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Aspartate transcarbamylase activity for the assessment of mesozooplankton production: new aspects from oceanic areas

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One method for assessing mesozooplankton production is based on measurements of the activity of an enzyme, aspartate transcarbamylase (ATC), in samples of the whole mesozooplankton community. The first field experiments were carried out in neritic areas, the south-western part of the English Channel and the west of Brittany. Previously published results have shown two main characteristics of ATC activity variations, i.e. an allometric relationship with biomass and a close correlation with the mesoscale changes with time of the mesozooplankton biomass. Other experiments were performed in two oceanic areas, the Ligurian Sea and the upwelling system off the southern coast of Portugal. They illustrated strongly different patterns of ATC activity variations. In the Ligurian Sea, it has not been possible to establish any allometric relationship, probably owing to either fairly complex hydrodynamics or disturbance of the mesozooplankton system caused by an unusual biotic environment. Off Portugal, however, allometric relationships clearly characterized two subsystems, one quite close to the shore and the other in offshore stratified oceanic waters. These results give an overview of different patterns of ATC activity variations in natural systems: some early hypotheses are confirmed, limits in applicability of the method are highlighted and promising prospects are becoming clearer.

Key words: aspartate transcarbamylase, mesozooplankton, pelagic ecosystem, production.

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Introduction

For several decades, the assessment of secondary production in pelagic ecosystems has been considered as a major concern for biological oceanographers, and nowadays it still remains a formidable challenge. Unfortunately, no existing method is fully satisfactory, yet accurate measurements become more and more urgent for both fisheries biologists and ecologists involved in climate regulation studies.

Some 10 years ago, a new biochemical method was suggested based on some conceptual considerations (Bergeron, 1983, 1986). In particular, strong unifying analogies found at the subcellular level in primary metabolic processes were put forward as a way for possible implementation of the method at the community level (Bergeron, 1983). The method depends on the measurement, carried out in whole mesozooplankton samples, of the activity of an enzyme, aspartate transcarbamylase (ATC). ATC is involved in the biosynthesis of pyrimidine bases used to build nucleic acids for cell multiplication and protein synthesis (Bergeron and Buestel, 1979). Early field results gathered in the south-western part of the English Channel were quite well in agreement with different aspects of system theory proposed by many authors (Bergeron, 1986) and besides showed a close correlation between ATC specific activities and mesoscale changes of the mesozooplankton biomass with time (Bergeron, 1990).

ATC activity variations are generally linked to protein biomass by an allometric relationship, which is considered as evidence of cybernetic regulatory processes in a dynamic steady state of the mesozooplankton community (Bergeron, 1986). The expression of such a fundamental feature naturally implies minimal conditions ensuring the spatio-temporal cohesion of the system. Two sets of so far unpublished data from oceanic areas illustrate this latter aspect and demonstrate different patterns of ATC activity variations in the field.

Materials and methods

The mesozooplankton samples were collected by vertical tows of WP2 net (200 μm mesh size) from 200 m depth

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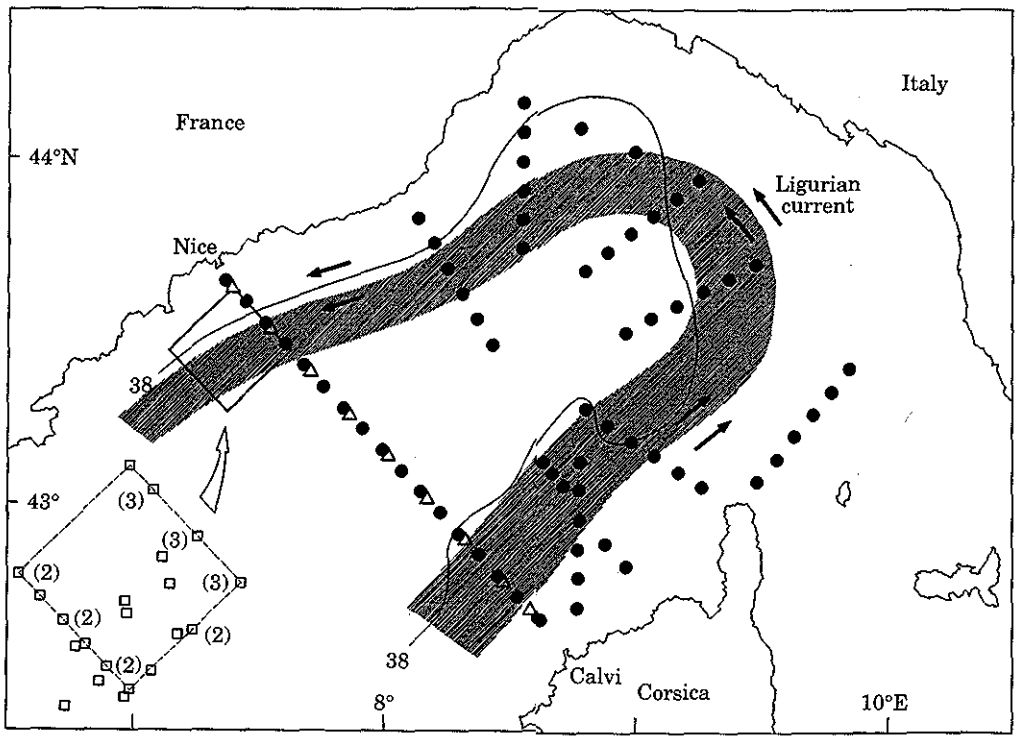

Figure 1. Sampling design for the Prolig I and II experiments in the Ligurian Sea: stations located along the square or marked by open triangles for Prolig I (March 1980), marked by dark circles for Prolig II (May 1985). The shaded area roughly indicates the standard position of the so-called frontal zone. The thin line represents the isohaline 38 observed at the surface during Prolig II (Louis Prieur, pers. comm.) and considered as coarsely depicting the limit of the peripheral zone (Ligurian current).

to surface. The macrozooplankton was eliminated by sieving through a 5 mm mesh. It is worth noting that, during the Prolig II cruise (Ligurian Sea, May 1985), a high abundance of gelatinous macrozooplankton (mainly salps) was found, coarsely estimated by measuring total volume and then discarded.

The samples were ground in iced distilled water with a Potter–Elvehjem homogenizer. The extracts were immediately frozen at -20°C and kept at this temperature until analysis in the laboratory. After thawing, this crude extract was used directly for ATC activity measurement according to Bergeron and Alayse-Danet (1981), modified as previously described in Bergeron (1986). An aliquot of the extract was centrifuged (10 min at 4000 r min^{-1}). Amylase activity and soluble proteins were measured in the supernatant with an autoanalyzer as described by Samain *et al.* (1977).

Results

Ligurian Sea

The physical structure and circulation of water masses in this area (Fig. 1) are chiefly driven by a large cyclonic gyre. Boucher *et al.* (1987) give a general description of the main hydrodynamic features, as well as their consequences to the zooplankton communities. Roughly three main hydrological zones may be identified: (1) a coastal and peripheral one governed by the so-called Ligurian current, whose mean speed is about 0.3 m s^{-1}; (2) a frontal zone characterized by a sharp horizontal change in density increasing seawards; and (3) an offshore central zone where the surface water density is high, close to that of the Levantine water. The spatial distribution and taxonomic composition of zooplankton are not closely related to these three features, because in the frontal zone contiguous divergence and convergence processes are found which vary greatly in time and space (Boucher *et al.*, 1987); moreover special behavioural patterns of some components of the zooplankton systems are likely to complicate further the general biological dynamics (Boucher, 1984; Ibanez and Boucher, 1987).

Two cruises enabled early attempts in measuring ATC activity in zooplankton samples from the Ligurian Sea. The first (Prolig I, March 1980) was devoted principally to the frontal zone with an intensive sampling design: two kinds of survey were carried out, discrete stations (where among other zooplankton was collected) along an "observation square" covered three times (Fig. 1) and multiparameter continuous recording surveys. These

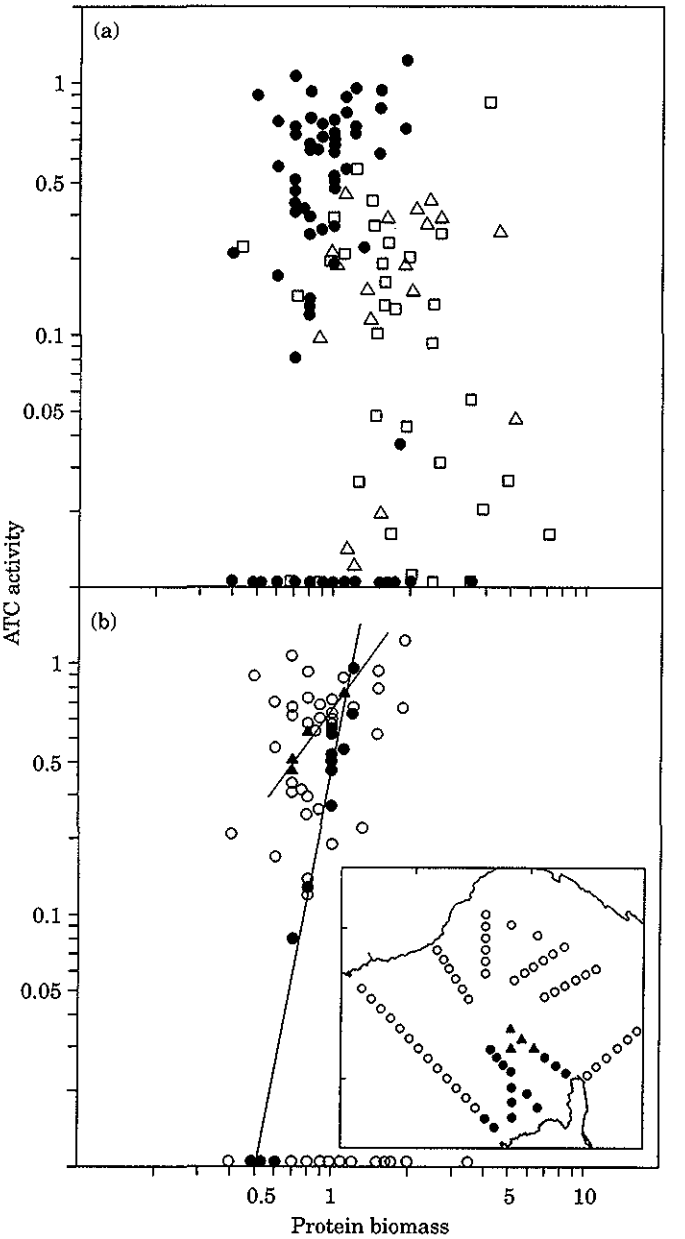

Figure 2. Ligurian Sea: variations in ln–ln coordinates of ATC activity (expressed in ATC units) in relation to protein biomass (expressed in mg). Both variables are expressed for one sampled m^3 of water. (a) Whole data for Prolig I (open squares and triangles) and II (dark circles) cruises. (b) Prolig II only, with special stress on data collected in the southern part of the area (sampling design in inset).

latter showed unambiguously the small-scale hydrological structure mentioned above (Belluau *et al.*, 1982); in fact the Prolig I cruise was an important step leading to a comprehensive view of the complex hydrodynamics in this area (Sournia *et al.*, 1990). It is not therefore surprising that vertical tows made from 200 m depth to the surface in such an environment were inappropriate for sampling a homogeneous zooplankton community. The respective variations of ATC activity and protein biomass give a highly scattered picture (Fig. 2a).

Nevertheless, with the aim of characterizing different communities despite these difficulties, a new special sampling strategy (Fig. 1) was used for a second cruise (Prolig II, late May 1985): a strong scattering of the data was again observed (Fig. 2a). Comparison of both data sets calls for two short comments. First, the scattering

Table 1. Ligurian Sea: variations of the ATC and amylase specific activities of the mesozooplankton for different abundance classes of the surrounding gelatinous macroplankton. (M=mean; SD=standard deviation; P=probability given by Student's *t*-test used to compare pairs of mean values).

Gelatinous macroplankton abundance	No. of stations	Mesozooplankton					
		ATC spe. act.			Amylase spe. act.		
		M	SD	P	M	SD	P
High (>60 ml)	10	0.07	0.12	<0.02	0.32	0.07	<0.1
Intermediate	24	0.33	0.33	<0.001	0.39	0.11	<0.01
Low (<20 ml)	12	0.89	0.40		0.50	0.09	

was notably less important than it was for Prolig I, which is consistent with the different observation scale; part of the "noise" due to small-scale heterogeneity has disappeared. Second, ATC activities are higher in spring than in late winter. Nevertheless, numerous values are equal to zero, or so low that they are not confidently measurable, and no allometric relationship obviously appears. Should further attempts be abandoned? Actually, during the bulk of the cruise, gelatinous macrozooplankton, mainly salps, were very abundant and many samples only contained few copepods. This is a relatively usual feature of the seasonal cycle in the Ligurian Sea (Braconnot, 1963; Ménard *et al.*, 1994). Salps are very effective filter-feeders (Andersen, 1985) and may represent potentially important competitors of copepods for grazing. This was obviously the case during the Prolig II cruise, because there was an inverse relationship between ATC specific activity levels of mesozooplankton and occurrence of macrozooplankton (Table 1), although the latter is badly sampled with a WP2 net and its abundance only roughly estimated. In particular, almost all ATC activity values equal to zero were recorded in stations where macrozooplankton was abundant. Moreover, amylase specific activity has been measured on the same samples as a global grazing estimator (Table 1); at the scale of the whole Ligurian basin, it exhibits a close correlation with ATC specific activity (least-squares regression: r=0.58 for 59 data pairs). This implies that production of living matter is closely dependent on assimilation rates from the trophic environment, which is quite consistent with a potential effect of competition of the macrozooplankton on the mesozooplankton, and suggests that the whole ecosystem is in an early productive period.

Additionally, by the end of the cruise, in the southern part of the area, salps disappeared while abundant young stages of copepods became dominant, which was especially striking in four clustered stations north of Corsica (dark triangles in inset of Fig. 2). The ATC activities measured in these samples gave a much more coherent picture (Fig. 2b), which was quite consistent with the change in the taxonomic composition. For a rather low biomass, there was a sharp increase of ATC activity as biomass increased, both variables being closely correlated. The four stations mentioned above seem to have reached higher levels following another relationship, which is most likely a transitional state towards a more steady one. This global pattern confirms some early results from 1979 (Bergeron, 1983) at the beginning of the spring production cycle and is likely to signal the start of a copepod outburst in the southern Ligurian Sea..

Coastal upwelling and adjacent oceanic area off Portugal

The upwelling system off the southern coast of Portugal was investigated in late summer 1981 (Coste *et al.*, 1986). The same west–east transect (38°N, off Cap Sines) was covered several times during the RCA (Résurgences Cotières Atlantiques) cruise, sampling stations being spaced out by 10 nautical miles, except both inshore ones (5 naut.m.). Actually, the wind conditions were not favourable and a decrease of the upwelling dynamics had not yet begun. This was indicated by a gentle warming of the surface waters of the coastal stations, while offshore oceanic waters were progressively getting closer to the shore (Fig. 3). High values of zooplankton biomass were still found in both inshore stations with a clear decrease towards the open sea. Here the respective variations of ATC activity and protein biomass are not at all scattered (Fig. 4a); two different allometric relationships clearly characterize the inshore stations, on the one hand, and the offshore stations, on the other. Moreover, at different distances from the coast in the offshore area, additional sampling was carried out in order to characterize the upper layer encompassing the thermocline (50 m depth to surface tows) and to compare with the classical 200–0 m tows. This established a third relationship (Fig. 4b) where a different perception level highlights another system showing different features, i.e. higher biomass and productive potential as indicated by the slope of the allometric relationship. Lastly, a comparison can be made with ATC activity

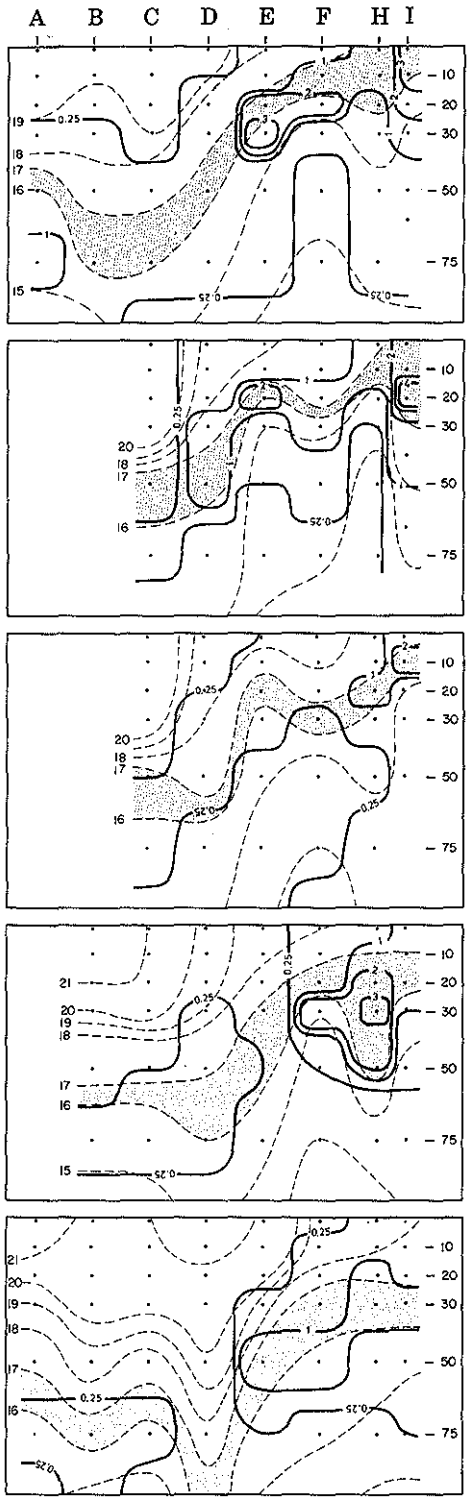

Figure 3. Vertical hydrobiological structure of the upper layer (100 m) along the W–E transect off the Portuguese coast and its variation during the RCA cruise. Isotherms in dotted lines (shaded area for the 16–17°C layer), chlorophyll concentrations in $\mu g\ l^{-1}$ in thick lines (data from Coste and Minas, 1983).

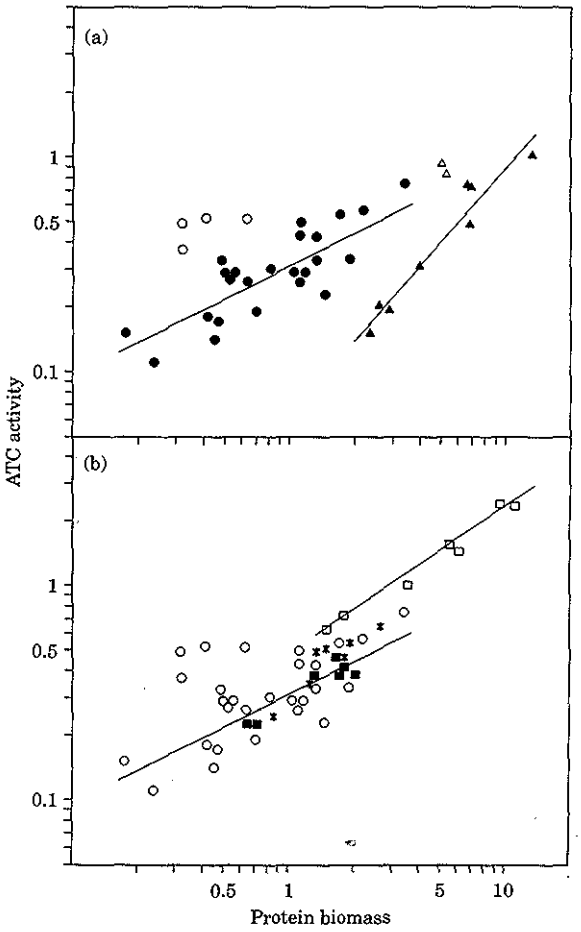

Figure 4. Coastal upwelling and adjacent oceanic area off Portugal: variations in ln–ln coordinates of ATC activity (expressed in ATC units) in relation to protein biomass (expressed in mg). Both variables are expressed for one sampled m^3 of water. (a) Whole data from 200–0 m sampling tows (circles for offshore A–F stations, triangles for inshore H and I stations; regression lines established with closed marks). (b) Offshore data with additional 50–0 m sampling (open circles for systematic sampling of A–F stations as in (a); squares for additional sampling: closed for 200–0 tows, open for 50–0 tows) and data (asterisks) from Biogas X cruise (late July 1980, 9°15′ and 40′W, 47°30′N).

values of samples (200–0 m tows) collected in a limited area in the open Atlantic (Biogas X cruise, late July 1980, same longitude, but 47°30′N). These latter values fit fairly well with the relationship established for the offshore stations (Fig. 4b). It may therefore by hypothesized that this is a general pattern typical of the temperate Atlantic Ocean in summer.

However, some data do not strictly fit these relationships, in particular four offshore samples showing higher ATC activity values (open circles in Fig. 4a). This leads to a consideration of the vertical hydrobiological structure of the area and its variation during the cruise

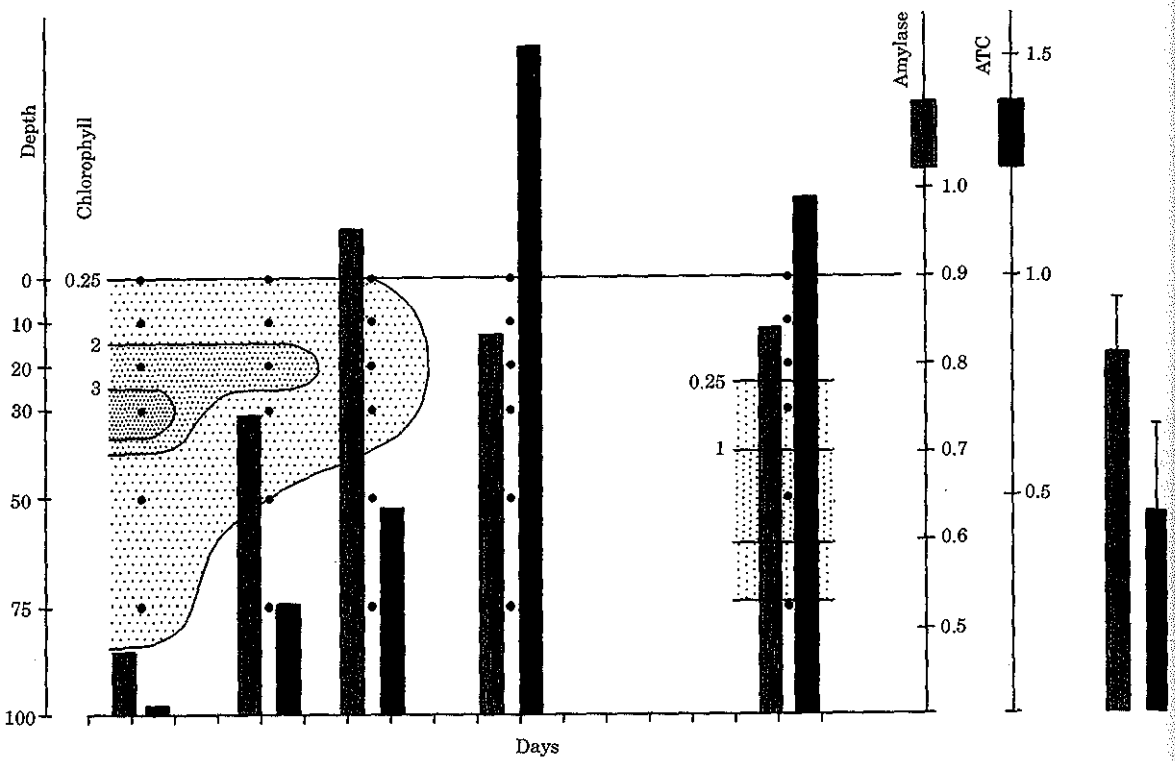

Figure 5. Temporal variation of chlorophyll concentration (in $\mu g\ l^{-1}$ of sea water: dotted areas) in the upper layer (100 m) and of metabolic descriptors of the mesozooplankton system sampled in stations E (cf. Fig. 3): amylase and ATC specific activity levels (in enzymatic unit mg^{-1} protein). Right: mean values and standard deviations for all of the other offshore stations.

(Fig. 3), especially station E, where high chlorophyll concentration may be noticed during the first transect. An important peak of zooplankton biomass was found at the same station. In addition, this is a general pattern observed for the whole area during the cruise, i.e., chlorophyll concentration and zooplankton biomass variations are strongly correlated (least-squares regression between protein biomass m^{-2} and 100–0 m integrated chlorophyll: $r=0.74$ for 42 data pairs). At station E, the phytoplankton biomass clearly shows a progressive decrease, just as if it was grazed by zooplankton. This hypothesis is strongly supported by the metabolic descriptors (Fig. 5), amylase as an index of digestive assimilation of carbohydrates and ATC for expressing the likely fate of this assimilated matter for secondary production. It should be noted that the values of both enzyme activities measured in all other offshore stations are very homogeneous and that consequently the levels observed in station E appear to be significantly different. A similar phenomenon appears in inshore station H from the fourth transect (Fig. 3), where there is a similar increase of both enzyme activity levels, so giving an explanation for two higher values observed inshore by the end of the cruise (open triangles in Fig. 4a). A time-lag exists between decrease of phytoplankton biomass and increase of amylase activity, and between this latter and subsequent increase of ATC activity, which is consistent with the literature data (e.g., Mayzaud and Poulet, 1978; Hirche, 1983). An important point must be emphasized: specific composition of zooplankton has been analysed in the same samples by Boucher (1987) and proved to be the same as that of the surrounding offshore stations. The variations in digestive enzyme and ATC activities are very probably the expression of a local stimulation of the metabolism of the mesozooplankton community.

Discussion

The establishment of an allometric relationship between ATC activity and protein biomass is undoubtedly a fundamental result; it principally shows that ATC activity variations within the mesozooplankton system are regulated by the same mechanisms as those found at lower levels of life, i.e. organs or organisms (Bergeron, 1982). This is in agreement with some attempts to search for common properties and general laws governing natural systems (Margalef, 1968; Patten and Odum, 1981; Platt, 1985). As previously stated (Bergeron, 1986), the allometry shows a dynamic steady state of a mesozooplankton system facing a given environment,

allowing the assumption that the ATC method works at a relevant perception level.

Allometric relations are only correlations that do not explain mechanisms; they do provide patterns which might reflect basic processes obscured by the diversity in the oceans (Calder, 1985). The ATC method is inherently "unaware" of the diversity of the sampled zooplankton community. It is quite obvious that changes in the specific composition of the zooplankton during the whole spring period in the English Channel (Bergeron, 1983, 1986) do not alter the allometric relationships that characterize ATC activity variations. On the contrary, the allometry "contains" the specific composition as one component, as well as the global emergent metabolism, of the adaptation of the system to its environment. A general result of this adaptation is complexity, "an apparent disorder in systems where we have reasons to believe that an order exists" (Atlan, 1985). At the subcellular level, one may also find some complexity in the mixture of numerous kinds of molecules and compounds, extremely numerous but not innumerable; and at this level one does not need to believe, we know that an order exists. If we consider a mixture of different species, it must basically be remembered that, after 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". Finally, the specificity and uniqueness of certain metabolic steps, such as that regulated by ATC, give the primary key to searching, identifying and pointing out common properties in complex molecular mixtures such as homogenates of samples of a whole mesozooplankton system (see, for example, Jones (1980) giving a fundamental point of view about pyrimidine bases biosynthesis).

Both experiments carried out in the Ligurian Sea illustrated that there are obvious limits to using the ATC method which are mainly linked to conditions for an appropriate sampling of a whole system. The clearest example of a possible obstacle is linked to the hydrodynamics of the area. It has been shown previously in the English Channel (Bergeron, 1986) that samples collected close to the shore, in small estuaries for instance, do not allow us to point out any allometric relationships; this is probably due to predominating high-frequency events, like tidal mixing (extremely strong in the English Channel), varying river outflow, winds, that create small-scale turbulence in shallow water areas with a very rugged coastline. One may come up against the same kind of problem in the open sea, on fairly larger scales, as illustrated above by the data from the Ligurian hydrological front (Prolig I cruise). In these two cases, difficulties arose from the variability of the physical environment, so they are not really attributable to the method itself. A mesozooplankton community inhabiting a highly fluctuating water mass has no stable spatio-temporal cohesion. Thus working on mixed species samples in such an environment cannot lead to reliable estimates of zooplankton production. However, the copepod egg production method should probably bring the most relevant perception level in systems, such as the Ligurian front, where high-frequency variability is the dominant feature, because the short-term and small-scale events that control the production process are integrated at this individual level.

The Prolig II cruise demonstrated a problem brought about by the biotic environment. A sudden occurrence of gelatinous macrozooplankton bloom disturbed a system whose bulk is usually made up of copepods. Different sized filter-feeders with strongly different metabolic rates and different spatial distribution patterns obviously cannot be sampled with comparable efficiencies by a unique sampling gear. Even if the mesozooplankton community retains some systemic features *in situ*, salps in the WP2 net prevent us from getting a suitable sample.

Although measured values are not really quantitative estimates of production (in terms of carbon mass per time unit and square metre for instance), ATC activity unit may prove a very useful tool for comparative studies. The main features of the seasonal development of an ecosystem, given by the parameters of the allometric relationship equation, show evidence of interannual fluctuations and their effect on important biological processes such as larval fish recruitment (Bergeron, 1993). In the last instance, ATC specific activity not only provides an assessment of potential secondary production, but also gives a global view of the "qualité du millésime", i.e. considering the common general generation time of most copepod species, an estimate of the mesoscale integrated effect of the whole environment on a biological system. In summing up, ATC in its ability to show semi-quantitative measurements must be considered as only an index, but an actual index, that would just need to be calibrated.

Regarding possible attempts at calibration, one may be tempted to follow Mayzaud (1986) in stating that conventional techniques involving the incubation of animals are most probably not the right ones. Without the least intention of questioning the usefulness of laboratory experiments, one must bear in mind that they have limitations, even on large scales (Grice *et al.*, 1980). One must accept that certain hypotheses cannot be tested in controlled enclosures whatever their size may be. Fortunately, oceanographers have not waited for an accurate laboratory calibration of the (highly fluctuating) relationship between pigment content and phytoplankton biomass before starting to measure chlorophyll in the field. For certain special perception levels, it is time to "forego experiments using isolated species and instead", as these pioneers several decades ago did, "conduct measurements on complex ensembles,

preferably in the field" (Platt *et al.*, 1981). From this point of view and as far as zooplankton communities are concerned, the promising C/N/P method of Le Borgne (1978) could solve this question, because theoretically it works at the community level and at similar scales as the ATC method. Therefore attempts to compare results from both methods would be highly relevant.

Flashback to some previous works

Bearing in mind some concepts put forward above, and especially the idea of "far greater differences existing within organisms than between them" (Stebbing and Heath, 1984), some methods are potentially of great interest and might profitably be reconsidered from a new point of view. What about the RNA/DNA ratio? Nucleic acids have been the subject of a great amount of work in marine biology. The earliest work was searching for an estimator of growth or productivity notably "in mixed populations of animals" (Sutcliffe, 1965). The idea has been rejected for zooplankton (Dagg and Littlepage, 1972), reintroduced (Båmstedt and Skjoldal, 1980) and rejected again (Ota and Landry, 1984). Much work has also been devoted to the RNA/DNA ratio in fish larvae and, despite the assertions of Buckley (1984), it has recently been demonstrated that this ratio is not an actual index of the growth process, at least in sole larvae (Bergeron and Boulhic, 1994). Why does it not work at this developmental level? Great changes are taking place during larval growth, i.e. different sorts of tissues belonging to different organs appear progressively during ontogeny and the result of a global measurement at the individual level looks confused. It is most likely to be the same for copepods (Ota and Landry, 1984), probably even more complicated by the discontinuous pattern typical of crustacean growth. Nevertheless, the basic concepts underlying these works remain fundamentally relevant and very strong. The problem lies in defining the appropriate conditions of applicability of the RNA/DNA ratio. For instance, it has proved to be successful in fish white muscle as a feeding condition index (several different studies quoted in Bergeron and Boulhic, 1994). Just as ATC activity measurement gives satisfactory results in the scallop gonad (Bergeron and Alayse-Danet, 1981), RNA/DNA ratio seems to be a good index as well (Robbins *et al.*, 1990). As far as copepods are concerned, a recent article by Nakata *et al.* (1994) gives further support to the potential interest of this ratio, which in adult females is most likely to be working at a relevant perception level. The common feature between a piece of a mollusc gonad and pooled adult females of copepods is the similarity, in each case, of the mixtures of molecules making up the samples to be compared. Thus, if one does assume that an homogenate made from a mixed copepod species sample is essentially closer to an homogeneous tissue, one may hypothesize that the RNA/DNA ratio should be a relevant tool at the whole community level. The work of Båmstedt and Skjoldal (1980) constitutes a first step supporting such an assumption (see also Båmstedt, 1983).

This flashback is a plea, based on a concept which involved a lot of work in the past, for introducing the statement of a fundamental point of view. ATC activity measurement might simultaneously be a poor index of copepod growth but, by reflecting the rate of pyrimidine bases synthesis at the community level, a good index of mesozooplankton production. Here is a challenging question.

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