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Interannual fluctuations in spring pelagic ecosystem productivity in the Bay of Biscay (northeast Atlantic) measured by mesozooplankton aspartate transcarbamylase activity and relationships with anchovy population dynamics

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Abstract:

The French part of the continental shelf of the Bay of Biscay (northeast Atlantic) is the habitat of an anchovy (*Engraulis encrasicolus* L.) population of scientific interest because of its economic importance and the trend towards greater interannual fluctuations in its abundance, particularly as a consequence of variations in recruitment. Each year a 1-month survey of this population and its pelagic environment is undertaken. Among the descriptors of ecosystem function characterized, mesozooplankton aspartate transcarbamylase (ATC) activity is measured with the goal of defining overall productivity of the mesozooplankton communities. Diverse physical forcing factors are responsible for the enhancement of productivity in the Bay of Biscay, and their respective influences vary at interannual scales. We present the results of ATC activity measurements carried out within the anchovy habitat during six consecutive breeding seasons (from 2000 to 2005). A strong correlation was found between mean ATC activity and variations in interannual biomass for the anchovy population ($R = 0.928$; $p < 0.01$). During the study period the anchovy population collapsed, and a particularly low level of ATC activity in the mesozooplankton preceded this event 1 year earlier. Conversely, an increase in anchovy abundance in the year following the collapse was preceded by a return to substantially higher levels of ATC activity. We hypothesize that this relationship may be robust and generally applicable. We speculate on the environmental descriptors necessary to confirm this result, in view of its potential application to the monitoring of this valuable fish population in the Bay of Biscay.

Keywords: Aspartate transcarbamylase ; Anchovy biomass ; Breeding season ; Mesozooplankton ; Pelagic fisheries ; Bay of Biscay

1. Introduction

Early studies of plankton were closely linked to fisheries research (Richardson, 2002). The seminal population model proposed by Beverton and Holt (1957) became the principal resource for scientists responsible for developing fisheries management rules, but limitations in the performance of the mathematical tools later became apparent, mainly related to environmental factors and their variability at different scales. It has recently been recognized that an ecosystem approach is essential for a better understanding of fish population dynamics (Hall and Mainprize, 2004; Jennings, 2005), and to address societal concerns (Horwood, 2008). This approach appears to be essential for small pelagic fish in general and anchovy in particular (Fréon et al., 2005), especially for the anchovy population inhabiting the Bay of Biscay (*Engraulis encrasicolus* L.) according to Borja et al. (2008). For example, because anchovy is a short-lived species (Uriarte et al., 1996), classical methods of stock assessment, including VPA (virtual population analysis), are unsuitable. In short-lived species a failure in recruitment can threaten the viability of the population. For this reason, improved knowledge of processes regulating the level of anchovy recruitment and the subsequent short-term sustainability of the fishery is essential. Recruitment generally fluctuates in response to various biotic and abiotic environmental factors.

In most cases changes in the biotic environment are linked to physical forcings acting at varying scales of time and space (Alheit and Hagen, 2002; Alheit, 2009). The temporal and spatial scales of relevance to the anchovy population exploited in the Bay of Biscay (northeast Atlantic) are broad. The spawning season extends from April to July, and more rarely to early August, with a peak in the May–June period (Motos et al. 1996), and the spawning area covers three degrees of latitude, mainly in the southern part of the continental shelf (Motos et al., 1996). The spawning region for this population is subject to many extrinsic drivers having mesoscale effects. The area includes a patchwork of different systems under the influence of numerous environmental factors that include the location and extent of river plumes, upwellings, wind regimes and residual currents (Koutsikopoulos and Le Cann, 1996; Bergeron, 2004; Bergeron et al., 2009), resulting in juxtaposed and changing hydrological structures (Planque et al., 2004, 2006). The resulting diversity of environmental conditions generates special adaptations in food web structures, and varying functional rates, which affect the mesozooplankton communities inhabiting these systems. This has substantial consequences for species composition and biomass (Albaina and Irigoien, 2004, 2007; Irigoien et al., 2009), but also for overall metabolism (e.g. Bergeron, 2004, 2006; Bergeron et al., 2009, 2010; Bergeron and Koueta, 2011). Mesozooplankton, which prey on small particles including phytoplankton and protozoans, are in turn prey for the abundant small pelagic fish. Thus, following Banse (1995), who included heterotrophic protozoans in the more general term „zooplankton", it is likely that mesozooplankton (*sensu* Sieburth et al., 1978) play a “pivotal role in the control of ocean production”.

The mesozooplankton community constitutes the first level of integration of hydroclimatic forcing in the pelagic food web (Banse, 1995), which provides a powerful tool for characterizing the basic processes on which the system relies. Such forcing factors primarily affect the metabolism of individuals (Båmstedt, 1986; Kleppel, 1993), and lead to overall changes in the functioning of the community at a higher level of systemic organization (e.g. Alcaraz et al., 2007). However ecological systems, contrary to mechanical systems, are far too complex to be specified in complete detail (Platt, 1981). Assessment of the biotic functioning of the environment in this study was based on metabolic descriptors of the mesozooplankton community, involving measurement of enzyme activity, in agreement with Smith (1981) who suggested that “one must forego experiments using isolated species and instead conduct measurements on complex ensembles, preferably in the field”. This approach that has been used for more than 20 years (Bergeron, 1983, 1986), and was more recently applied to the Bay of Biscay pelagic ecosystem (Bergeron et al., 2009, 2010). The enzyme activities in samples of the entire community were analyzed as initially advocated by Bergeron (1983, 1986), and in accordance with the „fully ataxonomic enzymatic approach‟ advocated notably by González and Quiñones (2009). The basic rationale for such an approach is founded on the permanence and omnipresence of the mesozooplankton community (primarily copepods) in the world ocean (Mauchline, 1998). The overall metabolism of this community results from biological integration at the mesoscale of the multiple environmental factors characterizing the ecosystem. While there are some grounds for criticism of Bergeron‟s methods (Berges et al., 1993), they remain relevant because they provide the fastest, simplest, and least expensive means for assessing mesoscale variations in important metabolic features. In this regard, see Packard (1985) and Packard et al.‟s (1996) study of ETS activity for estimating the respiration process. Moreover, the use of such methods is particularly relevant from a fisheries research perspective because they are compatible with the logistical constraints associated with fisheries research cruises, which typically involve large areas to be surveyed within as short a time as possible. This was particularly the case for the ecological studies of small pelagic fish populations carried out by our research team in the Bay of Biscay (Scalabrin and Massé, 1993; Petitgas et al., 2003).

Among the enzyme activities used by Bergeron et al. (2009, 2010), aspartate transcarbamylase (ATC) is particularly important (Bergeron and Koueta, 2011). ATC is involved in metabolic control of growth at the cellular level (Jones, 1980; Bergeron and Alayse-Danet, 1981). Growth results from various integrated physiological functions including nutrition and excretion, and respiration under various environmental conditions (e.g. temperature). Biological growth processes are underpinned by the biosynthesis of molecular purine and pyrimidine nucleotides, which are the building blocks of ribonucleic acid (RNA) and deoxyribonucleic acid (DNA) macromolecules; these are central to cell reproduction and protein biosynthesis. ATC participates in the first step of *de novo* biosynthesis of pyrimidine nucleotides, and was selected because pyrimidine biosynthesis follows a single metabolic pathway, whereas purines can be synthesized *de novo* or recycled from other metabolic pathways. Thus, ATC activity in mesozooplankton samples reflects production of the building blocks for the formation of new living biomass.

The basis of interest in enzymatic methods is their specificity for particular metabolic processes. While there may be uncertainties about the reliability of this approach from a biochemical perspective, it is assumed that the detection of enzyme activity reflects the activity of the related metabolic process. Although demonstrating stoichiometric relationships between enzyme activities measured in a sample of the mesozooplankton community and the ecosystem rate of specific metabolic processes is not currently feasible, enzyme activities represent a dynamic view of the processes involved (i.e. they have the invaluable property of dimension in, $time^{-1}$). Therefore, the activity of an enzyme can be used as a proxy for a metabolic process, providing an index of relative values that enable comparison among samples taken from a marine study area.

The European anchovy population in the Bay of Biscay (northeast Atlantic) is a small pelagic fishery that is shared by Spanish and French fishing fleets, and is of great economic importance. It has been monitored for more than 20 years, and has been the subject of extensive studies by scientists from both countries. Each year our fisheries research team undertakes a research cruise during the breeding season, which is mainly focused on stock assessment. From 2000 to 2005 we estimated ATC activity in samples of mesozooplankton communities collected throughout the continental shelf of the Bay of Biscay. We present here the results of our analysis of interannual variations in ATC activity during these six consecutive years, in relation to estimates of the annual biomass of the anchovy population.

2. Materials and methods

The anchovy population of the Bay of Biscay is surveyed annually by French and Spanish scientists with the objective of defining rules for the exploitation of this economically important resource. Annual assessments of this stock are based on research cruises undertaken by scientists of the AZTI (Basque Country, northern Spain) and IFREMER–Centre Atlantique (France) fisheries research laboratories. The combined results of these studies are analyzed by special Working Groups under the auspices of the ICES (International Council for the Exploration of the Sea). The French research team is largely focused on acoustics-based assessment of the spatial distribution and abundance of biomass of small pelagic fish (Scalabrin and Massé, 1993; Massé, 1996). The results presented here were obtained aboard the RV *Thalassa* during the „Pelgas" cruises, which occurred in approximately May in successive years from 2000 to 2005. These research expeditions encompassed the entire French part of the continental shelf of the Bay of Biscay, which extends slightly more than four degrees in latitude (Fig. 1).

2.1. Anchovy sampling: Acoustics and fishing

Anchovies usually disperse very close to the surface at night and occur in the so-called blind zone, where they are not able to be detected using an echo sounder (the echo sounder transducer is fixed to the hull of the RV *Thalassa*, which has a 6 m draft**,** and a „near field" estimated at 1 m under the transducer is considered as a confusion layer where echoes can not be taken into account; therefore, a 7 m high „blind zone" layer in sub-surface prevents from any observation of anchovy at night). To accommodate the anchovy behavior in this area, acoustic data were only collected during the day. Identification of species in the echo traces was achieved by fishing with a 76/70 pelagic trawl net with a 20 m vertical opening and a 10 mm mesh cod end (Petitgas et al., 2003).

Acoustic data were collected along transects at a vessel speed of 10 knots using a calibrated Simrad EK500 and EK60 split beam echo sounder. The frequency used was 38 kHz, the beam angles were 7°/7°, and the pulse duration was 1 ms. The acoustic data were processed in Hac standard format (ICES, 2005) using Movies software (Weill et al., 1993), and stored throughout each survey. For each ping the sampling rate was 10 cm vertically. The ping rate varied according to bottom depth (e.g. at a vessel speed of 10 knots, a ping rate of 0.5 s provides samples of approximately 0.1 m in the vertical direction and 5 m in the horizontal direction along the sampled transect). To develop the acoustic abundance index the data were processed according to the French sea survey protocol (ICES, 2009).

2.2. Mesozooplankton sampling and enzyme analyses

During the 2000 cruise and subsequently, the studies carried out at sea were extended to adopt an ecosystem approach. Within this framework, enzyme activities (Bergeron et al., 2009) in the mesozooplankton communities, including aspartate transcarbamylase (ATC) activity, were measured until 2005, with the goal of assessing overall pelagic secondary productivity and identifying possible relationships between enzyme activity and interannual fluctuations in the biomass of anchovies in the Bay of Biscay.

Mesozooplankton sampling occurred at stations located along transects that were arranged approximately perpendicular to the coastline (Fig. 1). Samples were collected during vertical tows at a speed of 1 knot (~50 cm sec^{-1}) using a standard WP2 net (0.25 m^2 mouth opening, 200 μm mesh size; Anon., 1974) that was hauled from 5 m above the benthos (or from 200 m depth in the case of the few stations located in the oceanic province) to the surface. On board the vessel the macrozooplankton were separated from the sample by sieving through a 5 mm mesh. In order to limit a possible influence of the protein content of the sample on the determination of enzyme specific activity, the volume of mesozooplankton in the filtrate was roughly estimated with a graduated test tube, the mesozooplankton were homogenized in varying volumes (adjusted to varying quantities of mesozooplankton collected) using a Polytron® grinder, and 2.5 ml aliquots of the homogenate were immediately frozen in liquid nitrogen, where they were retained throughout the cruise. In the laboratory they were stored at –80 °C until analysis; this storage procedure does not introduce any significant change in enzymatic activities (Biegala and Bergeron, 1998). Following thawing the crude extract was homogenized again using a Potter–Elvehjem tissue grinder, and three aliquots (200 μl) of the resulting homogenate were used in the ATC activity assay. The assay was carried out according to the method initially described by Bergeron and Alayse-Danet (1981) and revised by Biegala and Bergeron (1998). Each sample was essayed in triplicate. ATC specific activity was expressed as nM CA (carbamylaspartate) produced min^{-1} mg^{-1} protein. The method of Lowry et al. (1951) was used to quantify the amount of protein present in the sample, using bovine serum albumin as the standard.

3. Results and discussion

During breeding most of the anchovy population occurs in the southern part of the Bay of Biscay, but subsequently moves progressively northwards (Motos et al., 1996). In this study, the concentration of the population was considered most important because the stock declined markedly towards the end of the study period, particularly from 2003 to 2005. Therefore, in comparison with the size of the mesozooplankton community sampled each year in the entire Bay of Biscay (Fig. 1), the number of samples taken at locations where anchovies could be detected was quite low (Table 1).

The overall productivity of the pelagic ecosystem appeared to strongly influence the dynamics of the anchovy population in the Bay of Biscay, because variations in the estimated annual biomass of anchovy, calculated between two successive years, were significantly correlated (Fig. 2) with the mean values of ATC specific activity measured in the mesozooplankton community present in the anchovy habitat during the breeding season of the previous year ($R = 0.928$; $p < 0.01$).

Such a close relationship might be surprising and considered too simple in light of the enormous research effort invested in identifying mechanisms regulating variations in annual recruitment of anchovy and determining the biomass available to fishing (e.g. Borja et al., 1998; Allain et al., 2001; Borja et al., 2008). However, the unexpected collapse of the population that occurred during the study period (Ibaibarriaga et al., 2008; Irigoien et al., 2009; Petitgas et al., 2010) may have created conditions revealing the relationship, by amplifying signals reflecting the contrasted conditions that affected the population.

Actually the study period covered a kind of turning point in the history of the anchovy population in the Bay of Biscay. Two successive years, 2002 and 2003, show very contrasted features regarding two criteria: the mean values of ATC specific activities are strongly different, more than ten times higher in 2003 (Table 1, Fig. 2), and the standard deviations represent the extremes (0.14 and 1.57) in the data series (Table 1). This extremely low value of ATC specific activity in the breeding season in 2002 was most likely an early sign of the impending collapse of the anchovy population. The spatial distribution of the breeding anchovies also changed considerably: classical feature in 2002, quite in accordance with general schema presented by Motos et al. (1996) and comparable to that observed in 2000 by Bergeron et al. (2009), strongly scattered in 2003, after a drop of the total anchovy biomass (Table 1). Even if the difference in timing of both cruises carried out in 2002 and 2003 (Table 1) may have had a small influence, the collapse is closely connected with the lowest mean value of ATC specific activity in mesozooplankton community.

In 2002 the demographic structure of anchovy in the Bay of Biscay was very unusual (Fig. 3). As a result of poor recruitment, the two-year-old cohort (i.e. individuals from the 2001 recruitment) was far more abundant (almost a factor of two) than the one-year-old cohort (ICES, 2010). Consequently, despite weak recruitment the total population biomass was almost the same as that measured during 2000 and 2001, representing a significant reproductive potential for the population. However, a progressive decrease in the recruitment process began from 2000 onwards: the proportion of one-year-old individuals in 2001 decreased in comparison with the two-year-old cohort, and the proportion of this two-year-old cohort progressively increased during the 2000–2002 period. This resulted in very little change to the total anchovy biomass (Fig. 3), as older individuals are bigger, and their greater weight compensated for their smaller number in terms of the total biomass.

Between the Pelgas cruise in 2002 and the cruise in the following year the anchovy stock in the Bay of Biscay collapsed (Fig. 3). The biomass of 111 10^3 t in 2002 declined to 31 10^3 t in 2003, representing a decrease of 72% (ICES, 2010) and reducing the biomass to a critical level for dependable stock exploitation. From 2003 a succession of management decisions proved difficult for fishers. Following the advice of the ICES (International Council for the Exploration of the Sea), the EU recommended a number of harsh measures ranging from partial closure of the anchovy fishery in 2005, to markedly reduced total allowable catch (TAC) in 2006 (to 5000 t), and finally to total closure in 2007.

A brief review of the major environmental events that occurred and their possible influences on the pelagic ecosystem during the six years of the study explain the difficulties faced by the anchovy population in the Bay of Biscay during this period. Recruitment variability has a critical impact on the population biomass of short-lived species, including the anchovy. Among the environmental driving forces thought to influence anchovy recruitment are stratification of shelf waters, upwelling, and the extent of river plumes (Borja et al., 1998; Allain et al., 2001). Riverine discharge of freshwater causing nutrient enrichment or hydrodynamic effects appears to have been a major factor during the period of this study. The 2001 spawning season was characterized by extremely high outflow rates from the Gironde estuary. Despite the positive effects on the pelagic ecosystem through enrichment with nutrients, and the subsequent improvement in nutritional conditions for the anchovies (Bergeron et al., 2010), the discharge had negative consequences for recruitment, possibly linked to the scattering of eggs and larvae from the spawning ground. Bergeron et al. (2010) reported that patches of less saline water were present in front of the river mouths; these apparently moved away from the coast under the influence of northwesterly winds (P. Lazure, IFREMER-Centre Bretagne, pers. comm.). This is consistent with the results from quantile regression models of fish recruitment–environment relationships (Planque and Buffaz, 2008), which suggest that early mortality of larval stages is likely (Allain et al., 2007). Following a very dry winter over the southwestern part of the French territory, the spring period in 2002 was characterized by very low freshwater outflows from the Gironde estuary (Fig. 4). This is the main source of nutrient enrichment for the anchovy breeding area; nitrate presented as an index of this enrichment is obviously in close correlation with freshwater outflows. In 2002 the pelagic ecosystem was the least productive among the years of the study. Comparable conditions occurred in the spring 2003 breeding period (D. Delmas, IFREMER-Centre Bretagne, pers. comm.), when even lower river outflow occurred during the two months preceding the research cruise (data not shown). However, the influence of the Gironde outflow on the anchovy population was probably less evident because the cruise was carried out later in the year (cf. Table 1), and the anchovies were dispersed over the entire continental shelf and subject to other variable and unknown environmental conditions.

The notion of a strong relationship between recruitment of a short-lived species such as anchovy and its exploitable biomass justified the numerous studies cited above, but this relationship is debatable. In two of the six years (2002 and 2005) in the relatively short time period of this study, age 2 individuals were far more abundant than age 1 individuals, although this was the case to a lesser extent in 2005. Therefore, in both these years the exploitable biomass for fishing was substantially greater than that forecast by modelling of the recruitment levels. The year 2002 was particularly illustrative of this situation. The decrease in abundance of the anchovy population was a progressive process that began as early as 2001, probably for the reasons mentioned above. From the point of view of the abundance of the resource, the real collapse ("depletion", according to Petitgas et al., 2010) occurred in 2003.

There is a broad consensus that zooplankton play a major role in processes affecting the recruitment of anchovies (Irigoien et al., 2009), either because of its direct role in the nutrition of this essentially zooplanktophagous species, or by reflecting the main environmental conditions at the crucial breeding stage. The ATC method, implemented as suggested by Bergeron (1983), was not focused on the spatial distribution or variations in zooplankton biomass, or its species composition, as usual in most zooplankton studies (e.g. Albaina and Irigoien, 2004, 2007; Zarauz et al., 2007, for the Bay of Biscay). The specific activity of ATC in mesozooplankton communities provides a dynamic view of the overall productivity resulting from integrated metabolic activities controlled by environmental conditions. "Life is complicated" is the first sentence of an article published by Whitfield (2004), and all zooplanktonologists would agree that this observation is very pertinent to zooplankton communities. However, instead of *complication*, we prefer the term *complexity*, i.e "an apparent disorder in systems where we have reasons to believe that an order exists" (Atlan, 1985), quite in accordance with the notion expressed by Platt (1981) emphasizing the difference between ecological and mechanical systems. Whitfield (2004) adds: "yet look inside a cell and life takes on, if not simplicity, then at least a certain uniformity", which is a statement very relevant to the cells of copepod species. According to Stebbing and Heath (1984), "at higher levels of organization we see a constancy in subcellular ultrastructure and typically far greater differences exist within organisms than between them". Earlier, Schoffeniels (1973) stressed "the biochemical unity of biological systems", and according to Margalef (1968), from a cybernetic point of view the notion of the unity of biological systems can be widened to ecosystems and their functioning. This eminent planktonologist emphasized the multiplicity of possible perception scales in ecology, and linked this to the cybernetic nature of ecosystems through one of the fundamental properties of dissipative systems: their conceptual divisibility into dissipative sub-systems with the same statistical conditions of stability (Frontier, 1977). Consistent with the views of Margalef (1968), ecosystems and their sub-systems (including mesozooplankton communities) are not super-organisms, but they show cybernetic properties suggestive of this. However, the mechanisms governing their functioning are analogous to, but are not, cybernetic systems, as noted by Patten and Odum (1981), who observed that "analogy, and the willingness to accept it, are the keys to identifying the cybernetic machinery of the ecosystem". Such arguments are not readily accepted by the large majority of the scientific community, which tends to view analogy as not following sufficiently rigorous scientific processes. Nevertheless, the analogy with cybernetic systems brings a persuasive heuristic perspective to the infinite complexity (*sensu* De Rosnay, 1975) of ecological systems.

Analogous concepts were advanced almost three decades ago (Bergeron, 1983, 1986), mainly based on considering a mesozooplankton community as a system (*sensu* "system approach") or entity presenting overall detectable properties. Early field implementation of ATC activity measurements was made in ecosystems particularly favorable to this approach, including the western part of the English Channel and its entrance (Mer d'Iroise). As a consequence of the unique hydrodynamics of this region, notably a west–east residual circulation mainly driven by tidal currents (*la rivière Manche* of Salomon and Breton, 1991, 1993), mesozooplankton systems are homogenized by vertical mixing, which simplifies sampling of this sub-system. The early studies produced encouraging results (Bergeron, 1986, 1990, 1993). In the Bay of Biscay the hydrodynamics are much more complicated (Koutsikopoulos and Le Cann, 1996; Planque et al., 2004), particularly because of large estuarine outflows over the continental shelf (Lazure and Jegou, 1998). Nevertheless, studies carried out in the small pelagic fish program in the Bay of Biscay (particularly concerning the anchovy) clearly showed that ATC activity was enhanced at locations where conditions (often driven by physical factors) were favorable to greater mesozooplankton productivity, and *vice versa* (Bergeron et al., 2009, 2010; Bergeron and Koueta, 2011). Bergeron (1986) assumed the situation to not be so simple, based on results indicating that areas very close to the coast of the western English Channel are more complex. These areas are highly variable because of the very rugged coastline and extensive mixing linked to strong tides and winds. In contrast, in the Bay of Biscay there is great variability among the hydrological structures, but they are generally not so changeable. For instance, freshwater flowing from rivers overlays more saline and higher density water; this creates a double layer system that remains quite stable at the mesoscale level, provided that no strong or sudden disturbance occurs (as defined by Mann and Lazier, 1991).

The main interpretation of the results presented here appears very simple in light of the multiple variables potentially regulating the abundance of anchovies in the Bay of Biscay. However, several factors provide evidence for this relationship. First, this is thought to be a relatively small population with a spatially well-defined habitat, at least during the breeding season. Second, the effects of the unique events that occurred during the study period may have been amplified because of the reduced size of the population at this time. Clearly a longer time series will be necessary to confirm our findings and assess the value of including ATC measurements into surveys of the anchovy population in the Bay of Biscay.

More than thirty years ago, Mann (1981) stated that “for understanding biological oceanographic systems, it is necessary to have at least as much information on the fluxes as on the biomasses”. The results of this study suggest that determining the ATC activity in mesozooplankton samples could aim at following such a promising notion and provide a useful tool for directly assessing the dynamics of pelagic ecosystem productivity and its effect on the anchovy population dynamics.

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Tables

Table 1. Cruise and biomass data for the anchovy population in the Bay of Biscay.
The data are used to compare (1) the mean values of ATC specific activity measured in samples collected at locations where anchovies were detected through acoustics in spring of the year y_i and (2) the variation in anchovy biomass between this estimated in the year y_i and that estimated in spring of the following year y_{i+1}.

Date of cruise	No. samples analysed	Mean ATC specific activity	S.D.	Biomass* (x 1000 t.)	Yearly biomass variation (%)
17/4-13/5 **2000**	13	**0.758**	0.557	113	**-0.062**
27/4-5/6 **2001**	14	**1.291**	1.135	106	**0.047**
10/5-4/6 **2002**	15	**0.186**	0.138	111	**-0.721**
30/5-23/6 **2003**	13	**1.948**	1.569	31	**0.484**
29/4-22/5 **2004**	10	**0.981**	0.553	46	**-0.674**
5/5-25/5 **2005**	7	**2.589**	0.456	15	**1.067**
2006				31	

*from ICES (2010)

Figures

Figure 1. Chart of the study area over the Bay of Biscay continental shelf. Each black point represents a sampling station of the mesozooplankton community. Squares indicate the presence of anchovies (varying intensity of grey is function of the number of samples taken during the study period in proximity to shoals of anchovies detected through acoustics and confirmed by trawling). Major nutrient-enriched freshwater inflows are indicated by river names.

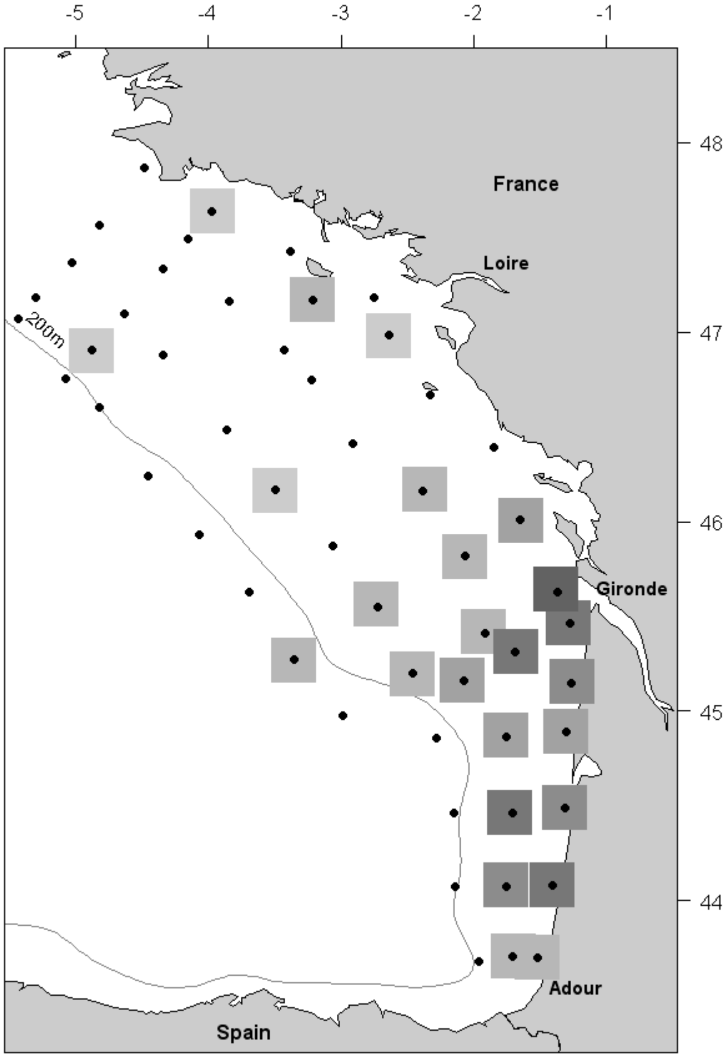

Figure 2. Least squares regression presenting the relationship between mean values of mesozooplankton ATC specific activity determined during spring of one year y_i and anchovy population biomass variation (y_{i+1} - y_i) until spring of the following year. Vertical bars indicate standard deviations (cf. Table 1).

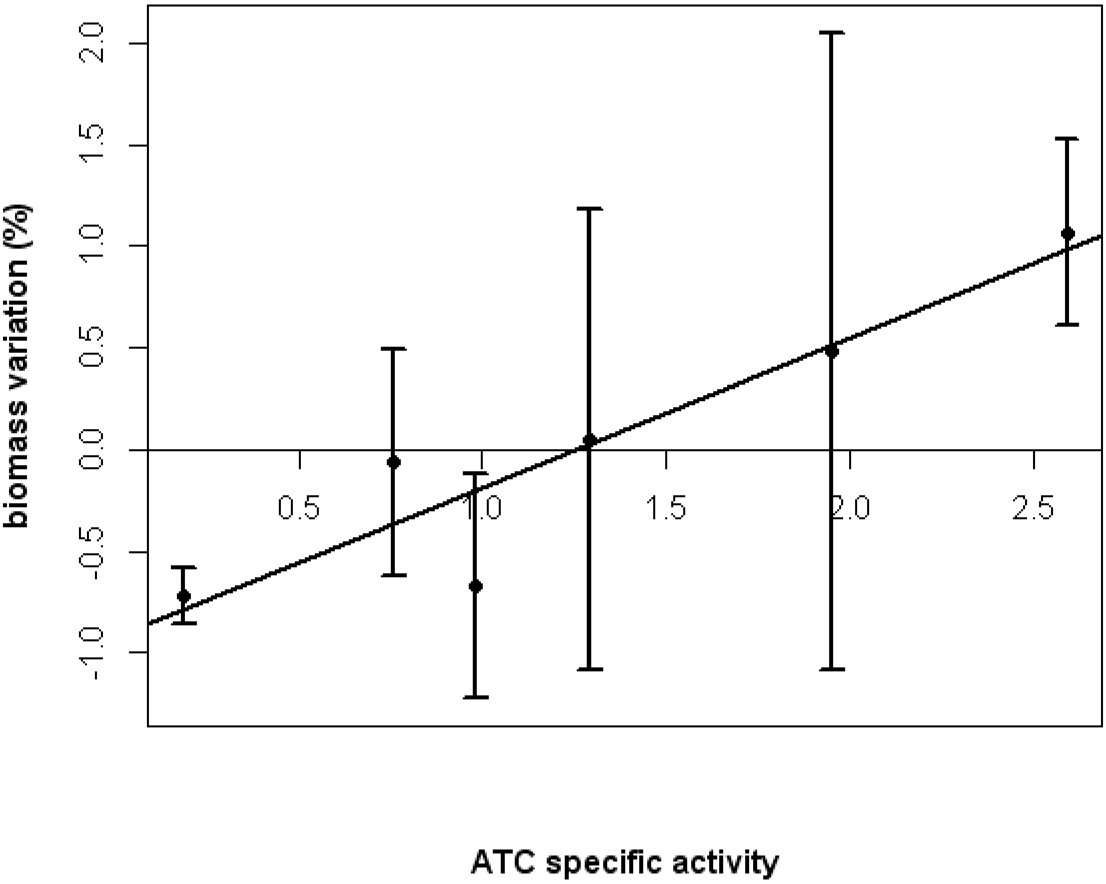

Figure 3. Anchovy biomass in tons (grey rectangles) and population demographic structure (hatched columns show the numbers of 1-, 2-, and 3-year-old individuals, from left to right in the grey columns) during the period 2000 to 2003.

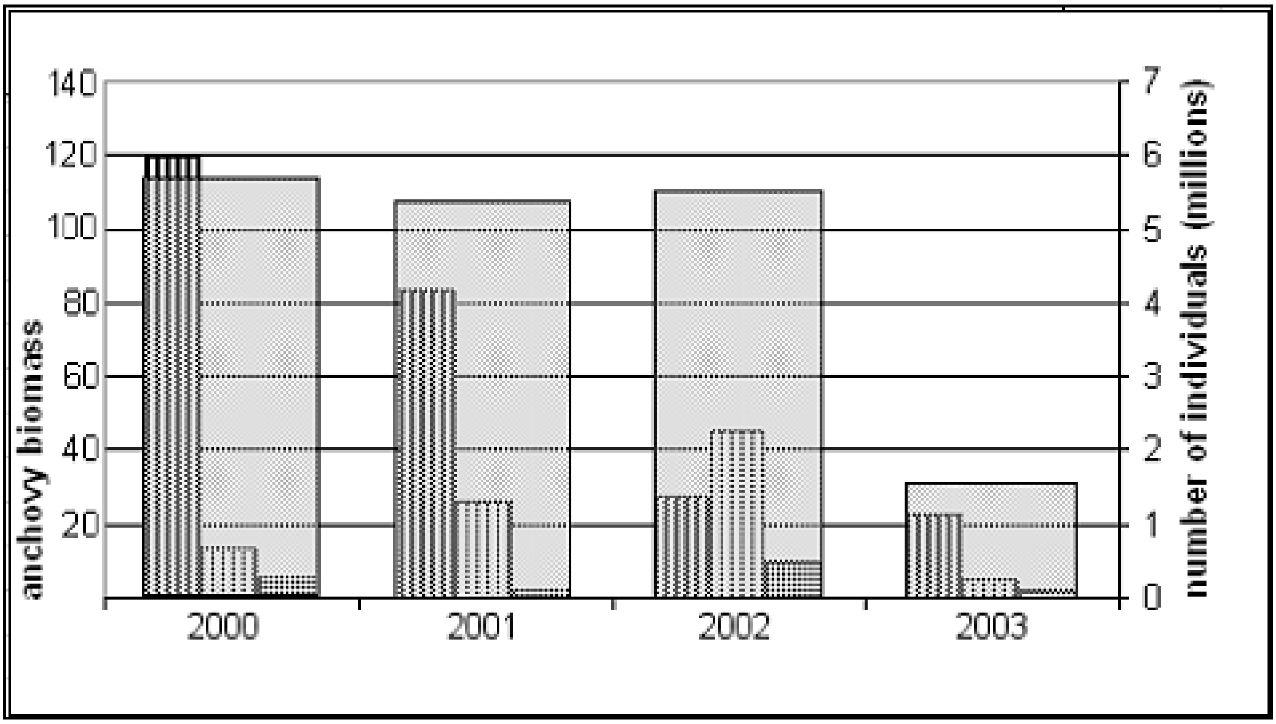

Figure 4. Late winter–early spring (1 January–1 May) variations in nitrate concentration in outflows from the Gironde Estuary during the period 2000 to 2002.