



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.

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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;

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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 (north-east 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 cannot 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

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