase in stock size. Based on annual otolith growth increments, we developed a growth chronology as a proxy for stock fecundity. Growth patterns were similar between geographically separate areas west and south of Ireland, with distinct years of good and bad growth. In both areas growth was significantly influenced by summer temperatures and autumn food abundances. These months are the primary growing season of the boarfish. Recruitment was not correlated with growth in the same year; it was however significantly correlated with adult growth the previous year, together with temperature during the months following spawning. The age structure shows that this species is very long lived (> 30 years), but that a considerable proportion of fish are only aged 4-6 years. These age classes correspond to the year with exceptionally high recruitment. This study has demonstrated that both adult growth as a proxy for reproductive potential and environmental conditions favouring early life stage survival may be the cause for the boom in boarfish abundance.*

Keywords: Boarfish, growth chronology, recruitment

Introduction

The boarfish (*Capros aper*, Linnaeus), is a small, planktivorous, pelagic shoaling species whose distribution covers a vast area of the Northeastern Atlantic from Norway to Senegal, the Mediterranean Sea and the offshore islands of the Azores, Madeira and Canaries, the Great Meteor Seamount and (Holgersen, 1954; Quéro, 1986; Froese and Pauly, 2010). They are primarily found on continental shelves and shelf edges, often in large, high density shoals, at depths ranging from 0 to 600m (Tidd and Warnes, 2006; O'Donnell *et al.*, 2009; O'Donnell *et al.*, 2011).

Historically the boarfish are considered rare in the Northeast Atlantic but with temporary increases in abundance. The first recorded capture was off the southwest coast of England in 1825 and numbers increased dramatically over the next 20 years (Cunningham, 1888). Between the 1840's and 1880's large numbers were captured sporadically until the numbers caught decreased again (Couch, 1844; Cunningham, 1888). In the mid 1900's, Cooper (1952) reported another increase which he hypothesised was caused by hydrographic features possible of sweeping shoals of fish up onto the shelf from depth. More recently, an overall increase in abundance has been noted between the 1980's and early 2000's on the Galician continental shelf and the Celtic Sea (Farina *et al.*, 1997; Pinnegar *et al.*, 2002), an increase which was also noted in the Bay of Biscay and attributed to enhanced recruitment as a result an increase in water temperature (Blanchard and Vandermeirsch, 2005). Based on an abundance index estimated from the Western International Bottom Trawl Survey (IBTS) data (Figure 1) this trend has persisted throughout the last decade, with apparent fluctuations possibly due to the shoaling nature of the species (ICES, 2011).

The annual growth pattern observed in boarfish otoliths has been validated by Hussy *et al.*, (2011). The strong seasonality of the environmental conditions of the temperate Northeast Atlantic waters and their effects on the growth patterns of this species, in addition to their

longevity, allows for the application of dendrochronology (tree-ring) techniques to boarfish sagittal otoliths. A growth chronology has been generated spanning the time period in which the increased abundance of this species is apparent.

The boarfish are a long-lived species, reaching a maximum age > 30 years (Hüssy *et al.*, 2012). Growth is initially fast in the first 2-3 years but then levels off, presumably as energy is allocated to other processes, possibly reproduction (Hüssy *et al.*, 2011). They are sexually dimorphic, batch spawners, most likely with asynchronous oocyte development and indeterminate fecundity that spawn on the shelf edge in June and July. They reach 50 % maturity at 9.7 cm total length, corresponding to an age of 3.5 years (Farrell *et al.*, 2012). Under aquarium conditions, similar to those observed in the Celtic Sea in the summer months, the males were observed to spawn daily and the females every 2-3 days for 9 consecutive months (J. Hemdal pers. comm.). Given the reproductive information available and under optimal conditions in regards to food and temperature, the boarfish are most likely capable of multiple spawning events throughout the spawning period.

Investigations into the diet of the boarfish have been conducted in the western Mediterranean, Portuguese waters and the Great Meteor Seamount. In all studies (MacPherson, 1979; Fock *et al.*, 2002; Lopes *et al.*, 2006) the composition of prey items varied daily and seasonally but the dominant items were the larger copepods, *Calanus* spp., specifically *Calanus helgolandicus* while other species included euphausiids and their larvae, mysid shrimp and gastropods. There has been a poleward movement of warmer water species such as *C. helgolandicus* since the early 1980's and these biogeographical shifts have been attributed to a changing climate and the coincident change in water temperatures, ocean currents and other physical mechanisms (Beaugrand *et al.*, 2002).

Although the general trend is an increase in temperatures, there have however been fluctuations occurring on many time scales and over the last century ecosystem shifts have

occurred which can be attributed to large scale ocean climate indices, such as the North Atlantic Oscillation (NAO) (Hurrell, 1995) and changes in the North Atlantic sub polar gyre (Hátún *et al.*, 2005), both which have strong influences on the physical processes of the area. Post 1995 the intensity of the gyre circulation decreased, possibly driven by a shift in the NAO (Häkkinen and Rhines, 2004; Lohmann *et al.*, 2009) which resulted in rapid warming and salinification (Hátún *et al.*, 2005). On a longer time frame, basin wide changes in temperature have been correlated with the Atlantic Multidecadal Oscillation (AMO) back to the latter part of the 19th century (Sutton and Hodson, 2005). Information on how the rising sea temperatures have altered the composition of fish species in the area has been documented in recent years (Quéro, 1998; Brander *et al.*, 2003). While observed changes have been linked to large scale ocean climate variability, through trophic dynamics occurring as a result of a persistent “bottom up” control throughout the ecosystem (Hátún *et al.*, 2009). The onset of the recent increase in the abundance of boarfish coincides with the post 1995 weakening of the sub polar gyre and the subsequent warming of the Northeast Atlantic. Stock size has important implications on the number of recruited fish (Cushing, 1990), while the number of young fish recruited to a fishery is highly dependent on the survival of the young of the year (Houde, 1987). In this study we investigate how environmental conditions (temperature and food availability) influence growth and recruitment dynamics of the boarfish.

Materials and methods

Sample selection

Both commercial and survey samples (n=40) were selected from 2010, where fish over 10 years with known geographical positions were chosen (Figure 2). Otoliths were visually

inspected and only otoliths where the transition from opaque to translucent zones was clearly defined were selected.

Stock data

Abundance estimates were those used by ICES WGWIDE 2011 and based on the following survey data: IGFS - Irish Groundfish Survey (ICES Subdivisions VIa, VIIb, VIIc, VIIg and VIIj), FR – EVHOE Groundfish Survey in the Celtic Sea and Bay of Biscay (ICES Subdivisions VIIf, VIIg, VIIh, VIIj, VIIIA and VIIIB) and SP - NGFS Spanish Groundfish Survey in Northern Spanish Shelf (ICES Subdivisions VIIIC and IXaN). Recruitment was based on the number of 1 year olds in the fishery (Figure 3). For each area a relative recruitment index (R_A) was estimated by back shifting recruitment by 1 year and dividing by the annual abundance (Figure 4).

Chronology

The left sagittal otoliths were cleaned in alcohol, immersed in undiluted propylene glycol for 6 minutes, placed on a black background under a circular reflected light source and viewed using a Leica MZ12 microscope at a magnification of 0.63 pixels μm^{-1} . Images were digitized using a Leica DFC290 camera: 8 bits per channel, 2048 \times 1536 pixel frame, 35 ms exposure. Image brightness and contrast were adjusted and filters applied in order to maximize the contrast between growth zones. Ages were estimated and the dorsal anterior axis chosen for measurements, following routine methods validated by Hüseyin *et al.* (2011). Measurements were taken from the outer edge towards the nucleus, from the beginning of one annulus to the beginning of the following annulus and always perpendicular to the growth axis, where 1 increment width (IW) comprised winter and summer growth from 1 year (Figure 5). Increment widths were measured using Image J (v. 1.44p available at

<http://rsbweb.nih.gov/ij/>. Due to unreliability of measurements from the inner highly opaque area of the otoliths, all IW greater than 150 microns were excluded. For each fish the IW were log transformed, a linear regression fit to each set of measurements and age related trends removed by dividing the residuals by the predicted values. The resulting individual, de-trended standardised residual time series were averaged to calculate mean growth and the master chronology, with residuals > 0 and < 0 indicating years of good and poor growth respectively.

Age effect

Residual analysis was conducted to check for an age effect which could bias the growth chronology. Residuals from the master chronology for a year of good (2004) and poor (2005) growth were regressed against fish age to check for age effects in each year, slope significance was tested and plots visually inspected.

Latitude effect

The same method was used to check for a latitudinal effect, with residuals regressed against sample position. Following visual inspection of the plots 2003 was included and in order to make a more conclusive analysis samples were split into “north” $> 52^{\circ}\text{N}$ and “south” $< 50^{\circ}\text{N}$.

Temperature data

SST was obtained from ICES at <http://www.ices.dk/ocean/data/surface/surface.htm> for 2000 to 2009. Datasets were chosen based on temporal and spatial resolution in the areas corresponding to “north” and “south”. Missing values were estimated using regression statistics obtained when a fourth order polynomial was fit to the measured data. Monthly average values were based on measured and estimated values and subsequently used to

calculate seasonal average values using the divisions: Spring = February, March, April (FMA); Summer = May, June, July (MJJ); Autumn = August, September, October (ASO); Winter = November, December, January (NDJ).

CTD data was obtained from ICES at <http://ocean.ices.dk/HydChem/HydChem.aspx?plot=yes> and a temperature at depth dataset compiled for the north. Data availability was too poor for the south.

When testing the effect of temperature on adult growth in the south, 2003 was excluded from the analysis as the exceptionally high temperatures in this year clearly lay outside the strong linear relationship.

Food data

Monthly average values of *Calanus helgolandicus* and *Calanus finmarchicus* for 2000-2008, estimated from the Continuous Plankton Survey (CPR) survey and corresponding to “north” and “south”, were provided by SAHFOS. Seasonal averages were calculated based on the same divisions used for temperature.

Data analysis

All analyses were carried out on the “north” and “south” separately and significance tested at the 0.05 level. For the recruitment analysis adult growth is used as a proxy for adult condition and thus potential stock fecundity.

Growth: The influence of temperature and food availability on growth was analysed with multiple linear regression analysis. The effect of each parameter alone was examined as well as their combined effect. The model fit was analysed for all combinations of the four seasonal

average values for temperature and food. The sub-models were then compared by likelihood ratio tests. The models analysed were.

$$G_y = a + b * T_{y,S} + \varepsilon$$

$$G_y = a + b * F_{y,i,S} + \varepsilon$$

$$G_y = a + b * T_{y,S} + c * F_{y,i,S} + \varepsilon$$

Where G_y = growth in year y , T = average seasonal temperature (SST for north and south and temperature at depth for north), F = availability of prey species i (*C. helgolandicus*, *C. finmarchicus* and their combined biomass *Calanus* spp.) and S = seasons within each year (FMA, MJJ, ASO, NDJ) and ε = residual model error.

Recruitment: The influence of growth, temperature and food availability on recruitment was tested in a similar approach. Prior to analysing the effect of the environmental factors, the hypothesis that growth the previous year and not growth in the same year influence reproductive output was tested:

$$R_{A,y} = a + b * G_y + c * G_{y-1} + \varepsilon$$

Where $R_{A,y}$ = relative recruitment index from area (A), G_y = growth in year (y) and G_{y-1} = growth in the previous year (Figure 7). In the following analyses, only growth the previous year G_{y-1} was used. For each added term, the model fit was analysed for all combinations of the four seasonal average values for temperature and food. The best fit sub-models were then compared by likelihood ratio tests. The model with the lowest AIC is the model that best fits the data. The models analysed were.

$$R_{A,y} = a + b * G_{y-1} + \varepsilon$$

$$R_{A,y} = a + b * T_{y,S} + \varepsilon$$

$$R_{A,y} = a + b * F_{y,i,S} + \varepsilon$$

$$R_{A,y} = a + b * G_{y-1} + c * T_{y,S} + \varepsilon$$

$$R_{A,y} = a + b * G_{y-1} + c * F_{y,i,S} + \varepsilon$$

$$R_{A,y} = a + b * T_{y,S} + c * F_{y,i,S} + \varepsilon$$

Where R = recruitment index of area A, G_{y-1} = growth the previous year T = average seasonal temperature (SST for north and south and temperature at depth for north), F = availability of prey species *i* (*C. helgolandicus*, *C. finmarchicus* and their combined biomass *Calanus* spp.) and S = seasons within each year (FMA, MJJ, ASO, NDJ) and ε = residual model error.

Results

Growth

In both areas, growth of the adult fish was correlated with a combination of temperature and food conditions during summer and autumn.

South: Surface temperature during summer alone explained 82% of the interannual variation in growth (Figure 6), while a combination of summer temperatures and autumn availability of *C. helgolandicus* increased the degree of explained variability to 91%.

North: The picture is less clear, particularly with respect to sea surface temperature. However, in general, the results are very similar to those in the south with *C. helgolandicus* abundance during autumn explaining 80% of the interannual variability in growth, while the combination of temperature at depth in summer and autumn abundance of *C. helgolandicus* explained as much as 90%. Sea surface temperature explained far less of that variability than temperature at depth.

Recruitment

South: The effect of growth in the same year as well as in the previous year was analysed with multiple linear regression analysis for each area and recruitment index separately. In all analyses, growth the previous year explained a higher degree of the variability in recruitment

than growth in the same year. Consequently, G_{y-1} and not G_y was used in all subsequent analyses.

A clear pattern was evident with the Spanish recruitment index and conditions in the south, where growth alone explained 54 % and autumn and winter temperatures explained 60 % of the interannual recruitment variability. Together, they explained as much as 72 %, while a combination of autumn temperature and *C. finmarchicus* explained 76 %. With the French recruitment index a similar picture was observed, albeit only autumn *C. finmarchicus* had a significant effect (55 %). None of the variables were found to be significantly correlated with the Irish recruitment index.

North: Growth (neither in the same, nor in the previous year) had a significant effect on any of the recruitment indices, even though growth the previous year had a higher influence in all analyses. None of the parameters examined were significantly correlated with the Spanish and the French recruitment indices. However, the Irish index was significantly correlated with spring and autumn temperatures explaining 63 % of recruitment variability. Adding growth increased the degree of explanation to 83 %. Food could not be analysed, as only there were only 4 years of data with both recruitment and food data.

Discussion

Growth

This study demonstrates the value of using growth chronology techniques for investigations into climatic effects on a fishery with a wide geographical range. Black *et al.*, (2008) conducted a similar study using this approach on the long lived yelloweye rockfish (*Sebastes ruberrimus*) in which the annual periodicity of growth-increment deposition had been validated. The seasonal pattern of otolith increment formation in boarfish has been verified by Hussy *et al.*, (2011). The summer months were observed to be the peak growing

period and correspond to the results of this study where a strong correlation exists between growth and temperature in the summer months. Thus the suitability of Boarfish otoliths to growth chronology analysis has been established. Boarfish reach a maximum age of > 30 years and as no age dependent growth differences exist, having a larger sample of older fish would allow for comparison of growth and environmental variables over the period which the present boom in abundance was initiated.

Overall the chronologies for the north and south are synchronised with exceptions attributable to differing summer temperature regimes. Growth in the north is poorer and displaying a greater magnitude in variation. Given that the recent increase in this “sub-tropical” species abundance has been linked to an increase in water temperature (Blanchard and Vandermeirsch, 2005; Farina *et al.*, 1997), this is a possible indication of temperature limitation on growth and a higher degree of susceptibility to environmental variation for the fish which inhabit the more northern latitudes. This was shown to be the case with north Atlantic cod stocks where differential growth and condition between stocks was partly due to the different temperature regimes (Rätz and Lloret, 2003).

The boarfish are generally found below 40m depths (O’ Donnell *et al.*, 2011) and thus the stronger relationship between growth and temperature at depth is expected. In the north, the relationship between growth and SST was non-significant but temperature at depth combined with food abundance in autumn could explain 90% of the variation observed in adult growth. These results correspond to those in the south where summer temperatures and autumn food abundances were utilised in the strongest models and thus allows for the use of SST as a proxy for temperature at depth.

In both areas a strong correlation exists between adult growth and *C. helgolandicus* in the autumn months. While the otolith growth pattern showed growth to be strongest in the summer months, the growing period continues through to November (Hussy *et al.*, 2011).

Farrell *et al.*, (2012), described the boarfish as an asynchronous batch spawner whose annual reproductive cycle begins between February and April and ends between October and December. This reproductive strategy is energy intensive and requires a continuous intake of food (Hunter and Leong, 1981) and therefore when active spawning has ceased high food abundances at this time of year are likely to be invested in growth and reproductive potential.

Recruitment

Initial stock size (Cushing, 1990) and young of the year survival year (Houde, 1987) will have important implications on the number of young recruits to a fishery. This study incorporates adult growth/condition and reproductive strategies, with environmental factors effecting survival of the young of the year. Interestingly, growth in the year prior to recruitment explained a higher degree of variability in all recruitment indices in comparison to growth in the corresponding year. Reduced recruitment in the South African anchovy, *Engraulis capensis*, with a similar reproductive strategy to the boarfish, has been linked to, among other things, high rates of gonad atresia or reabsorption as a result of starvation and poor adult condition (Hutchings *et al.*, 1998). While poorly conditioned females of some species will reduce their reproductive potential in order to limit somatic energy losses (Lambert and Dutil, 2000). When using adult growth as a proxy for adult condition, and considering that the boarfish reproductive cycle can begin as early as February, starvation due to low levels of food in the autumn months the previous year could have negative effects on gonad maturation, oocyte viability, egg production and spawning, and thus provide an explanation for the relationship between recruitment and growth in the previous year.

Survival of the young of the year is imperative for recruitment and this critical period is highly influenced by the physical and biological environment (Hjort, 1914; Lasker, 1975; Iles and Sinclair, 1982; Cushing, 1990). The peak spawning period for the boarfish is July (Farrell

et al., 2012) and thus the significant relationships between recruitment and post spawning autumn and winter temperatures and autumn food abundance in both areas document the impact of environmental conditions on larval survival. In the north, the significance of spring temperatures may be attributable to atypical oceanographic conditions which occur at this time of year (Pingree and LeCann, 1990) or an indication of mixing and subsequent spring bloom production providing the energy required to initiate the reproductive cycle.

The final combined models show area specific relationships between adult growth and environmental conditions, and the coincident recruitment indices. Spawning takes place along the continental shelf edge (O' Donnell *et al.*, 2011) and observations from the Mackerel Egg Survey (MEGS), 2010 identified the highest concentration of boarfish eggs in the Celtic Sea, south of 50°N (Farrell, unpublished data). Spatial patterns of mackerel egg and larvae drift have shown transport along the shelf edge in a south-eastwards direction south of 51°N and a concentration of eggs and larvae over the Porcupine Bank north of 51°N (Bartsch and Coombs, 2004). A southeasterly counter flow is observed close to the Celtic shelf-break (Pingree and LeCann, 1989) while in the north a retentive circulation pattern exists in the Porcupine Bank area (Mohn *et al.*, 2002). Using these patterns it is possible to infer a hypothesis that it is the eggs spawned in the Celtic Sea and transported to the warmer waters in the south which are driving the stronger recruitment in the area, while those spawned to the west of Ireland are retained in the area and benefit from the nutrient rich waters of the Taylor cap (Mohn and White, 2007). The poleward flow of the SEC (Pingree and LeCann, 1989, 1990) may then be a mechanism for the northward drift or migration of fish as size and age increases.

At present both areas appear to be highly suitable for successful reproduction and survival of the boarfish but with optimal environmental conditions in the south. The age frequency

distribution shows a peak in the 4-6 year olds (O'Donnell *et al.*, 2011; Hussy *et al.*, 2012) and not surprisingly, all recruitment indices were strongest in 2005. Using 2005 as an example the model results can be confirmed. Strong adult growth in 2004 promoted recruitment in 2005 and post spawning autumn temperatures and food abundances were high. In the south, average winter SST was however poor due to low December values and a negative NAO index. January values were above average and possibly attributable to a strong "Navidad" poleward flow, a consequence of a negative NAO index linked to winter warming in the southern Bay of Biscay (deCastro *et al.*, 2011) and northern seas in exceptional years (Garcia-Soto *et al.*, 2002).

The co-occurrence of historical booms in abundance of this species and ocean climate indices cannot go unmentioned, such as the warm phases of the AMO in the mid 1800's, mid 1900's (Gray *et al.*, 2004) and post 1990 (Sutton and Hodson, 2005). The shift in the sub-polar gyre circulation post 1995 resulted in a warming of the Northeast Atlantic and has been linked to the changes in distribution of other species and their food sources (Hátún *et al.*, 2009). The results of this study show clear relationships between temperature, both in terms of adult growth and survival of the young of the year. When considering the above links to climate records it would appear that water temperature has a profound effect on the increase in stock size of this species, while the temperature effect on the prevalence of its preferred prey has already been confirmed (Beaugrand *et al.*, 2002).

The results of this study demonstrate that adult growth in the year prior to spawning, and the dependency of egg and larvae survival on environmental conditions, are two major factors contributing to boarfish recruitment success in the Northeast Atlantic. Adult growth is strongly influenced by summer temperatures and autumn food abundances, while young of the year survival is dependent on temperature in the months following spawning. Conditions in the south are more suitable in comparison to the north and area specific relationships exist

between adult growth, the environment, and their respective recruitment indices, with climate being an intrinsic factor. Many obscurities prevail in our knowledge of this species, including an explanation for the presence of a large number of older fish. Possible future complimenting studies should include Individual Based Modelling of early life stages, genetic and stomach analyses of boarfish in the Northeast Atlantic and the development of an extended growth chronology.

Acknowledgements

We gratefully acknowledge the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) who run the CPR survey and who provided the zooplankton data. We would like to thank all the skippers and crew of the Killybegs Pelagic fleet, the Danish Pelagic Producers Organisation/FF Skagen and the scientists and crew of the RVs “Celtic Explorer”, “Walther Herwig II”, “Johan Hjort”, “Scotia” and “Antarctic” for helping with sample collection.

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Figures

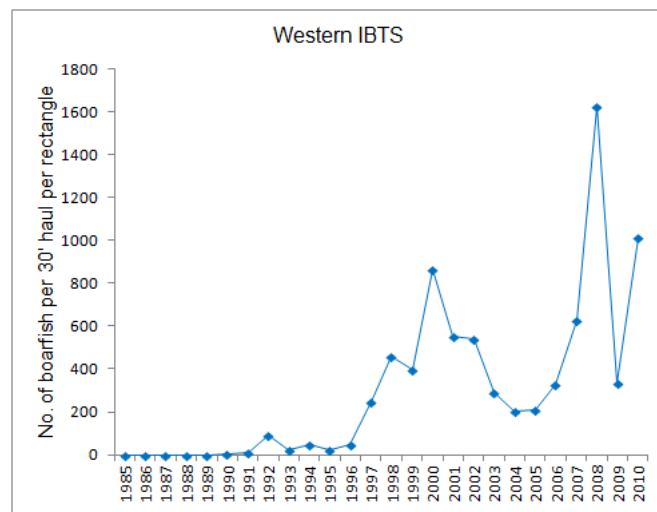


Figure 1 Boarfish in ICES Subareas VI, VII, VIII. CPUE in number per 30 minute haul of boarfish per rectangle in the western IBTS survey 1985 to 2010. From ICES, 2011.

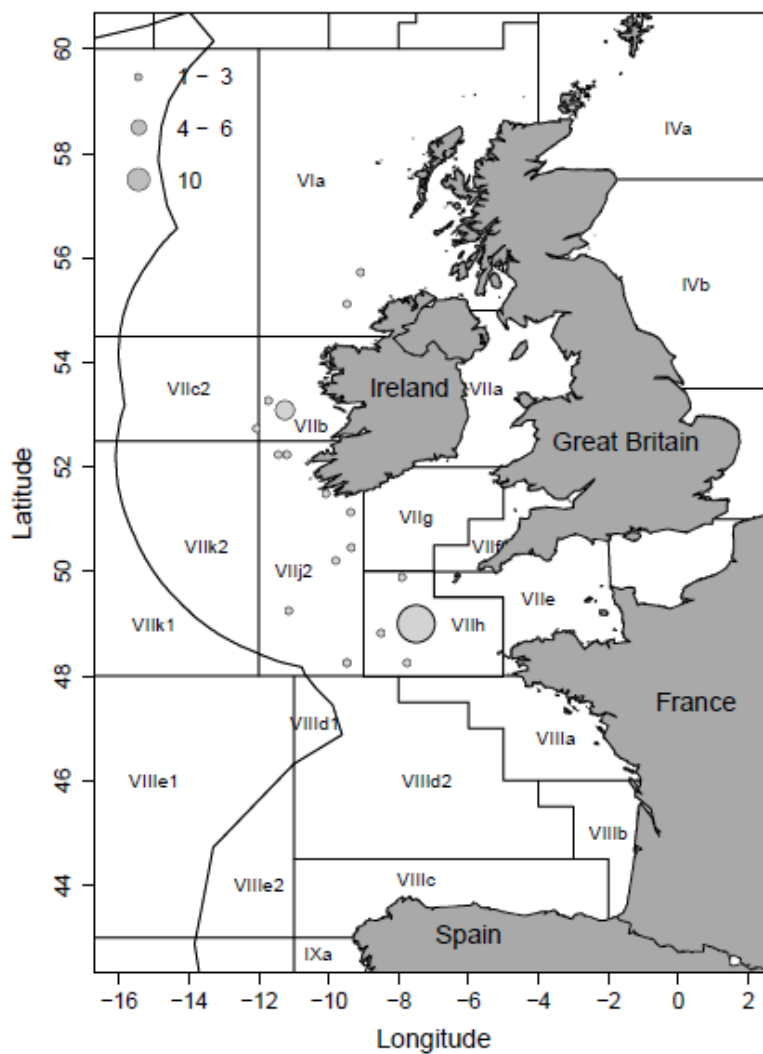


Figure 2 Map of the study area with sample positions and ICES Subdivisions.

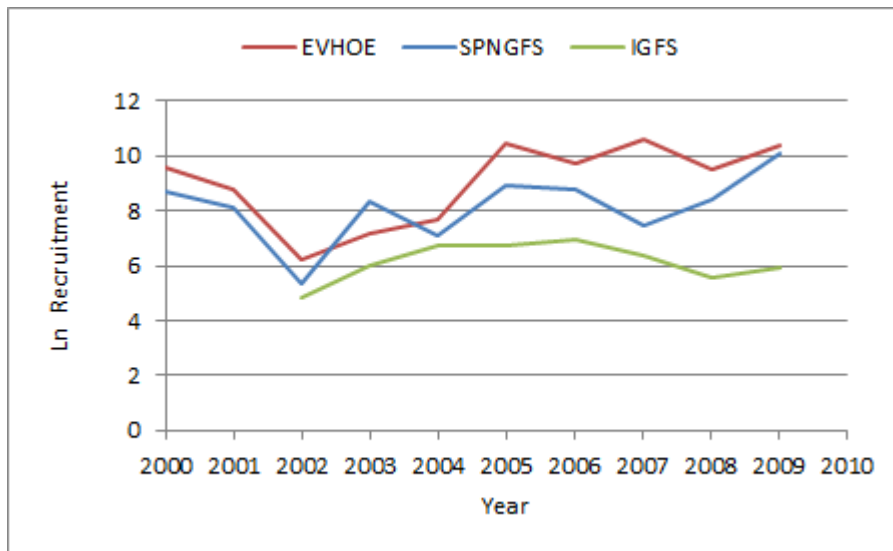


Figure 3 Recruitment indices for the EVHOE (French), SPNGFS (Spanish) and the IGFS (Irish).

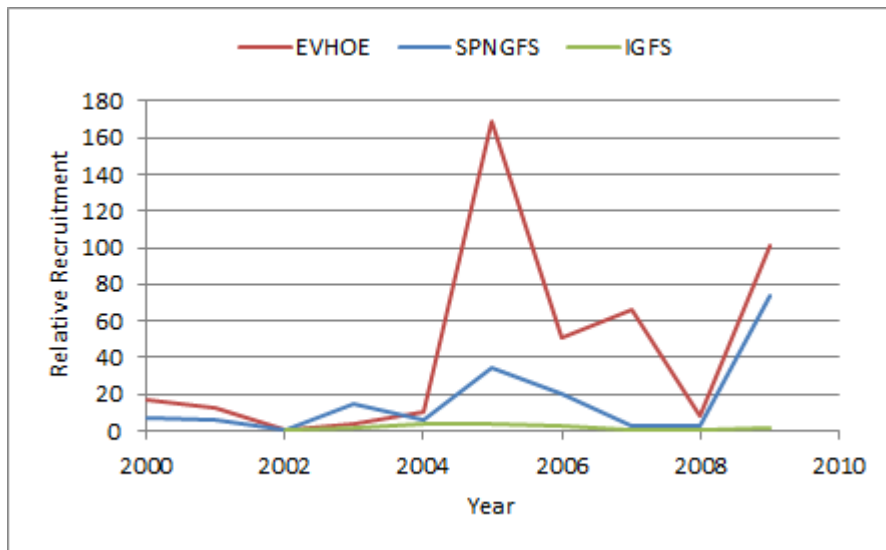


Figure 4 Relative Recruitment for the EVHOE (French), SPNGFS (Spanish) and IGFS (Irish).

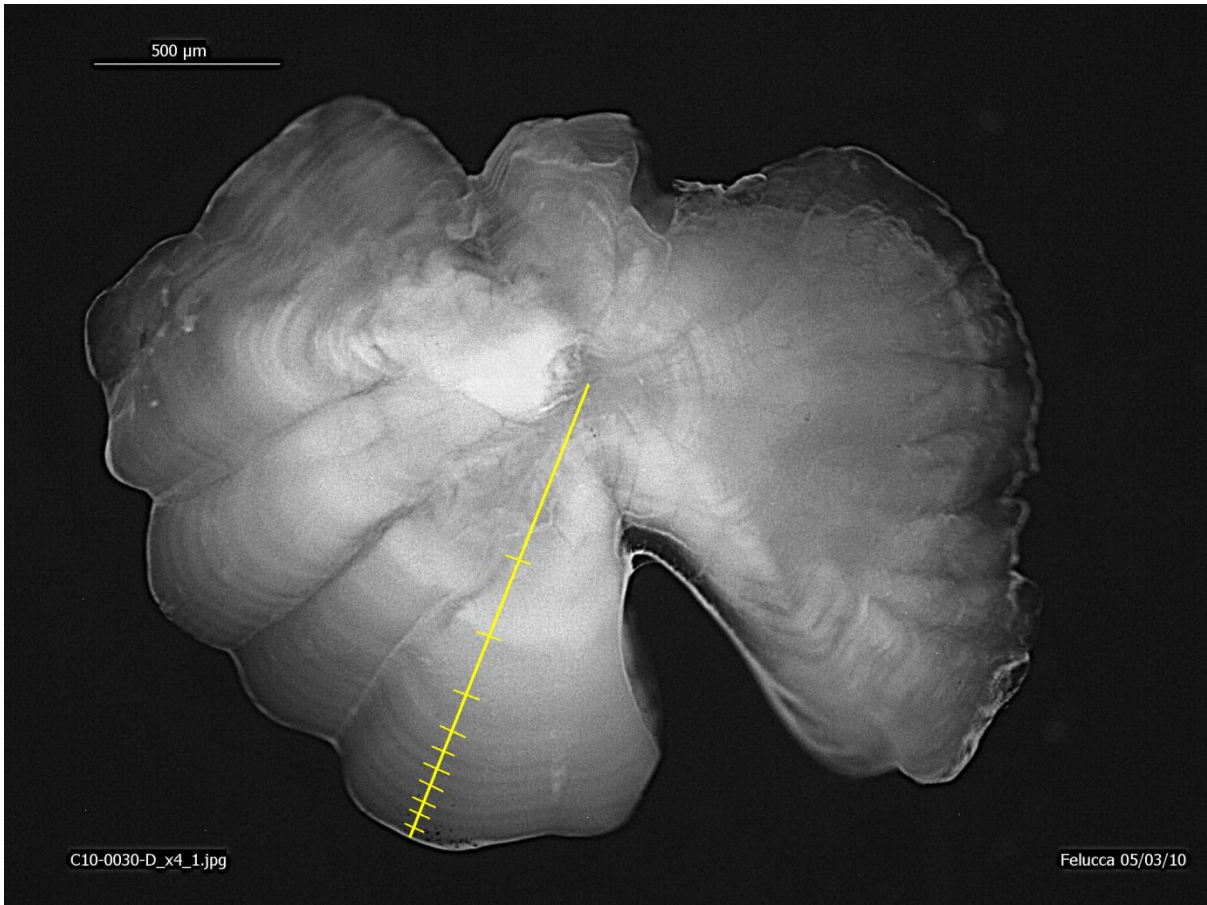


Figure 5 Left sagittal otolith. The diagonal yellow line represents the optimal measuring axis and the perpendicular lines indicate where measurements were taken.

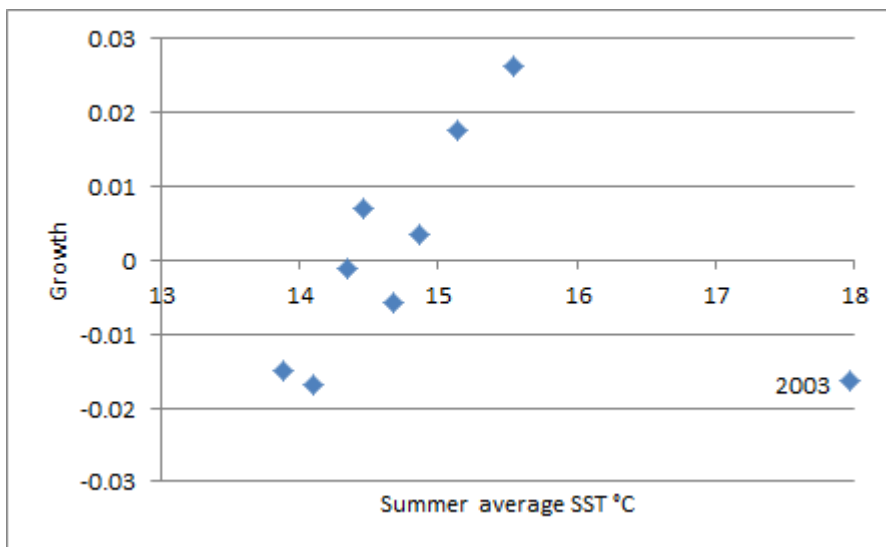


Figure 6 The relationship between and summer SST and growth in the south clearly showing the very high temperatures in 2003 which lie outside the linear relationship.

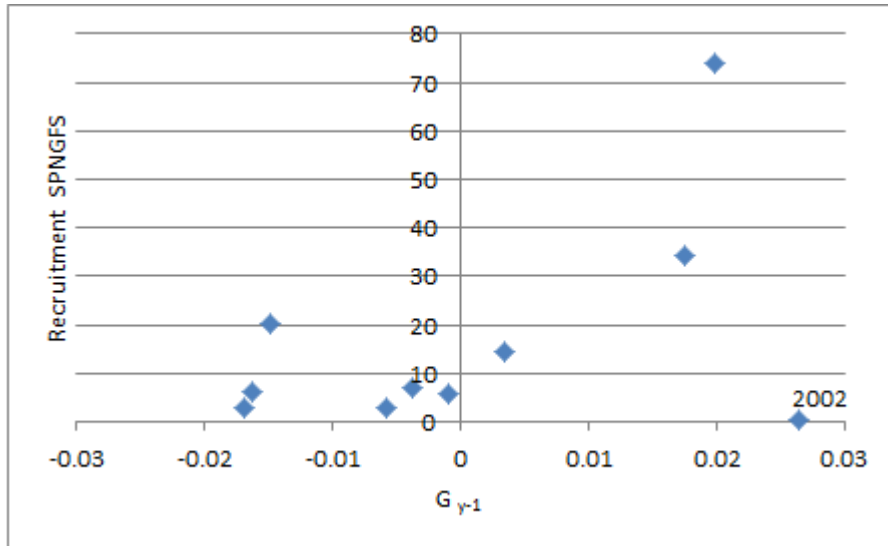


Figure 7 The relationship between recruitment from the SPNGFS and G_{y-1} in the south showing 2002 lying outside the linear relationship.