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Determining how the pelagic ecosystem over the continental shelf of the Bay of Biscay (NE Atlantic) functions: An approach using mesozooplankton enzyme activities as descriptors

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Abstract:

A fisheries research cruise conducted in 2000 offered a first opportunity to take simultaneous measurements of the activities of three enzymes in mesozooplankton samples collected at a regional scale over the continental shelf of the Bay of Biscay in the NE Atlantic, with the aim of characterizing main aspects of the functioning of the biotic environment of small pelagic fish populations. The activity of the digestive endopeptidase trypsin was selected to characterize the assimilation rate of proteins, whereas pyruvate kinase (PK) was chosen as an indicator of carbohydrate assimilation and aspartate transcarbamylase (ATC) provided an overall assessment of mesozooplankton productivity. The Bay of Biscay region is subject to various strong physical driving forces that directly affect the primary structure of the pelagic food web. On our cruise, the phytoplankton biomass distribution reflected these different physical influences: diatoms dominated the nutrient-enriched coastal water; picoplankton dominated the northern-central part where nutrients were depleted; and nanoplankton were abundant at the shelf break where internal waves provided an input of nutrients. These and other results (on bacteria, particulate organic carbon distribution, among others) illustrate the differences that exist in the microbial food webs of different sectors of the bay. The living matter produced was characterized by the quality and quantity of the smallest prey items that were available to higher trophic levels. Variations in mesozooplankton enzyme activities may agree well not only with classically expected results, but also present unexpected special features: high ATC specific activities were measured around the mouth of the Gironde, in the nutrient-rich desalted water of the plume, but surprisingly not in front of the Loire river. PK specific activities reflected preponderantly the balance between phytoplankton cells sizes and the related bacterial abundance resulting from nutrient limitation (mainly P), that induces varying carbohydrates production potential. Trypsin specific activities were moderately variable, except in a restricted area where a highly abundant protein content characterized the particulate matter and in the plume of water flowing out of the Gironde. It is concluded that the presented approach of the metabolism of mesozooplankton communities may provide novel views on crucial processes occurring at the mesoscale, which fits in generally well with the scales of ecological factors mostly influential on small pelagic fish populations.

Keywords: aspartate transcarbamylase; Bay of Biscay; mesozooplankton; metabolic descriptors; pyruvate kinase; trypsin

1. Introduction

Pelagic marine systems have quite different characteristics according to their location in the world's ocean. As recently demonstrated for the Bay of Biscay in the NE Atlantic (Bergeron, 2004), the pelagic environment over its continental shelf experiences many extrinsic physical drivers. It is a patchwork of different ecosystems, including (1) coastal systems influenced either by river plumes or local upwelling caused by special wind regimes and (2) oceanic systems along the shelf break, where deep water may be up-welled or large eddies may form. 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 (Albaina and Irigoien, 2004; 2007). Different environmental conditions can result in substantially different mesozooplankton species composition, biomass, and metabolism (e.g. Bergeron, 2004; 2006). Mesozooplankton, which prey on small particles such as phytoplankton and protozoans, in turn serve as prey for the abundant small pelagic fishes. Thus, following Banse (1995) (although he included heterotrophic protozoans in the more general term "zooplankton"), one may consider that mesozooplankton (*sensu* Sieburth et al., 1978) play a "pivotal role in the control of ocean production".

The bulk of mesozooplankton consist of copepods; these small crustaceans often constitute as much as 80% of the biomass, and often even more for the Bay of Biscay (i.e., 92–98% according to Plounevez and Champalbert, 1999). Copepods are probably the most numerous multicellular organisms on earth (Mauchline, 1998). Marine copepods form a relatively homogeneous zoological group, occupying a strategic place in pelagic food webs. Moreover, some aspects of their life cycle are especially interesting, such as their

103 permanence and omnipresence in marine systems and the fact that their generation time fits
104 in generally well with the duration of mesoscale events and spatial structures occurring in
105 pelagic systems. Such mesoscale events and features are often those most crucial for the
106 study of the environment of marine fish populations. The position of the mesozooplankton
107 in the complex organisation of pelagic ecosystems suggests their importance for generating
108 an integrated view of the channelling of energy and organic matter through the autotrophic
109 and heterotrophic components of the pelagic food web into marine resources, both to direct
110 consumers of mesozooplankton and to predators higher in the ecological hierarchy.
111
112 With the aim of easily assessing basic processes in pelagic ecosystems, a number of
113 conceptual assumptions (Bergeron 1983; 1986; 1995) have been advanced to justify
114 enzymatic activity measurements of samples of the whole mesozooplankton community.
115 While it must be acknowledged that such methods are grounds for some criticisms (e.g.,
116 Berges et al., 1993), interest in their implementation endures because they provide the
117 fastest, simplest, and least expensive means of assessing mesoscale variations in important
118 metabolic features (e.g., Packard et al.'s (1996) study of ETS activity for estimating the
119 respiration process). The use of such methods is especially important from a fisheries
120 research perspective, because synoptic cruises must generally be performed over broad
121 areas as quickly as possible; this is notably the case for the ecological studies of small
122 pelagic fish populations carried out by our research team in the Bay of Biscay (Scalabrin
123 and Massé, 1993).
124
125 The fundamental basis of enzymatic methods is their specificity with regard to the targeted
126 metabolic process. If uncertainties about the reliability of such an approach persist from a
127 fundamental view of biochemical practice, the hope is that assessing enzyme activities is

essentially monitoring rates of realization of metabolic steps. Accepting that stoichiometric relationships between enzyme activities measured in a sample of the whole mesozooplankton community and the ecosystem rates of specific metabolic processes are most probably out of reach, nevertheless enzyme activities theoretically express a dynamic view of the processes involved (i.e., they have the dimension of $time^{-1}$, which is a highly valuable property). Therefore, an enzyme's activity can be used as a proxy for a metabolic process; it is an index that uses relative values, which permits comparisons of samples taken in the marine area under study.

The goal of this study was to measure the activities of three enzymes to assess two main processes: (1) the transfer of particles into the mesozooplanktonic compartment by feeding, and (2) the secondary productivity resulting from the assimilation of food. Proteins and carbohydrates are two of the main components of living particulate organic matter, and they represent the largest quantity of the food ingested by copepods. Protein ingestion and assimilation have been classically estimated through the activity of the digestive enzyme trypsin, as initially suggested by Boucher et al. (1976) and measured by many others (e.g., Båmstedt, 1988; Hirche, 1989; more recently Lischka et al., 2007). Because of the diversity of the macromolecular structure of carbohydrates, their crude molecules require specific digestive enzymes to be assimilated in a first step (cf. p. 168, Table 4.1., in Mayzaud, 1986). In this study, we did not follow the methods based on digestive enzymes used by previous authors (cf. Mayzaud, 1986), but preferred measures of pyruvate kinase (PK) activity, according to concepts advanced by Bergeron and Herbland (2001), as an indicator of carbohydrate assimilation. PK operates at the end of the glycolysis chain, an intracellular catabolic pathway common to all classes of carbohydrates. Finally, the overall bulk mesozooplankton productivity was estimated with aspartate transcarbamylase (ATC),

153 an enzyme involved in the biosynthesis of pyrimidine bases used to build nucleic acids for
154 cell multiplication and protein synthesis. In short, trypsin activity should indicate protein-
155 rich diet assimilation by mesozooplankton (dominance of a microbial loop or presence of
156 heterotrophic protozoans for instance, among other protein-rich food items); PK activity
157 should indicate carbohydrate assimilation (grazing on phytoplankton, or other
158 carbohydrate-rich prey); and ATC activity should permit the characterization of the overall
159 mesozooplankton productivity resulting from the assimilation of these two classes of
160 molecules.
161

162 We present here the results of our first opportunity to measure activities of all three
163 enzymes simultaneously in the same mesozooplankton samples collected over a relatively
164 large scale (about 4° in latitude) across the continental shelf of a temperate area in spring
165 of the year 2000. Petitgas et al. (2006) previously incorporated these enzyme activities into
166 a set of more than fifty variables, permitting data processing based on statistics. Their aim
167 was to cluster stations according to different hydroplankton characteristics in an attempt to
168 define the environment of two populations of small pelagic fish in the Bay of Biscay. We
169 reconsider these data here in an alternative spirit, in a more naturalistic way, in search of a
170 way to characterize different food web functional types and rates of channelling matter and
171 energy from primary producers (here defined as phytoplankton and bacteria) to higher
172 trophic levels. The ultimate target of the present work is determining to what extent this
173 small set of three enzyme activities is able to give a coherent and reliable picture of the
174 overall functioning of the pelagic ecosystem providing useful information on the factors
175 influential on the zooplanktivorous small pelagic fish populations of the Bay of Biscay.

176

2. Materials and methods

The PEL2000 research cruise, which also was devoted to the study of the abundance and spatial distribution of small pelagic fishes using acoustic tools (Scalabrin and Massé, 1993), occurred from April 17 to May 13, 2000 aboard the RV Thalassa. It covered the entire French part of the continental shelf of the Bay of Biscay (i.e., a little more than 4° in latitude). Mesozooplankton sampling occurred at stations located along transects that ran roughly perpendicular to the coast line: 69 mesozooplankton samples were collected (Figure 1).

Water samples

Water samples were collected at five depths for measurements of nutrients, chlorophyll, bacteria, and particulate organic carbon (POC), following a reduced sampling grid (46 stations, cf. Figure 1). The methods used for nutrient and primary producer analyses followed Petitgas et al. (2006) and will not be described here. Phytoplankton carbon was estimated from Chl *a* concentrations assuming a constant C:Chl *a* ratio of 50:1; bacterial numbers were converted into bacterial carbon assuming a standard cell content of 16 fg C that corresponds to the range of values (10–18 fg C) previously measured by Artigas (1998) in the Bay of Biscay. Because phytoplankton and bacteria constitute the main component of the microbial assemblage, we assumed that their carbon represented an approximation of the microbial carbon.

We determined two ratios from these data:

(1) (microbial C)/POC gives a picture of the living carbon in micro-organisms in relation to the total POC. The difference, total POC – microbial C roughly represents detrital carbon.

(2) (bacterial C)/(phytoplankton C) represents an index of ecosystem development through different physiological states of the phytoplankton community.

Mesozooplankton samples and enzyme analyses

Mesozooplankton samples were collected by 50 cm sec^{-1} vertical tows with a WP2 net (200-µm mesh size) from the bottom (or from 200 m depth in the case of the few stations located in the oceanic province) to the surface. On board, the macrozooplankton collected were separated by sieving through a 5-mm mesh. The mesozooplankton in the filtrate were homogenised in iced distilled water with a Polytron® grinder. Then, 2.5-ml aliquots were immediately frozen in liquid nitrogen and kept in liquid nitrogen until the end of the cruise. Thereafter, they were stored at –80 °C until analysis in the laboratory, as this storage procedure does not introduce any significant change in enzymatic activities (Biegala and Bergeron, 1998). After thawing, the crude extract was homogenised again with a Potter–Elvehjem tissue grinder, and a 200-µl aliquot of the resulting homogenate was reserved for the ATC activity assay. The rest of this homogenate was centrifuged (10 min at 4000 rev min^{-1}, 3 °C) and 200-µl aliquots of the supernatant fluid were assayed for other enzymes or for protein content. Trypsin activity was estimated by the classical "BAPNA method" adapted to zooplankton extracts by Samain et al. (1977), pyruvate kinase activity according to Bücher and Pfleiderer (1955), modified by Bergeron and Herbland (2001), and ATC activity as initially described by Bergeron and Alayse-Danet (1981) and revised by Biegala and Bergeron (1998).

PK specific activity is expressed in μM NADH oxidised min^{-1} mg^{-1} protein; trypsin specific activity in μM *p*NA (paranitroaniline) released min^{-1} mg^{-1} protein; and ATC specific activity in nM CA (carbamylaspartate) produced min^{-1} mg^{-1} protein.

227 In the figures below, specific activities of enzymes measured in mesozooplankton samples
228 are presented as square symbols. For each enzyme, three classes of values were arbitrarily
229 defined according to the frequencies of these values in each class in order to have a well-
230 balanced distribution.

3. Results

Hydrobiological environment

Among the strong physical drivers in the Bay of Biscay, two are permanent but vary in their effects according to seasonal conditions. Moreover, they exert opposing influences because one brings freshwater, the other high salinity waters. However, they both provide inorganic nutrients to surface waters over the Bay of Biscay shelf. First, two large rivers, the Loire and the Gironde, debouch into the middle-northern part of the region. There is also a smaller river in the south, the Adour, which is generally at its outflow maximum during the breeding season (around May) of the anchovy population; this is water issuing from the spring thaw of snow in the nearby Pyrenees Mountains. The influx of freshwater is clearly indicated by the low salinity of surface waters along the coast (Figure 2). The consequent enrichment in inorganic nutrients (e.g., nitrate, cf. Figure 3) is also evident in the coastal area. The spatial variations of nitrate concentration in surface waters (Figure 3) show that another source of nutrients exists over the shelf break, the up-welling of deep waters (highest surface salinity for the region, 35.6) induced by strong tidally induced internal waves. The phenomenon is revealed by satellite imagery (Figure 4 shows a view at the same stage of the seasonal cycle, though not from the year of the cruise; Gohin et al. (2005) demonstrated that this process is recurrent, at least for the period 1998–2003 and that the picture presented is reliably representative) and its effect on primary production, in terms of Chl *a*, appears clearly in a vertical hydrological section along the continental slope (Figure 4). This surface layer enrichment plays a prominent role in this oceanic-like part of the bay. From satellite imagery, it is possible to infer that an area ~50 km wide and several hundred km long and over a depth of about 40 m is enriched by this internal wave process.

The size structure of the phytoplankton community can be described by three categories: microphytoplankton (cells > 20 μm); nanophytoplankton (cell sizes between 3 and 20 μm); and picophytoplankton (cells < 3 μm). Microphytoplankton, which is essentially composed of diatoms, dominated in nutrient-enriched coastal waters and in the southern part of the bay (Figure 5). Nanophytoplanktonic cells were mainly present in the northwest. Picophytoplankton were absent along the coast but were abundant in the northern and central part of the bay. In this latter area, nutrients were almost exhausted (Figure 3) and picophytoplankton were dominant. The low percentage of microbial carbon (Figure 6) suggested that the POC was essentially detrital. The bacterial biomass was high in comparison with the phytoplankton biomass (> 25%, cf. Figure 7), which indicated that a microbial loop was actively operating and that regenerated production was significant.

Mesozooplankton enzymatic indices

PK specific activities did not appear to be enhanced by inflow of nutrient-rich freshwater from rivers in coastal areas (Figure 8a), despite conditions favourable *a priori* for stimulating photosynthetic carbohydrate production. Conversely, stations along the shelf-break exhibited some of the highest PK activities, which were probably enhanced by ingestion of phytoplankton cells enriched in carbohydrates produced by active photosynthesis through the supply of nutrients in up-welled deep waters; here PK activities were clearly influenced by variations in phytoplankton biomass in terms of Chl *a* (Figure 4). However, a highly significant correlation ($R = 0.639$, $DF = 45$, $p < 0.001$) linked the spatial variations of PK specific activities to the ratio of (bacterial C)/(phytoplankton C), and this relationship was valid for all of the stations sampled during the cruise.

A small group of four stations in the northwest sector of the sampled area (in the region of 47°N, 5°W; see open circles in Figure 1 that specify the positions accurately) exhibited some of the highest values of trypsin specific activity (Figure 8b). The mean value for these stations was 5.77 (S.D. = 0.18), whereas the mean for the whole (82 stations) was 4.10 (S.D. = 1.03); these four stations were situated close to the one where the water column sampling had the highest value of integrated particulate protein: 3.81 g m^2. The mean for the other 44 hydrobiological stations was 1.64 (S.D. = 0.34). Such a strong coincidence is worth noting. Except for this special case, trypsin activities did not vary greatly across the bay as a whole. There were, however, three high values along the coast, especially in less saline water flowing from the Gironde estuary (Figure 2); this difference could be related to the higher abundance of detrital POC in this water (Figure 6), as mentioned above.

Theoretically, ATC specific activities reveal the global productivity of mesozooplankton communities and should be partly conditioned by the efficiency of primary processes represented by the enzymes PK and trypsin. The ATC activities were weak everywhere in the Bay of Biscay, except over the shelf break and along the coast, where moderate or high values were observed (Figure 8c). Taking into account the width of the area enriched by up-welled deep waters along the shelf break, it may be considered that the two high and four moderate values of ATC activity in this area resulted from this enrichment. Along the coast we found the highest ATC activities, and these were related to less saline waters entering from rivers. Moderate activities were not much lower than the highest ones, especially in front of the mouth of the Gironde estuary. In contrast, the stations around the mouth of the Loire River did not show any remarkable features. It should be noted that, along the coast, ATC activity variations were somewhat correlated with those of trypsin

306 and were inversely related to the mean values of the (microbial C)/POC ratio found in the
307 three major plumes (shown in Figure 6) estimated for waters influenced by freshwater
308 from the rivers.
309

4. Discussion

A highly important point has to be raised first, as a preliminary of the discussion section. Phytoplanktonologists and zooplanktonologists generally do not use the same language, i.e. similar expressions to present their descriptors. This is because the spatial variation scales are strongly different and most of the small particles (in a generic sense) they study often are presented as integrated values (per m^2) for the photic layer in the case of particles produced at the primary level. In contrast, because of the well-known patchiness distribution of zooplankton (e.g. Steele, 1977; Williamson et al., 1986), their descriptors must be related to a weight-linked reference, i.e. dry weight or, as in the present study, protein content. Otherwise, an expression of enzyme activities analogous to that of primary producers (per m^2) would be essentially representative of values influenced by spatial variations of zooplankton biomass. For this reason, formal relationships valid for the whole studied region between both main types of descriptors are difficult to establish, in particular to test statistically, except for instance in the case of the bacterial C / phytoplankton C ratio, which is typically a descriptor based on relative values. A statistical treatment of this data set has been previously presented by Petitgas et al. (2006). These data are reconsidered here in an alternative spirit: what the hydrobiological descriptors tell us about the structure and functioning of the pelagic ecosystem and how the mesozooplankton communities adapt to this environment.

4.1. Significance of the metabolic descriptors

Among the three descriptors used in the present study, PK activity is the newest enzymatic tool for evaluating the metabolic ecology of mesozooplankton. It was initially promoted with the hope of obtaining a global assessment of carbohydrate assimilation by mesozooplankton (Bergeron and Herbland, 2001). The underlying concept was that the

generic reaction occurring under the catalytic action of chlorophyll may be summarized as $CO_2 + H_2O \rightarrow HCHO + O_2$, where HCHO symbolizes the basic elemental ratio of carbohydrates. However, phytoplankton actively growing in exponential phase are also very rich in protein (Haug et al., 1973; Granum et al., 2002); this could explain why large phytoplankton cells in the river plumes did not contain carbohydrate in sufficient quantity to induce enhanced PK activity. The observed correlation between PK specific activities and the ratio of bacterial C to phytoplankton C suggests a highly valuable significance of PK specific activity: it is able to provide an overall view of ecosystem development through different physiological states of the phytoplankton community. This ratio is low when phytoplankton are blooming in nutrient replete waters (Cho and Azam, 1990; Simon et al., 1992). In contrast, the ratio is high in post-bloom periods, when phytoplankton are severely nutrient limited. Under nutrient limitation (N or P), phytoplankton cells respond with high production of both particulate and dissolved carbohydrates, in relation to proteins, and carbohydrates are favourable to development of bacteria (Granum et al., 2002; Børsheim et al., 2005). During such post-bloom periods, regeneration processes control phytoplankton growth. The potential interest of PK application has previously been demonstrated in a special case of very low enrichment in nutrients of a river plume (Bergeron, 2006). Anyhow, the significance of enhanced carbohydrate assimilation by mesozooplankton through an increase of the PK specific activity does not seem to be fundamentally disputable from a theoretical point of view.

Certainly it is dangerous to draw definite conclusions from one single data set; nevertheless, in the present study high PK activities occurred in locations where mesozooplankton could graze on large phytoplankton cells (> 20 µm) under conditions apparently permitting new production: enhanced PK activity occurred in such conditions in

361 the south of the bay, but also where phytoplankton were small and nutrient limited, a
362 condition favourable to hyper-production of carbohydrates according to an abundant
363 literature (e.g., Granéli et al., 1999; Alderkamp et al., 2006). Between these two radically
364 contrasting ecological contexts, intermediate situations obviously contribute to the global
365 correlation that links variations in PK specific activities to the ratio of bacterial C to
366 phytoplankton C. A continuum exists, like that advanced by Legendre and Rassoulzadegan
367 (1995), between two contrasting pathways for the flux of biogenic carbon (i.e., the
368 herbivorous and the microbial food webs). Therefore, results from PK activity
369 measurements in mesozooplankton might require to be interpreted cautiously, at least with
370 respect to evaluating assimilation of autotrophic cells.
371
372 But in another respect, one may wonder what is the most important information to obtain
373 about the function of a pelagic ecosystem. Is it crucial to demonstrate that a certain type of
374 phytoplankton cells constitutes a principal food source to mesozooplankton compared to
375 other types, or can the process be viewed from another angle, as recommended in recent
376 essays on ecological thinking (Whitfield, 2004): with respect to the purely metabolic
377 process, the essential question is what quantity of carbohydrates enters the
378 mesozooplankton compartment, a pivotal link of the pelagic food web (in accordance with
379 Banse, 1995). The basic concept may be restated: a measurement of PK activity in a
380 mesozooplankton sample evaluates a process working at the cellular level (i.e., the
381 functional rate of the last enzyme of the glycolysis chain, which depends on the
382 assimilation of all ingested carbohydrates).
383
384 In the estuary plumes, we found relatively high activities of trypsin in accordance with the
385 richness in protein of actively growing autotrophic cells. However, living particles do not

386 offer a sole type of prey for mesozooplankton (e.g., Poulet, 1976) and another source of
387 organic matter might explain high trypsin and ATC activities. For example, the suspended
388 particulate matter (SPM) present in estuarine waters to variable extents (Tackx et al., 1995;
389 Gasparini et al., 1999) may play, with associated micro-organisms and notably ciliated
390 protozoans, an important role in copepods feeding (Heinle et al., 1977). As recently
391 pointed out (Håkanson, 2006), the carbon content of SPM is crucial at low trophic levels:
392 the SPM in the water column is also a metabolically active component of the food web. In
393 our study, the Gironde estuary is well known for its high levels of SPM (e.g., Castel and
394 Feurtet, 1989; David et al., 2005) mainly made up of a large fraction of particulate organic
395 carbon (Irigoien and Castel, 1995). This could explain why the (microbial C)/POC ratio is
396 in front the Gironde estuary is the lowest out of the three estuaries, it means that the POC
397 is essentially detrital, it is quite in agreement with the generally accepted concept of the
398 Gironde carrying seaward much more SPM than does the Loire estuary. Accordingly, we
399 also found large differences in the trypsin and ATC activity levels in mesozooplankton
400 collected immediately offshore from them. Thus, we hypothesize that detrital matter
401 released from rivers induces a strong local enhancement of mesozooplankton productivity,
402 as revealed by high ATC specific activities, particularly offshore of the Gironde estuary.
403
404 In contrast with coastal mesozooplankton, which are contained along the coast by a
405 residual circulation driving waters to the north (cf. isohalines in Figure 2), the up-welled
406 deep waters along the shelf break tend to spread beyond the slope, inducing a relatively
407 wider but more diluted enrichment, which is revealed by the extent of higher nitrate
408 concentrations at the surface. This phenomenon has an effect on PK activity and to a lesser
409 extent on trypsin. The consequence for ATC activity appears to be a dilution effect; we
410 found two high values on the fringe of the area concerned.

411

412 All of the data presented in this study were gathered during a fisheries research cruise
413 devoted to small pelagic fishes in the Bay of Biscay. Abundance and spatial distribution of
414 these populations were estimated through acoustic tools (Jacques Massé, Dept. EMH,
415 IFREMER, Manager). Sardines (*Sardina pilchardus*) and anchovies (*Engraulis*
416 *encrasicolus*) are by far the dominant small pelagic species in this region, and results of
417 this investigation provide indices about spatial variation of pelagic productivity (Figure 9).
418 Anchovies mainly accumulate along the southeastern part of the coast, whereas sardines
419 are more scattered throughout the bay, with low abundance in the south, greater abundance
420 in the middle-northern part along the shelf break, and only a few echoes detected in the
421 northeast along the coast. Anchovies are strictly zoophagous throughout their life.
422 Although small sardines (no longer than 18 cm) also are zoophagous, as they grow they
423 develop a filter feeding system, and individuals longer than 18 cm become
424 phytozoophagous, or mixed feeders (Garrido et al., 2007). Sardines show differential
425 behaviours according to their size: Small individuals live in surface layers and larger
426 individuals live in deeper layers (Jacques Massé, Dept. EMH, IFREMER, pers. comm.).
427 Therefore, anchovies and small sardines occur in relatively shallow waters in coastal areas.
428 In the open sea, and especially over the shelf break, anchovies are scarce, small sardines
429 live in surface layers, and large sardines inhabit deeper layers where they feed on the deep
430 phytoplankton (as indicated by the presence of Chl *a*, cf. Figure 4). The greatest abundance
431 of the carnivorous anchovy occurred near the mouth of the Gironde estuary (Figure 9),
432 which most likely indicates a strong attractive effect of the enrichment of the adjacent
433 marine area upon the breeding anchovy population. This is in itself an index of
434 zooplankton productivity, which also is clearly supported by high ATC activities.
435 Accumulation of anchovy biomass coincident with high ATC activities extended to the

436 southern part of the bay (i.e., from 44°30 N until the northern limit of low salinity coastal
437 water flowing out from the Gironde).
438
439 The respective distributions of the two fish species illustrate that the central-northern part
440 of the bay is a biological desert in regard to fish spawning in spring, an observation made
441 often in previous years and even over several decades (Arbault and Lacroix, 1977). From
442 recent work on the typology of hydrological structures over the Bay of Biscay shelf,
443 Planque et al. (2006) characterized six main hydrological zones, of which one presents
444 strongly distinctive features, notably a deep mixed layer and the greatest stability over
445 time. This zone coincides with the desert, where surface nutrients are almost exhausted,
446 picophytoplankton are dominant, and high PK specific activities were measured in
447 mesozooplankton samples in this study. In this nutrient-limited area, small-sized
448 phytoplankton cells control regeneration production and the apparent hyper-productivity of
449 carbohydrates is linked to an actively working microbial loop. However, the final
450 disposition in the ecosystem of the excess carbohydrate production implied by the
451 enhanced PK activity is unknown, at least so far as the pelagic ecosystem is concerned.
452 This hydrographic zone coincides with La Grande Vasière, a benthic area well known by
453 fishermen for its enhanced biological productivity and where intense fisheries activity,
454 mostly by trawlers, occurs (Léauté, 1998). Thus, this vast area may well serve as a trap for
455 products sinking from the diatom late winter bloom that occurs in the distal plume of the
456 Loire river (Gohin et al., 2003). Lateral transport from higher on the shelf also may be
457 important, playing the role of a kind of rack for feeding of fishes inhabiting the immediate
458 vicinity.
459
460 *4.2. Ecological regionalism of the Bay of Biscay*

In this study, we found substantial differences in the levels of both metabolic descriptors and ecological processes at different sites in the Bay of Biscay. It is important to keep in mind, however, that the depths of sampling stations ranged from 15–20 m in estuary mouths to more than 200 m over and beyond the shelf break. If one accepts the assumptions presented in the introduction inherent in the use of our metabolic assessment tools as proxies for the main processes involved in the functioning of mesozooplankton communities, then our data lead us to propose the following spatial compartmentalization.

4.2.1. Estuaries and marine areas under their influence

Outflow rates of the two large estuaries responsible for an enrichment in nutrients along the continental shelf are similar (i.e., slightly higher than 10^3 (around 1200) m^3 s^{-1}; Anne-Marie Jegou, Dept. DYNECO, IFREMER, pers. comm.). Moreover, they do not differ in either the extent of low surface salinity or high nitrate concentrations. Nevertheless, we found great differences in trypsin and ATC specific activities between the Loire and the Gironde estuaries. Differences in abundance of particulate organic carbon are patent and might explain why trypsin activity in mesozooplankton was higher in water flowing out from the Gironde. ATC activities in this same area also were among the highest measured in our study, which indicates a strong mesozooplankton productivity potential. Therefore, this site seemed to be characterized not by a classical (i.e., based on primary production) food chain but by an efficient short food chain in which protein-rich particulate matter constituted the main food source for an actively growing mesozooplankton community; this community, in turn, is of benefit to breeding anchovies. This difference between the Loire and Gironde estuaries' attractive effect on anchovy biomass has been studied annually for many years, but the following question remains: Why are anchovies almost never present near the Loire estuary? Even if the particulate matter brought by the Gironde

has a different nutritive value, it is more abundant and the results from our study bring substantial elements for the coherence of this observation.

4.2.2. La Grande Vasière, the silt-rich region

Small-sized phytoplankton cells dominate in the northern-central part of the continental shelf. The limitation in nutrients in this area favours the development of an active microbial loop and creates conditions for high production of both particulate and dissolved carbohydrates, which induces an enhancement of PK activity in mesozooplankton. However, we found no evidence for increased ATC activity. The relatively intense biological activity within the superficial layers of the water, indicated by the high PK activities, likely is beneficial to the underlying muddy seafloor that is well known for the abundance of its benthic fauna.

4.2.3. The continental slope

Along the shelf break, strong tidally induced internal waves provide a nutrient supply to the surface layers via up-welling. Thus, higher phytoplankton biomass (Chl. *a*) indicates most probably that the primary productivity is enhanced and it is used by the sardine population. The strongest effects of these internal waves occur in the Celtic Sea, in front of the entrance of the English Channel, a region located just at the northwestern limit of our sampling area in the Bay of Biscay; there is a decreasing trend in these effects towards the southeastern part of the bay. Enzyme activities measured in this study seemed to reflect this trend: The high trypsin activities found at the northwest limit likely are evidence of a massive supply of protein-rich matter, then high PK activities (three stations corresponding with a core of nitrates in Figure 3) were found, followed by a decrease when moving to the SE.

511

512 *4.2.4. The southern region of the Bay of Biscay*

513 Large (> 20 µm) phytoplankton cells inhabit the southern region of the bay. The moderate
514 or high activities of either PK or trypsin found in this area indicate the presence of a
515 classical food chain, in which the balance between carbohydrate and protein as the
516 dominant cell content varies from one station to the other. Along the coast, where surface
517 water is less saline, both trypsin and ATC specific activities had high values. Clearly,
518 environmental conditions encountered along this southern part of the coast and continuing
519 until the northern limit of less saline water out flowing from the Gironde, appear
520 favourable to high mesozooplankton productivity. These conditions exert an evident
521 attractive power on the anchovy population, which needs to feed actively in order to
522 maintain fecundity throughout the breeding season.

523

524 *4.3. Established from literature and promising perspectives*

525 The relationships between variations in activities of the three enzymes studied in the
526 mesozooplankton and the descriptors of environmental conditions, both abiotic and biotic,
527 are not always simple. Particulate matter (bacteria, microprotozoans, and phytoplankton)
528 and mesozooplankton communities have complex composition, behaviour, distribution,
529 and abundance at multiple spatial and temporal scales (Link et al., 2005). Furthermore,
530 great differences exist in generation times between microbial cells (a few hours to a day,
531 not much more) and the main components of mesozooplankton communities (i.e., for
532 copepods, most often several weeks). The generation time of most species of copepods fits
533 in generally well with the duration of the mesoscale events that influence ecosystem
534 functioning, and this temporal agreement could be very important for a better
535 comprehension of the real natural processes. For instance, storage of carbohydrates such as

β-1,3 glucan in a phytoplankton cell varies on a temporal scale of a few hours (e.g. between 17 % and 42 % of cellular organic C in a marine diatom species: Granum et al., 2002), which means that a C:N ratio determined in such a cell in the evening would not be the same as that determined the preceding morning. It is very unlikely, if not impossible, that copepod cells could adapt their PK activity to such a high frequency variation because there is a latent period between the ingestion of the phytoplankton cell and its assimilation (Mayzaud and Poulet, 1978) through the adaptation of digestive enzyme activities involved in the assimilation of crude molecules of carbohydrates and requiring a time-lag period for acclimatization to quantitative or qualitative change in available prey (Roche-Mayzaud et al., 1991; Mayzaud et al., 1992); therefore, high frequency phenomena tend to be smoothed at the mesozooplankton level of the organization of pelagic ecosystems. As a consequence, the following assumption might be boldly conceived: the indices of mesozooplankton community metabolism most probably provide the best view of the basic processes essentially involved in the functioning of the pelagic ecosystem at the mesoscale.

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Figure captions

Figure 1
Map of the stations sampled in the Bay of Biscay. Black dots represent stations where all t the operations were carried out, open symbols indicate stations where only vertical temperature and salinity profiles were recorded and mesozooplankton samples were collected. The dotted line over the shelf break shows approximately the location of the chlorophyll section presented in Figure 4.

Figure 2
Map of the spatial variation of salinity in surface waters (numbers outside of the frame are indicative of geographic coordinates).

Figure 3
Map of the spatial variation in surface waters of nitrate concentrations expressed in $\mu M\ l^{-1}$ (numbers outside of the frame are indicative of geographic coordinates).

Figure 4
Remote sensing of sea surface Chl a and vertical section (following the dotted line presented in Figure 1) over the shelf break showing measured Chl a concentrations expressed in $\mu g\ l^{-1}$ according to depth (Z in m)

Figure 5
Map showing spatial variation of three main size classes in % of phytoplankton cells (integrated values through the photic layer, numbers outside of the frame are indicative of geographic coordinates).

Figure 6
Map showing the spatial variation of the ratio (microbial C)/POC (integrated values through the photic layer). Three numbers in larger and bold type are mean values for four stations in less saline water obviously issuing from each of the three rivers (the numbers outside of the frame are indicative of geographic coordinates).

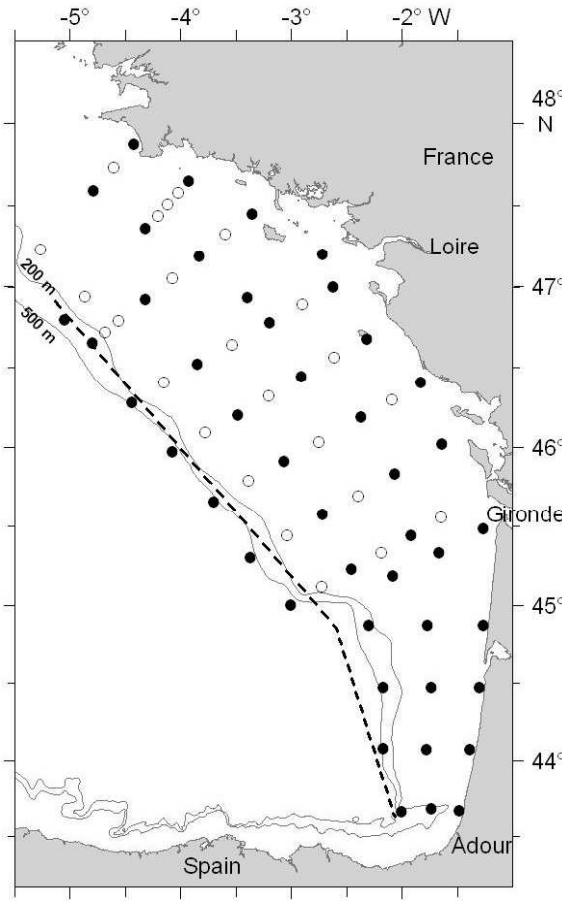
Figure 7
Map of the spatial variation of the ratio (bacterial C)/(phytoplankton C), values integrated through the photic layer (numbers outside of the frame are indicative of geographic coordinates). Note similarities with the spatial variations of PK specific activities shown in Figure 8a.

Figure 8

Spatial distribution of values of the three enzymatic specific activities (see “Material and methods” section for definitions) measured in samples of the whole mesozooplankton communities, PK (a), trypsin (b) and ATC (c). Both 200 and 500 m depths isobaths indicate the limits of the continental shelf.

Figure 9

Abundance and spatial distribution of the populations of the two main fish species representing a trophic level just above mesozooplankton in the Bay of Biscay: anchovy (*Engraulis encrasicolus*) in grey on the left and sardine (*Sardina pilchardus*) in white on the right (Jacques Massé, Dept. EMH, IFREMER, pers. comm.). Varying sizes of symbols are proportional to estimated fish biomass expressed in tonnes nautical mile^{-2}. 50, 100 and 200m depths isobaths are shown.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Adour
Spain

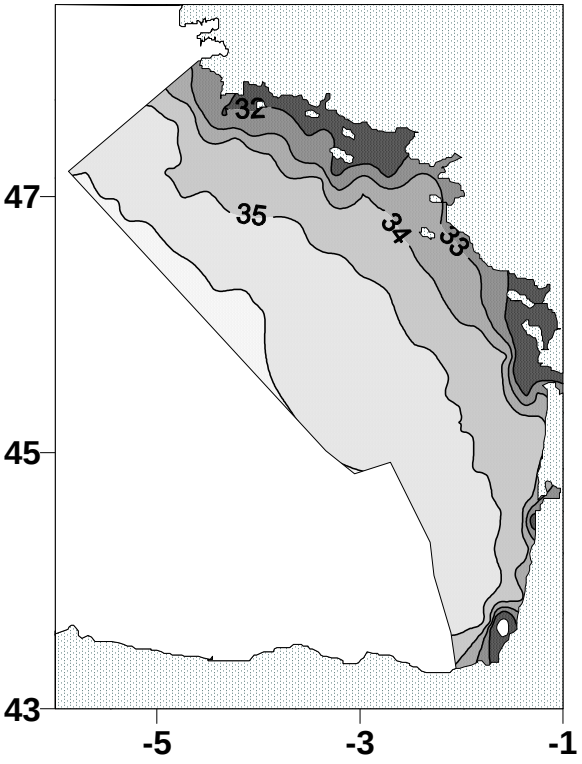


Fig 2

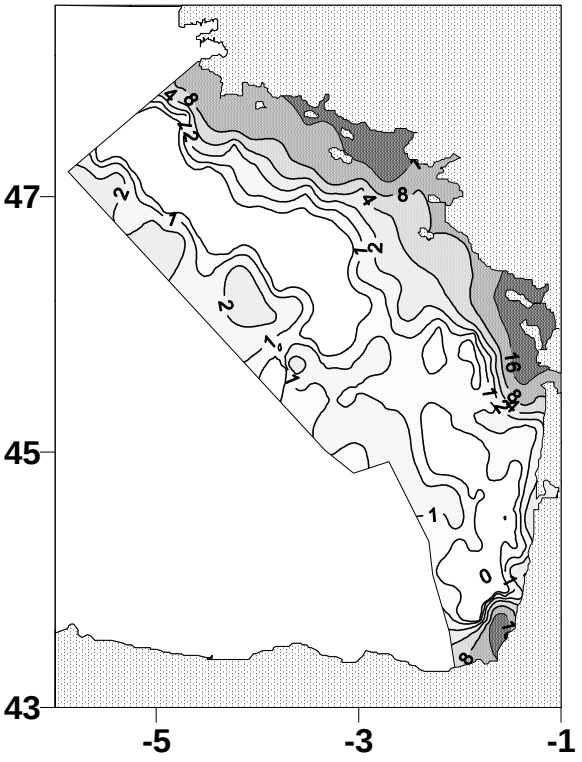
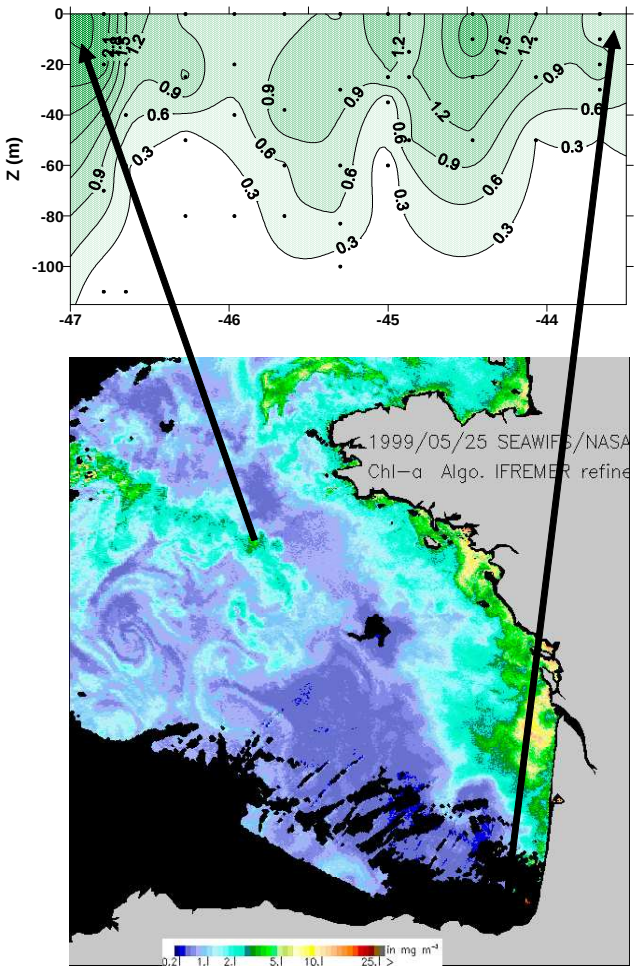


Fig 3

Fig 4


Z (m)
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-80
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-46
-45
-44
1999/05/25 SEAWIFS/NASA
Chl-a Algo. IFREMER refine
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0.9
1.2
1.5

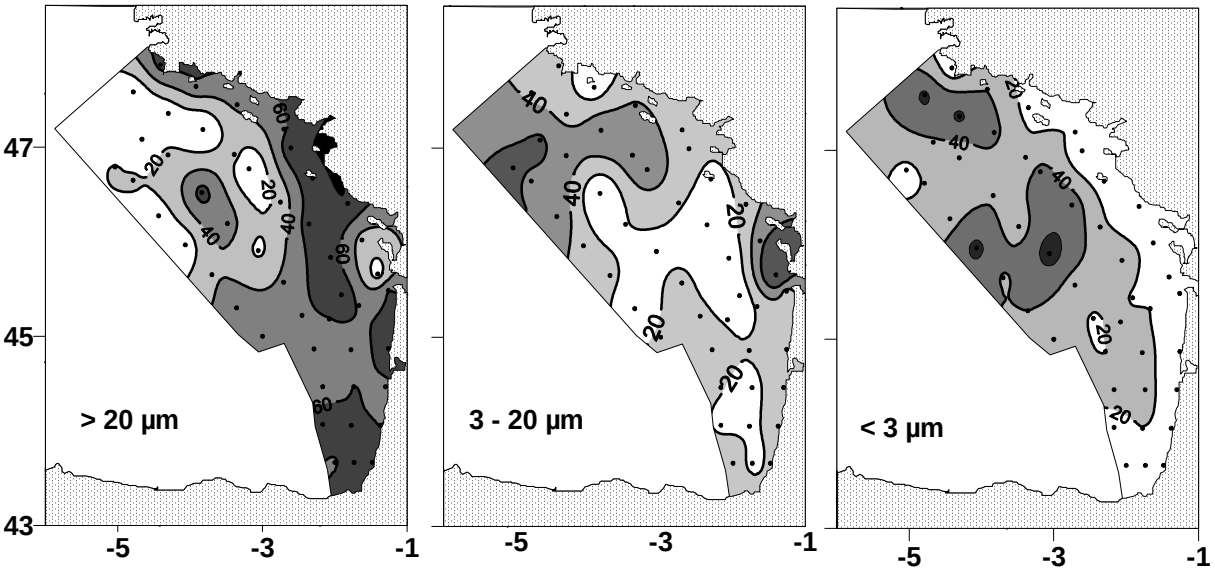


Fig 5

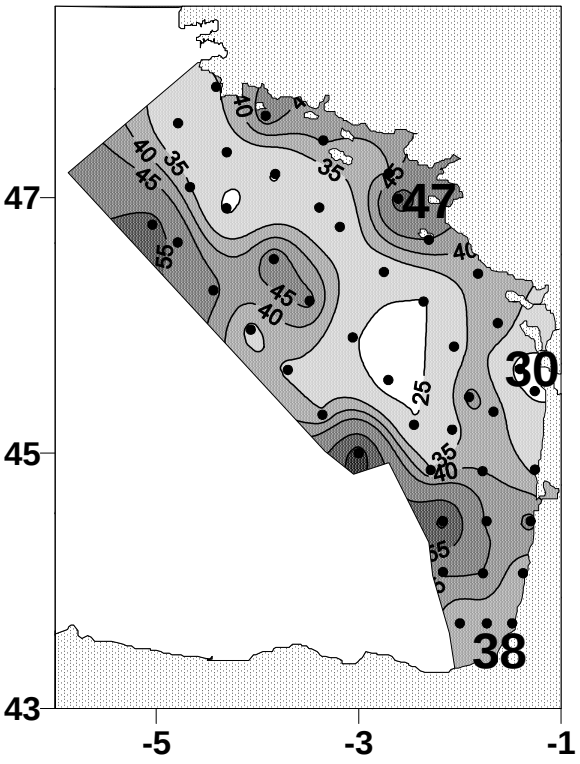


Fig 6

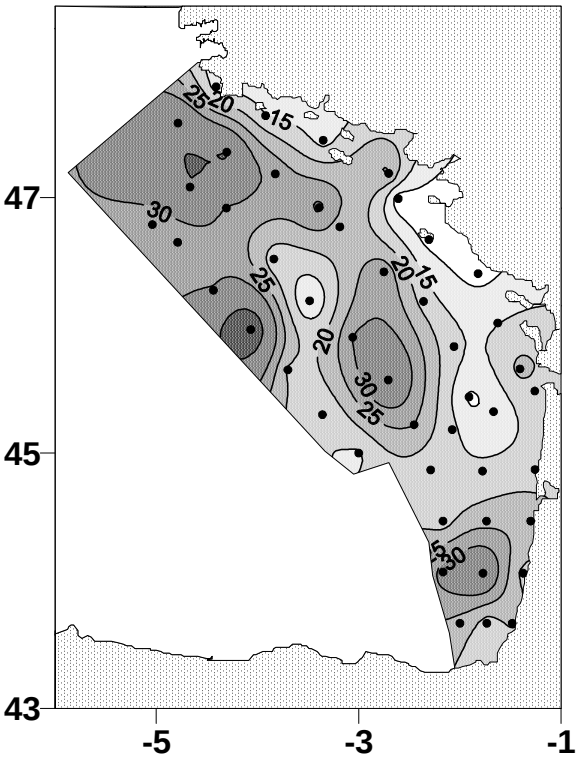
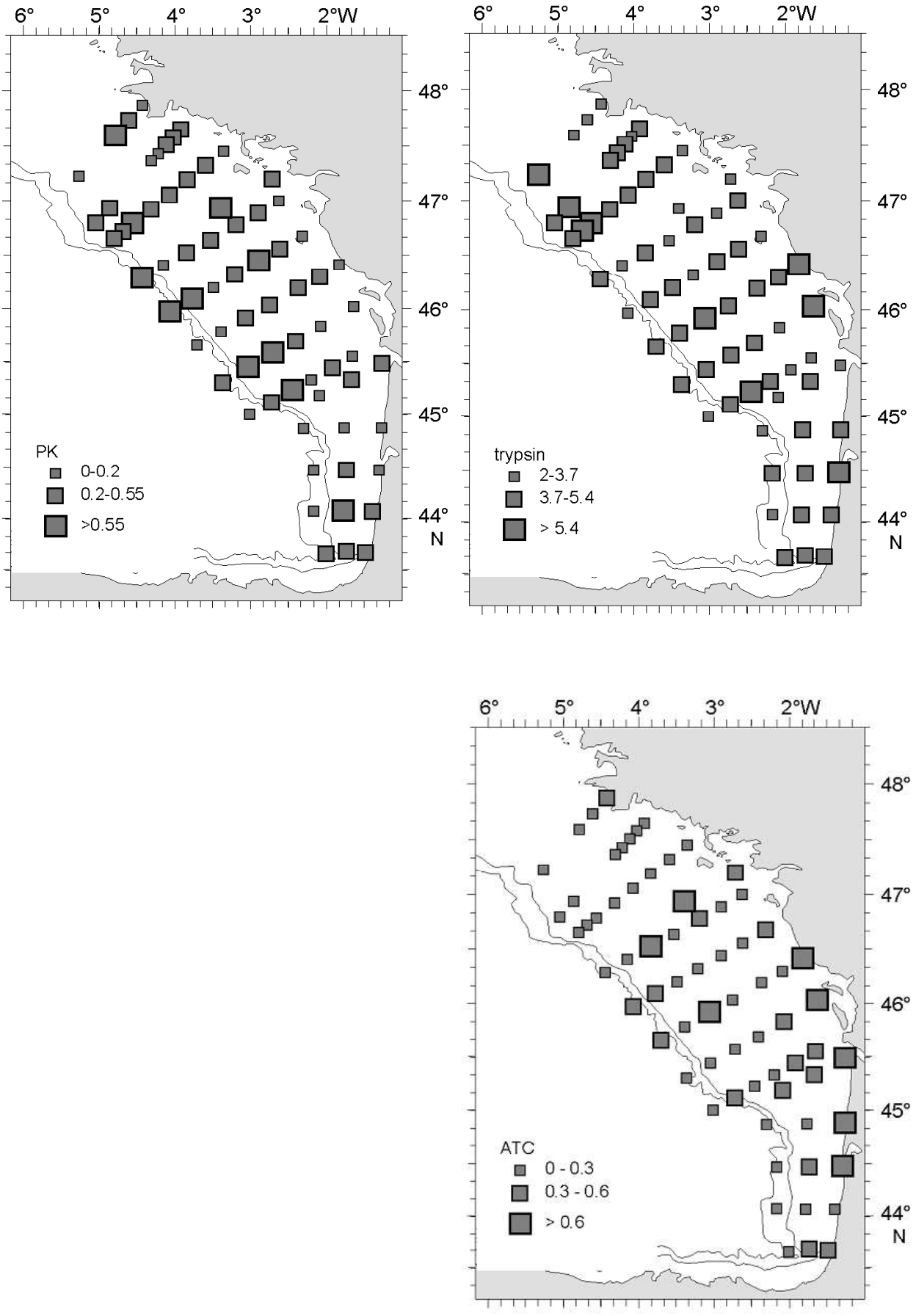


Fig 7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46°
45°
44°
N
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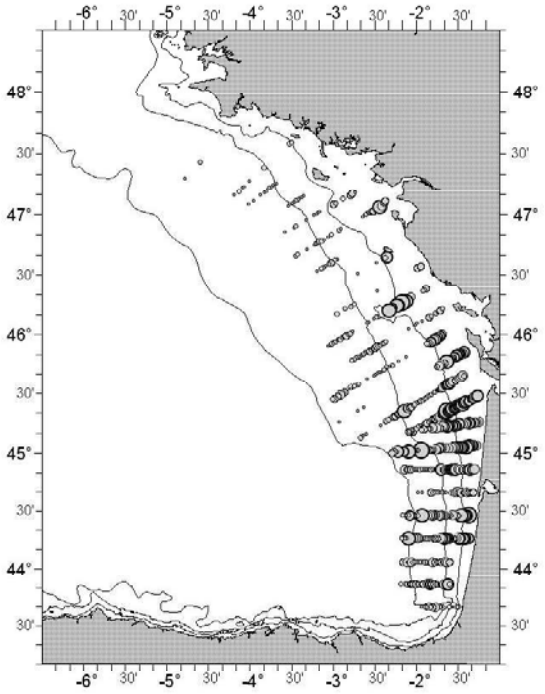
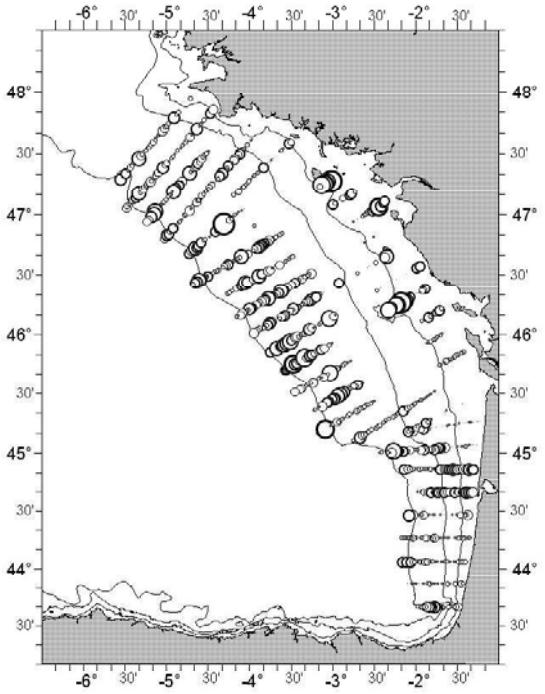
0-0.2
0.2-0.55
>0.55
trypsin
2-3.7
3.7-5.4
> 5.4
ATC
0 - 0.3
0.3 - 0.6
> 0.6

Fig 8



anchovy



sardine

Fig 9