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Characteristic features of zooplankton in the Bay of Biscay

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SUMMARY: Three hundred species of zooplankton have been identified in the Bay of Biscay, among which 10% are copepods. Diversity and variability of taxa, with time and space at all scales, are remarkable. Biology, ecology and biomass of species belonging to mesozooplankton are best known, whereas studies on micro- and macrozooplankton species are scarce. Field estimates of growth and secondary production, even of the most frequent and abundant species, are also scarce. Mesozooplankton carbon biomass represents 4-20% of total particulate organic carbon (POC) and ranges between 2 and 300 $mgC.m^{-3}$. Highest values of zooplankton standing stock are generally found either in spring, summer or autumn, depending on stations located in mixed and frontal waters, or in the vicinity of estuaries. Values for density and biomass of zooplankton are not linearly related in time and vary by 1 to 2 orders of magnitude in relation to hydrological conditions and seasons. Based on literature and chlorophyll regimes, it appears that zooplankton in the Bay of Biscay is generally food limited; so that, zooplankton (i.e. copepods) may not reach optimum growth and production rates, except in specific water conditions enhancing primary production or high standing stock (≥ 2 μg Chlo a. l^{-1}) of phytoplankton. Growth of anchovy larvae and reproduction of adults are critical phases in the life cycle of anchovy, which both rely on different and specific food categories. Matching between anchovy spawning, nursery sites and areas with high standing stock and productivity of zooplankton have never been evaluated in the Bay of Biscay.

Key words: Zooplankton, composition, production, Bay of Biscay.

RESUMEN: Rasgos característicos del zooplancton en el golfo de Vizcaya. – Se han identificado trescientas especies del zooplancton en el golfo de Vizcaya, de las cuales el 10% son copépodos. La diversidad y variabilidad taxonómicas, en el tiempo y en el espacio, son notables. Se conoce bien la biología, ecología y biomasa de las especies pertenecientes al mesozooplancton, mientras que los estudios sobre las especies del micro y macrozooplancton son escasos. Escasean asimismo las estimaciones de campo de crecimiento y de producción secundaria, aún de las especies más frecuentes y abundantes. La biomasa de carbono del mesozooplancton representa el 4-20% del carbono orgánico particulado (POC) y varía entre 2 y 300 $mgC.m^{-3}$ .Los valores más altos de biomasa zooplanctónica se encuentran generalmente en primavera, verano u otoño, según se trate de estaciones situadas en aguas de mezcla o frontales, o en la proximidad de estuarios. Los valores de densidad y biomasa zooplanctónica no tienen una relación lineal en el tiempo y varían en 1 a 2 órdenes de magnitud en relación con las condiciones hidrológicas y estacionales. En base a la literatura y a los regímenes de clorofila, parece que el zooplancton del golfo de Vizcaya está generalmente limitado por el alimento; así, el zooplancton (esto es, los copépodos) no pueden alcanzar tasas óptimas de crecimiento y producción, excepto en condiciones específicas del agua que favorezcan la producción primaria o una densidad elevada ($\geq 2\mu$g Chlo $a.l^{-1}$) de fitoplancton. El crecimiento de las larvas de anchoa y la reproducción de los adultos son fases críticas en el ciclo vital de la anchoa, dependiendo ambas de categorías de alimentos distintas y específicas. La coincidencia entre la puesta de la anchoa, las áreas de cría y las zonas de gran densidad y productividad zooplanctónicas no ha sido nunca evaluada en el golfo de Vizcaya. (Traducido por los editores).

Palabras clave: Zooplancton, composición, producción, golfo de Vizcaya.

INTRODUCTION

The link between physical oceanography, marine food chains and fish stock have been the subject of many studies in fisheries. As a logical approach, multiple correlation analyses have been carried out on fish abundance and a suite of hydro-biological measurements. However, correlations between changes in physical factors and fish stocks are viewed with suspicion, because the problem with such an approach is that there is no limit to the number of comparisons and that the presence of correlation does not necessarily imply cause and effect (Shepherd *et al.*, 1984; Mann, 1993). It is now considered appropriate to focus on the biological production process which represents a better link between physical oceanography and fish recruitment (Mann, 1993; Cushing, 1995). As stated by Mann (1993): "Among the myriad of complex interactions, there is one sequence which appears again and again. It is the alternation of vertical mixing and stratification, leading to enhanced production, mainly by diatoms. The vertical mixing may be generated from above by wind stress or from below by tidal currents impinging on the bottom. The stratification may be in response to surface warming, or a result of an influx of low-salinity water. The sequence appears in habitats as diverse as the open ocean, continental shelf waters, coastal upwelling areas and estuaries", including the Bay of Biscay. "The common feature of them all are bursts of diatom production, which is the basis of the traditional food chain, by which primary production is passed through mesozooplankton to fish".

As a major component of this group of zooplankton, copepods act as "filters" between phytoplankton and fish (Runge, 1988). Consequently, part of the recruitment mechanism of O-group and year-class strength of anchovy, as shown in many other planktivorous fish, are now believed to depend on secondary production processes.

In contrast, "Well-stratified conditions prevailing in tropical and in temperate waters in summer and fall, lead mainly to production of flagellates, which are dissipated in a more complex microbial food web, which is assumed to be inefficient in supporting fish production" (Mann, 1993). A quiet different understanding of these relationships between physical oceanography and the food environment has been developed in the past decade. As stated by Kleppel (1993): "At least 3 novel concepts about trophic structure have affected the classic perception of the marine food chains - (1): energy flows through complex food webs rather than along simple food chains; -(2): nanoplankton and microzooplankton are important in metazoan food webs, including copepods ; and - (3): fluxes of food materials and energy through ecosystems are governed by the relationships between food nutritional composition and the nutritional needs of the feeders, rather than simply by the carbon balance between them. The overwhelming body of evidence suggests that copepod diets are extremely diverse and variable, with significant differences in nutritional value existing between taxonomic groups of phytoplankton". As a consequence, diversity in phytoplankton, combined with differential nutritional composition and shifts in copepod diet are assumed to be the real biological driving forces, which in turn strongly influence growth rates and the fate of secondary production (e.g. Kleppel *et al.*, 1991; Poulet *et al.*, 1995; Laabir *et al.,* 1995).

The purpose of this paper is to review the relevant information on zooplankton to estimate regional conditions of food in different areas prevailing in the anchovy (*Engraulis encrasicolus*) habitats in the Bay of Biscay. Our aim is to address several aspects relevant to secondary production which could be necessary for estimating the productivity of the feeding and nursery grounds of fish.

THE BAY OF BISCAY

The Bay of Biscay 1°- 10° N, 43°- 48° W (Fig. 1) is a part of the sub-temperate eastern North Atlantic, and is surrounded by the French-Spanish coast. Topography, hydrological characteristics, origin and variations of water masses in the Bay are reviewed elsewhere (see Koutsikopoulos and Le Cann, 1996). Due to its location and size, coastlines and topography, the Bay is affected by a variety of micro- and mesoscale physical forces, including decadal north Atlantic climatic oscillations (Rogers, 1984; Fromentin and Ibáñez, 1994), upwelling/downwelling, tidal front and river discharges. These physical events affect both the population dynamics and productivity of plankton (see LeFèvre, 1986; Legendre and LeFèvre, 1989; Southward *et al.*, 1995).

An overview of the ecology of zooplankton, number of taxa and species, abundance and distribution of specimens in the Bay of Biscay before the seventies has been published by Thiriot (1976). He
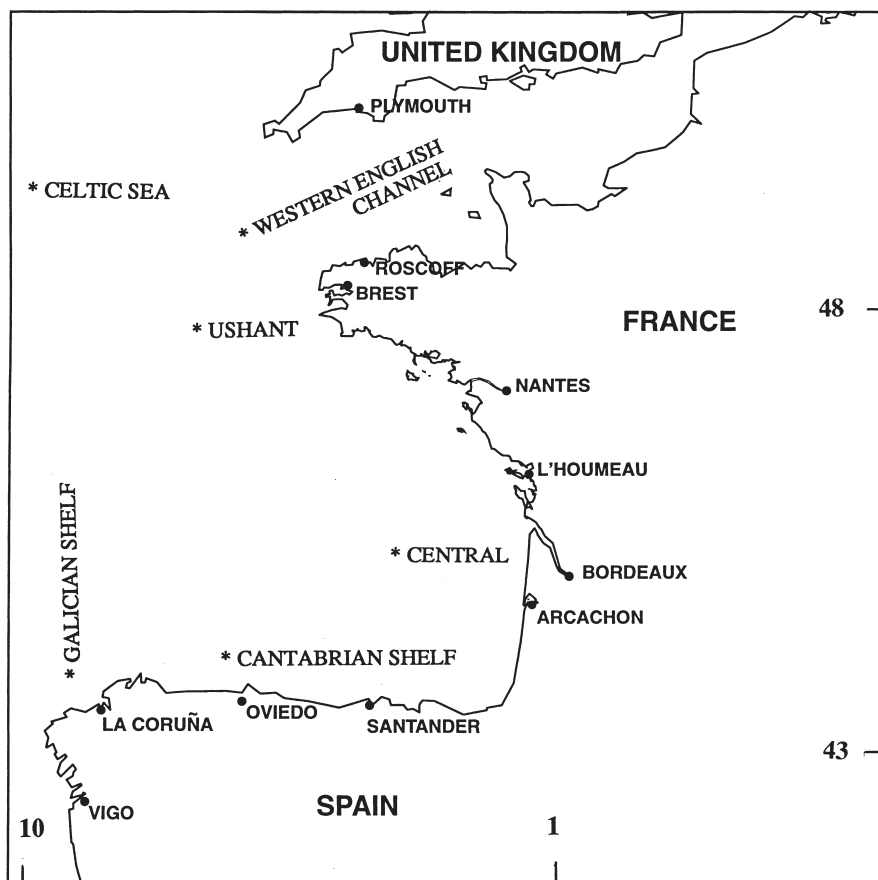
Fig. 1. – Bay of Biscay. Stars show the areas where observations, selected from the literature, were made and which correspond to data shown in Figures 2 to 7 and Tables 1 to 6.

reported that the Bay is a zone of transition and mixing, where several taxa belonging up to 300 species (i.e. oceanic, deep water, coastal, neritic) can be found.

RELATIVE PROPORTIONS OF PARTICULATE ORGANIC CARBON IN THE PLANKTON COMMUNITIES

Estimates of both the representative and relative proportions of particulate organic carbon (POC) in this region, is given by Holligan *et al.* (1984) for the western area of the English Channel, Varela *et al.* (1988) for the Galician continental shelf, and by Fernández *et al.* (1993) for stations located in the central Cantabrian shelf. The relative distribution of POC during early- and midsummer varies according to hydrological conditions. Detritus is the major part of the POC, ranging from 45 to 90% of total. It is evenly distributed in all the Bay, although absolute values are, at times, relatively higher in specific stations (i.e. stratified waters and coastal areas: Table 1). In contrast, phytoplankton and zooplankton carbon correspond to 4-40% and 4-20% of total POC, respectively (i.e. micro- and mesozooplankton are generally less than 15% of total POC). Their biomass are the highest in the productive stations, located in upwelling and frontal regions, or those influenced by rivers, estuary and close to shore (i.e. mixed waters). Bacterial carbon is about 2% of total POC. Ranges of carbon values (Table 1) are more or less overlapping, and do not show any drastic difference in term of proportions between stratified, frontal and mixed water conditions, since high and low biomass of zooplankton are occurring in each area. However, frontal and mixed waters present slightly higher POC values compared to stratified ones. The fact that detritus is proportionally less abundant in both frontal and mixed water conditions compared to stratified ones, suggests that plankton communities are likely more productive in the former ones. In addition, total concentrations of POC in both mixed and frontal areas are at times equal and often 2-3 times higher than values observed in stratified waters, at similar depths or stations. These pat-

TABLE 1. – Relative proportion and range of seston biomass in two extreme areas, located at the northern and southern boundaries of the Bay of Biscay. Data from: (1)- Holligan *et al*. (1984) and (2)- Varela *et al*. (1988).

| | LOCATIONS | | | | | |
| | Western English Channel (1) (depth 0 - 60m) | | | Galician continental shelf (2) (depth 0 - 200m) | | |
Water conditions	Stratified	Frontal	Mixed	Stratified	Frontal	Mixed
Type of seston (% of total POC)						
Detritus	87 - 95	20 - 70	53 - 68	85 - 88	56 - 73	47 - 80
Bacteria	1.4 - 1.7	2 - 7	7 - 10	1 - 3	1.3 - 2.4	0.04 - 2
Phytoplankton	1.8 - 2.5	7 - 9	7.0 - 7.5	4 - 6	15 - 22	15 - 40
Mesozooplankton (80 to $< 200\mu$m)	4 - 6	1 - 12	12 - 18	4 - 8	9 - 20	5 - 12
Range of total POC (mg C $\cdot$ m^{-3})	246 - 1,488			225 - 807		

terns are summarised in Table 1, eventhough they are modified according to seasons, specific areas or depths (see Fernández *et al*., 1993 ; Tenore *et al*., 1995). The C: N ratio ranges between 7.7 to 10.3 for frontal and stratified waters, respectively. For micro- and mesozooplankton it is 4.4 (Holligan *et al*., 1984). These data are necessary to estimate efficiency of egg production of copepods in the field (see below).

THE SIZE FRACTIONS OF ZOOPLANKTON

Zooplankton size spectrum (Fig. 2-A) has been measured in samples collected during an annual cycle in 1988-89, at stations located on the continental shelf off La Coruña (Valdés *et al*., 1990). The sizes of most zooplankters (ca. 98.5%) sampled in the entire Bay, fall within the range of 0.2 to 2.5 mm. The taxonomic groups of zooplankton corresponding to each size range have been identified and are presented in Figure 2-B. Results indicate that the spectrum is polymodal, characterised by three major peaks in the 0.3-0.5, 0.7-1.1 and ≥ 1.6 mm size ranges, respectively (Fig. 2-A). Highest frequency (ca. 70%: mesozooplankton) occurs in the 0.7-1.1 mm range. The two other peaks correspond to macrozoopankton (7 to 12% of total) and to microzooplankton (≤ 2% of total), respectively.

The comparison between the size and type of food filtered by anchovy (Fig. 2-C) and the actual size spectrum of planktonic prey in the Bay of Biscay (Fig. 2-A, C) is important, since O-group clupeoids rely firstly on both phytoplankton and microzooplankton (i.e. eggs, nauplii, copepodites). In contrast, pre-recruits and adults rely on larger size prey which belong to meso- (ca. copepods) and macro-

zooplankton (ca. euphausiids) (e.g. Blaxter and Hunter, 1982; Smith, 1985). These authors have shown that the prey size spectrum screened by anchovy varies during ontogenic development. As fish grow older from O-group to adulthood, the diet shifts progressively from micro- to macrozooplankton. Fecundity and quality of eggs spawned by adult anchovy, which determines survival of their offspring, as shown for other fish (e.g. Kjørsvik *et al*., 1990), relies also on the type, abundance and chemical composition of food, belonging to macrozooplankton.

Therefore, an overview and full understanding of anchovy recruitment, in relation to trophodynamic processes, relies on the measurements of both the biomass and production of each of these three zooplankton components. These characteristics for micro- and macrozooplankton are still poorly known in the Bay of Biscay, as most of the studies carried out have been based on zooplankton samples collected almost exclusively with ≤ 250 mm mesh size nets.

VARIATIONS OF ZOOPLANKTON BIOMASS

In most regions of the Bay of Biscay, zooplankton biomass vary in space (mainly along both horizontal, at the mesoscale: ≥ 1-10 Km, and vertical axis, at the microscale: 1-100 m) and with time (mesoscale: month-year variation, and macroscale: decadal variation). With space, there are 1 to 3 orders of magnitude difference between minimum and maximum values recorded in a given area. With time, values vary with 1 to 2 orders of magnitude between months or years. These characteristics are reported in Figures 3, 4 and 5. In principle, highest
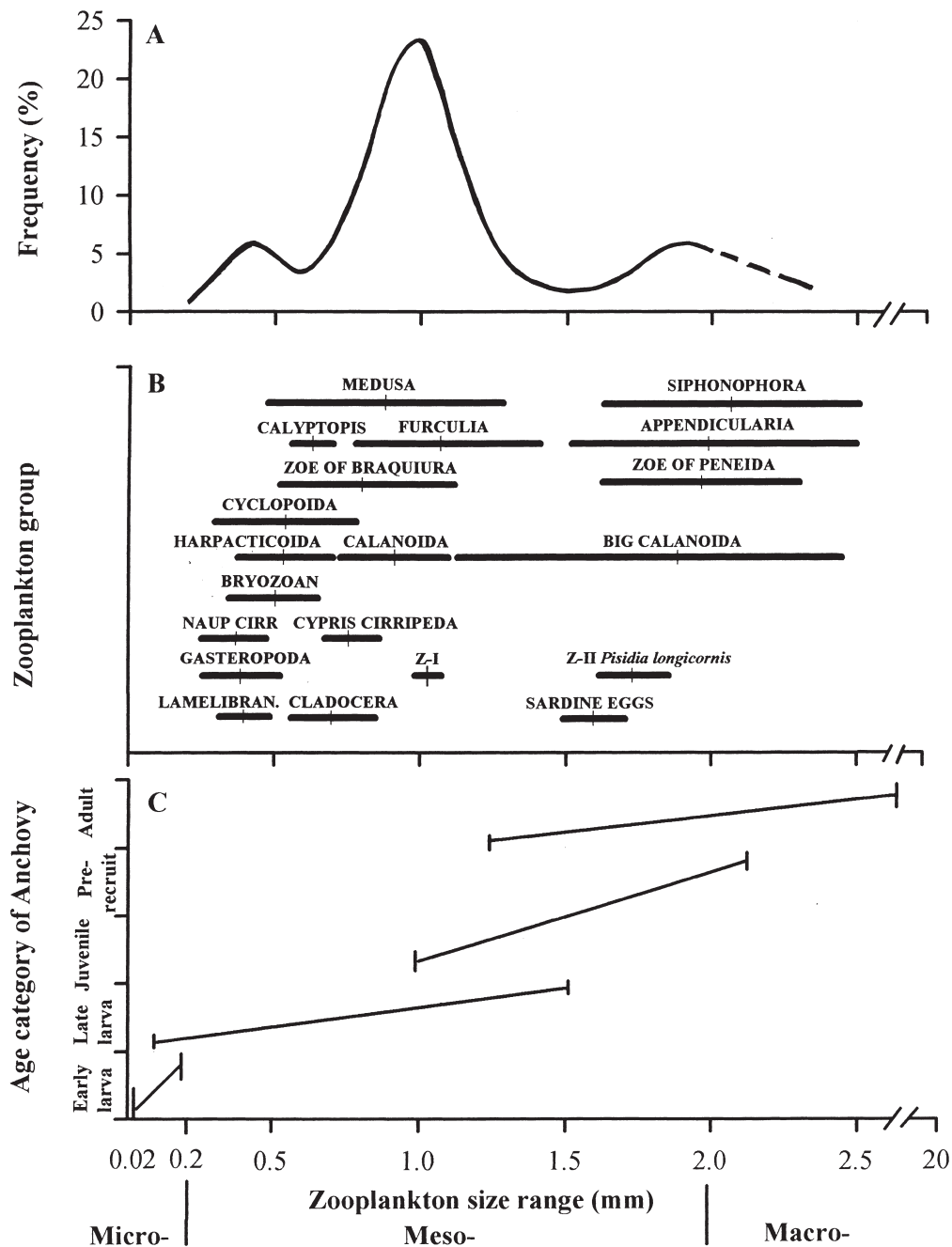
FIG. 2. – Size spectrum (A) and corresponding taxa (B) of zooplankton on the continental shelf off La Coruña, in the Bay of Biscay (from Valdés *et al.*, 1990). The size of prey selected by anchovy during the ontogenic development is given in (C) (from Smith, 1985).

biomass should match food requirement of anchovy mainly during larval growth and reproduction of adults.

Variation with space

At the micro- and mesoscale (m to Km), an example of these variations is well documented by Fernández *et al.* (1993) for the central Cantabrian coast. Their data (Fig. 3-A) show that at a given season, the variability of zooplankton biomass over the horizontal axis is less than between depths in the water column (Fig. 3-B). The extreme values of 10-320 μgC.m^{-3} found in this area are representative of the amplitude of zooplankton biomass, characterising shelf and oceanic regions in the Bay of Biscay (Fig. 3-C ; see also Fernández de Puelles *et al.*, 1995).
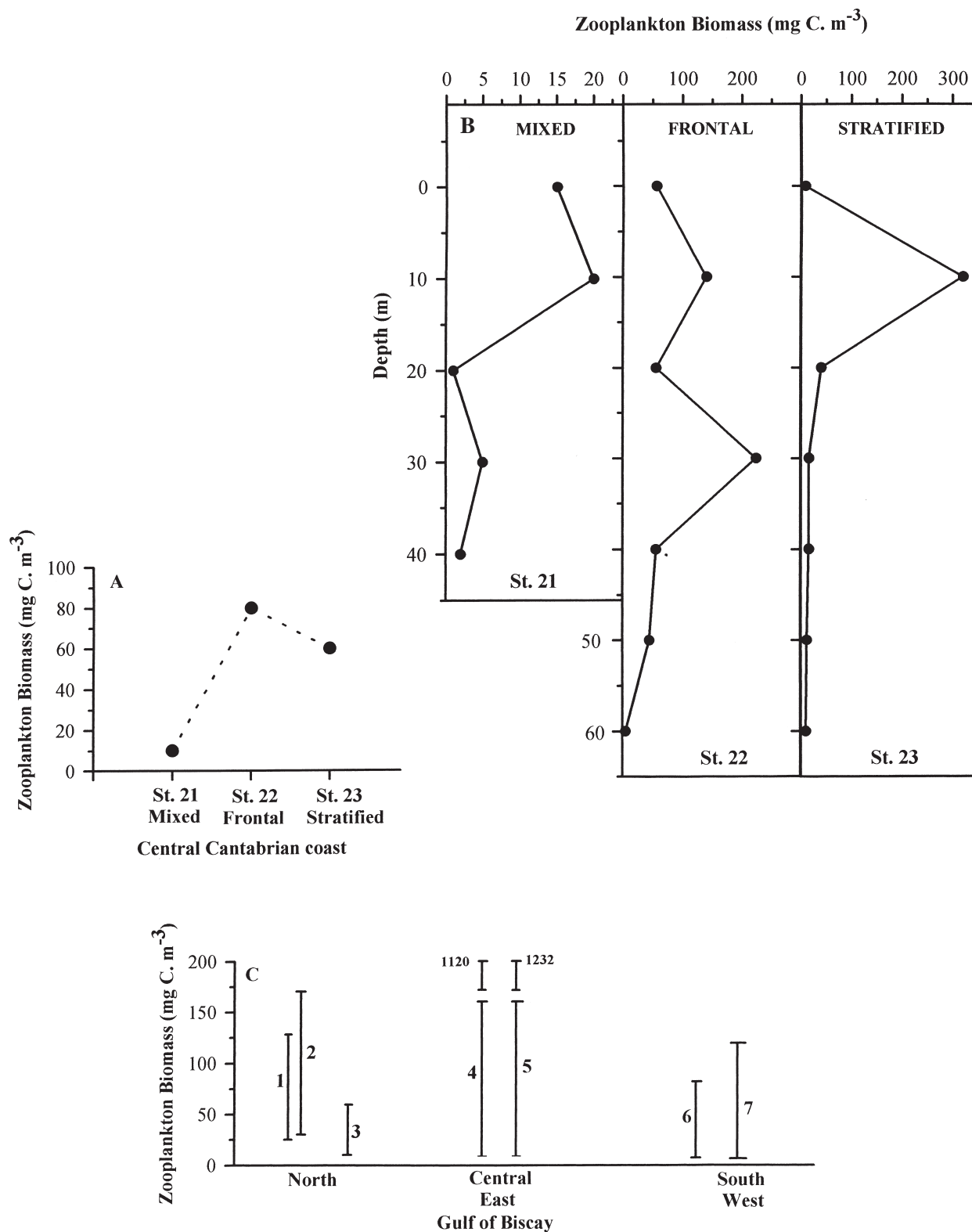
FIG. 3. – Variations of the biomass of zooplankton in space at different scales. A- Mesoscale: comparison between biomass measured in spring at stations located in the central Cantabrian coast and corresponding to mixed (stat. 21), frontal (stat. 22), and stratified (stat. 23) water conditions (from Fernandez *et al.*, 1993). B- Microscale: Comparison between biomass measured at different depths at three stations, same as in (A). C- Macroscale: comparison between minimum- maximum values measured in the northern, central and southern areas of the Bay of Biscay. Data are from: 1- Western English Channel (Holligan *et al.*, 1984); 2- Celtic Sea (Poulet *et al.*, 1991); 3- Ushant region (Moal *et al.*, 1985); 4- Continental shelf offshore Arcachon (D'Elbée and Castel, 1991); 5- Arcachon Basin (D'Elbée and Castel, 1991); 6- Central Cantabrian coast (Fernández *et al.*, 1993); 7- Coast of Galicia (Valdés *et al.*, 1990).
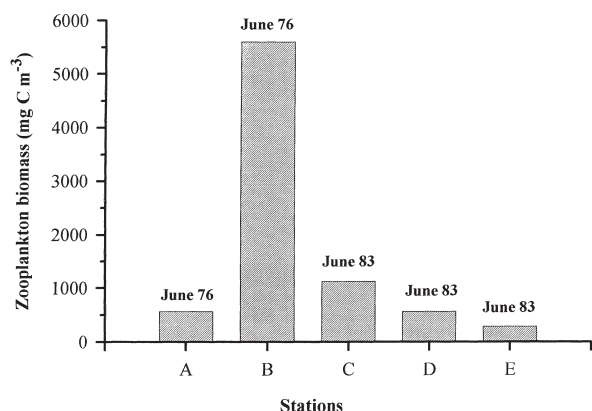
FIG. 4. – Changes of zooplankton biomass during summer conditions between stations, located in the central east region of the Bay. Gradients of standing stocks between bay, estuarine and coastal waters. Position of stations is: A- Inside Arcachon Basin (June 1976 ; Castel and Courties, 1982), B- Mouth of Arcachon Basin (June 1976; Castel and Courties, 1982), C- Off Gironde estuary (mixed conditions, June 1983; D'Elbée and Castel, 1991), D- Continental shelf (stratified conditions, June 1983; D'Elbée and Castel, 1991), E- Shelf break (frontal zone, June 1983; D'Elbée and Castel, 1991).

At a larger scale, variations of biomass are given in Figure 3-C. These values were borrowed from several authors and converted into carbon (conversion factors are 0.01, 0.056 or 0.08 corresponding to the ratios between biomass in μgC/ number of copepods.m^{-3}, calculated from Fernández et al., 1993 data), in order to homogenise and compare the available data. Several interesting patterns emerge. First, variations of the biomass values and ranges are about the same between northern, central and Southern areas, generally comprised between 5 to 200 μgC.m^{-3}. Second, exception to this pattern is found in the central-east area, where biomass measured in near shore, estuarine and basin waters, in Arcachon and in the Gironde are > 1000 μgC.m^{-3}. These very high zooplankton biomass are representative of the important biological activity and patchiness occurring in these neritic environments, and probably as well, in the rivers along the Cantabrian and Galician coasts (e.g. Corral and Álvarez-Osorio, 1978).

The situation in the Gironde area deserves some attention, since it is likely one of the most productive environment, influenced by both estuarine and rivers. Zooplankton biomass estimated in samples collected in shallow and deep waters are given in Figure 4. (Castel and Courties, 1982; D'Elbée and Castel, 1991). Along the inshore-offshore A-E transect, values vary by 1 order of magnitude in June. However, high values are observed both at the mouth of Arcachon Basin (e.g. Stat. B), on entrance of Gironde Estuary (e.g. Stat. C) and even at station D located close to shore on the continental shelf.

Estimates of zooplankton biomass reported earlier (see review by Boucher, 1985) range on the average between 2 and 90 μg.m^{-3} dry weight, 30% of which is carbon. These examples of vertical and horizontal gradients of zooplankton biomass underline the well known fact that zooplankton assemblages are either extremely patchy (i.e. at specific depth-horizons, or stations during spring-summer), or very dilute. Along the northern coast of Spain, zooplankton patchiness has been clearly identified (López-Jamar et al., 1991). These authors have shown that patchiness is very variable in space. The onset, as well as the decay of patchiness in the Bay deserve a thorough investigation in order to understand and evaluate the variations of the standing stock of available food, fitting the feeding requirements of anchovies.

Variation with time

Most of the highest biomass values in the Bay are generally observed during late spring and summer, while minimum values are found in winter. Subsidiary biomass peaks are found in September (see Boucher, 1985). Variations with time are illustrated in Figure 5, for short (i.e. mesoscale: month-year ; Fig. 5-A) and long (i.e. macroscale: decadal ; Fig. 5-B) periods of observation. Valdès et al. (1991) have found at various stations located on the continental shelf off La Coruña, that zooplankton biomass varies seasonally between 9 and 336 μgC.m^{-3} (Fig. 5-A). Again, this range of annual variation is likely representative of some other closed areas, where plankton surveys were restricted to spring, summer or autumn (e.g. Varela et al., 1988; Tenore et al., 1995; Fernández de Puelles et al., 1995).

Measurements for periods that span longer than a year are scarce in the literature (see Arbault and Lacroix-Boutin, 1970). Nonetheless, information is available for several species of zooplankton collected from 1978 to 1991 in the Gironde Estuary (Castel, 1993, Fig. 5-B). In the case of the copepod Acartia bifilosa, decadal variation is 1 order of magnitude. Acartia spp. are among the most abundant zooplanktonic crustaceans found in the Bay (see below) ; and thus, the pattern described in Figure 5-B is interesting, since similar inter-annual variability may also apply to other species.

The causes of these variations (Figs. 3 to 5) are likely driven by climate change, physical oceanography, phytoplankton patterns or predation pressure
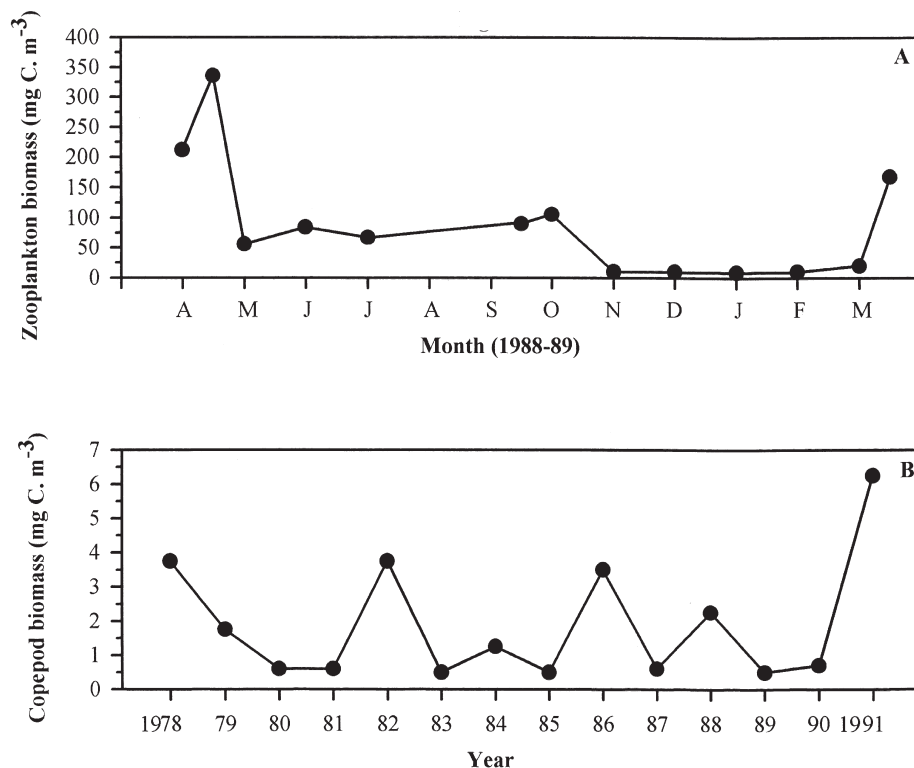
FIG. 5. – A- Short-time variations of total zooplankton biomass during the year 1988-89, representative of stations located on the continental shelf off La Coruña (Valdés *et al.*, 1991), (conversion factor: μgC.m^{-3}/Nb. Ind. m^{-3} = 0.056). B- Long term variations of the biomass of one copepod (i.e. *Acartia bifilosa*) in the Gironde Estuary (from Castel, 1993), (conversion factor: 1 copepod = 2.5 μgC).

existing in the Bay of Biscay at different scales of time and space. However, this general assumption has never been clearly investigated, or a clear cause and effect relationship well defined between forcing factors and zooplankton population dynamics (e.g. Colebrook, 1982).

Variation of the biomass / density ratio

Three linear regressions between zooplankton abundance and biomass are plotted in Figure 6. Regression for March 1987 applies to data obtained at 3 stations located along a transect in the Cantabrian coast (Fernández *et al.*, 1993). It shows that approximately the same density resulted in biomass values 10 times higher as compared to position of stations, highest values being found near frontal and upwelling stations. Similar regressions, computed by Valdès *et al.* (1990) for June and September 1984 for stations located along the Galician coast, are also shown in Figure 6. In that case, twice as many individuals per m^{-3} in September resulted in the same biomass as compared to June. These correlations also show that for a given area (e.g. northern coast of Spain: Fig. 6), biomass is not necessarily propor-
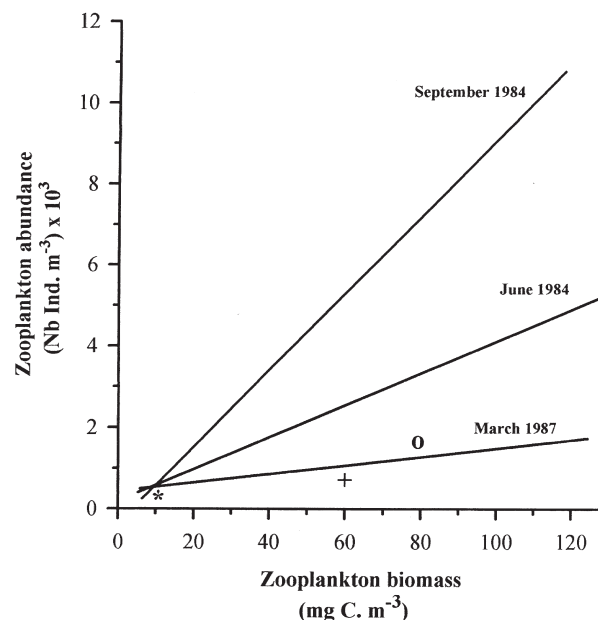

FIG. 6. – Relationship between density (Y) and biomass of zooplankton (X) in the Bay of Biscay. March 1987 (Y = 0.5 + 0.01 X , r = 0.8): data from Fernández *et al.*, (1993), corresponding to mixed (*), stratified shelf break (+) and stratified (o) continental shelf. June (Y = 0.099 + 0.033 X , r = 0.78) and September (Y = - 0.372 + 0.094 X , r = 0.81) 1984 data, corresponding to all stations and water conditions combined (from Valdés *et al.*, 1990).

TABLE 2. – Representative list of the most abundant and frequent taxa and species of zooplankton found in the Bay of Biscay (from D'*e*lbée and Castel, 1991).

ARTHROPODA

BRANCHIOPODA

Podon polyphenioides (Leuckhart, 1859)
Podon intermedius (Lilljeborg, 1853)
Podon leuickharti (Sars, 1861)
Evadne spinifera (P.E. Müller, 1867)
Evadne nordmanni (Loven, 1836)
Evadne tergestina (Claus, 1877)
Penilia avirostis (Dana, 1849)

OSTRACODA

Conchoecia curta (Lubbock, 1860)
Conchoecia elegans (Sars, 1865)
Conchoecia rotundata (G.W. Müller, 1891)
Conchoecia spinirostris (Claus, 1874)
Conchoecia parthenoda (G.W. Müller, 1906)
Conchoecia daphnoides (Claus, 1890)
Conchoecia subarcuata (Claus, 1890)

COPEPODA

Calanoida
Calanoides carinatus (Kröyer, 1849)
Calanus helgolandicus (Claus, 1863)
Calanus tenuicornis (Dana, 1849)
Neocalanus gracilis (Dana, 1849)
Eucalanus elongatus (Dana, 1849)
Eucalanus crassus (Giesbrecht, 1888)
Rhincalanus nasutus (Giesbrecht, 1888)
Paracalanus parvu (Claus, 1863)
Ischnocalanus tenuis (Farran, 1926)
Calocalanus contractus (Farran, 1926)
Calocalanus styliremis (Giesbrecht, 1888)
Calocalanus pavo (Dana, 1849)
Clausocalanus sp.
Pseudocalanus elongatus (Boeck, 1872)
Ctenocalanus vanus (Giesbrecht, 1888)
Aetideus armatus (Boeck, 1872)
Euchirella rostrata (Claus, 1866)
Euchaeta hebes (Giesbrecht, 1892)
Euchaeta acuta (Giesbrecht, 1892)
Scolecithricella dentata (Giesbrecht, 1892)
Diaxis hibernica (A. Scott, 1896)
Centropages typicus (Kröyer, 1849)
Centropages hamatus (Lilljeborg, 1853)
Centropages violaceus (Claus, 1863)
Centropages chierchiae (Giesbrecht, 1889)
Isias clavipes (Boeck, 1864)
Temora stylifera (Dana, 1849)
Temora longicornis (0.F. Müller, 1785)
Metridia lucens (Boeck, 1864)
Pleuromamma gracilis (Claun 1863)
Pleuromamma robusta (Dahl, 1893)
Heterorhabdus papilliger (Claus, 1863)
Candacia armata (Boeck, 1872)
Anomalocera patersoni (Templeton, 1837)
Labidocera wollastoni (Lubbock, 1857)
Parapontella brevicornis (Lubbock, 1857)
Acartia clausi (Giesbrecht 1889)
Acartia discaudata (Giesbrecht, 1881)
Acartia bifilosa (Giesbrecht, 1881)
Acartia grani (Sars, 1904)
Acartia tonsa (Dana, 1848)
Acartia margalefi (Alcaraz, 1976)

Cyclopoida
Oithona nana (Giesbrecht, 1892)
Oithona helgolandica (Claus, 1863)
Oithona plumifera (Baird, 1843)
Cyclopina littoralis (Brady, 1872)

Poecilostomatoida
Oncaea media (Gies.brecht, 1891)
Oncaea curta (Sars, 1916)
Oncaea conifera (Giesbrecht, 1891)
Ditrichocorycaeus anglicus (Lubbock, 1857)
Urocorycaeus furcifer (Claus, 1863)

Harpacticoida
Harpacticus littoralis (Sars, 1910)
Tisbe sp.
Pseudobradya sp.
Paradactylopodia sp.
Altheuta sp.
Microsetella rosea (Dana, 1852)
Euterpina acutifrons (Dana, 1852)
Clytemnestra rostrata (Brady, 1883)
Clytemnestra scutellata (Dana, 1852)

CIRRIPEDIA

Chthalamus sp.
Balanus sp.

PERACARIDA

Mysidacea
Gastrosaccus spinifer (Goes, 1864)
Schistomysis spiritus (Norman, 1860)
Neomysis integer (Leach, 1814)
Mesopodopsis slabberi (Van Beneden, 1861)
Anchialina agilis (Sars, 1877)
Erythrops elegans Sars, 1863
Gastrosaccus lobatus (Nouvel, 1950)
Leptomysis gracilis (Sars, 1864)
Mysideis parva (Zimmer, 1915)
Schistomysis kervillei (Sars, 1885)
Schistomysis ornata (Sars, 1864)

Cumacea
Nannastacus longirostris (Sars, 1879)
Bodotria sp.
Diastylis sp.

Isopoda
Epicarid microniscian larvae

Amphipoda
Caprella sp.
Phronima sp.
Argissa hamatipes (Norrnan, 1869)
Atylus swammerdami (Milne Edwards, 1830)
Atylus sp.
Cheirocratus sundevalli (Rathke, 1843)
Hyperia sp.
Megaloropus agilis (Hoek, 1889)
Melphidippella macra (Norrnan, 1869)
Phtisica marina (Slabber, 1749)
Tryphosites longipes (Bate & Westwood, 1861)
Urothoe elegans (Bate, 1856)
Westwoodilla caecula (Bate, 1856)
Apherusa ovalipes (Norman & Scott, 1906)

EUCARIDA

Euphausiacea
Nyctiphanes couchi (Bell, 1853)
Stylocheiron sp.

Decapoda
All larval stages

CHAETOGNATHA

Sagitta friderici (Ritter-Zahony, 1911)
Sagitta lyra (Krohn, 1853)

CNIDARIA

Gymnoblastid Anthomedusae
Calyptoblastid leptomedusae
Physalia physalis (Linne, 1758)
Physophora hydrostatica (Forskal, 1775)
Lensia conoidea (Keferstein & Ehlers, 1860)
Lensia fowleri (Bigelow, 1911)
Lensia multicristata (Moser, 1925)
Chelophyes appendiculata (Eschscholtz, 1829)
Velella velella (Linne, 1758)

CTENOPHORA

Pleurobrachia pileus (0. F. Müller, 1776)
Beroe cucimis (Fabricius, 1780)

NEMERTEA

Pilidium larvae

ANNELIDA

Metatrochophore and nectochete larvae
Tomopteris sp.

MOLLUSCA

Gasteropod and Bivalve veligers

ECHINODERMATA

Echinopluteus
Ophiopluteus
Auricularia
Bipinnaria,
Doliolaria larvae

UROCHORDATA

APPENDICULARIA

Oikopleura dioica (Fol, 1872)
Fritillaria pellucida (Bush, 1851)

THALIACEA

Salps and Doliols

VERTEBRATA

Fish eggs
Larvae

tional to the number of organisms per m^{-3}, simply because the size and species categories of zooplankton change seasonally or spatially. Furthermore, results in Figure 6 show that for a given biomass, the corresponding densities increase by a factor of 1 to 6 from spring to fall. This set of data illustrates the changes occurring in the zooplankton biomass mediated either by shifts of taxa, species and sizes or developmental stages containing different amounts of carbon per individual.

In this region, the carbon biomass/zooplankton density ratio (i.e. units: μgC.m^{-3} / Nb. Ind. m^{-3}), extrapolated from data published by Fernández *et al.* (1993), varies between 0.01 and 0.08. The biomass varies by 1 order of magnitude in comparison to 3 orders of magnitude for density (Fig. 6). From a trophodynamic point of view, it means that the standing stock of zooplankton in term of organic matter (i.e. carbon) and the corresponding number of individuals and species in each sample must be carefully identified in any case, in order to minimise erroneous estimates of flux of energy between zooplankton and fish. At the present time, we do not know how the anchovy react to these variations.

IDENTIFICATION AND RELATIVE PROPORTION OF TAXA AND SPECIES OF ZOOPLANKTON

In the Bay of Biscay, oceanic (e.g. Farran,1926: see D'Elbée and Castel,1991), coastal-neritic (e.g. Vives,1979; 1980; Alcaraz,1981 ; Le Tareau *et al.,* 1983; Moal *et al.*, 1985; Valdès *et al.*, 1990; D'Elbée and Castel, 1991), and estuarine zooplankton (e.g. Corral and Álvarez-Osorio, 1978; Castel and Courties, 1982; D'Elbée and Castel, 1991) have been extensively studied. An exhaustive list of identified taxa and species is given in Table 2 (D'Elbée and Castel, 1991). It is based on the analyses of plankton hauls (2 m; 0-180 m) achieved during 1983-1984 in the southern Bay of Biscay. It probably incorporates all zooplankton taxa known in the entire Bay of Biscay, occurring over the year. However, this list has some weak points regarding several taxa, belonging to meroplankton (e.g. Annelida, Cirripedia, Decapoda), holoplankton (e.g. Thaliacea, Chaetognatha, Pteropoda, Heteropoda, Euphausiacea) and ichthyoplankton (e.g. fish eggs and larvae). This is unfortunate, since species belonging to the two former groups are often numer-
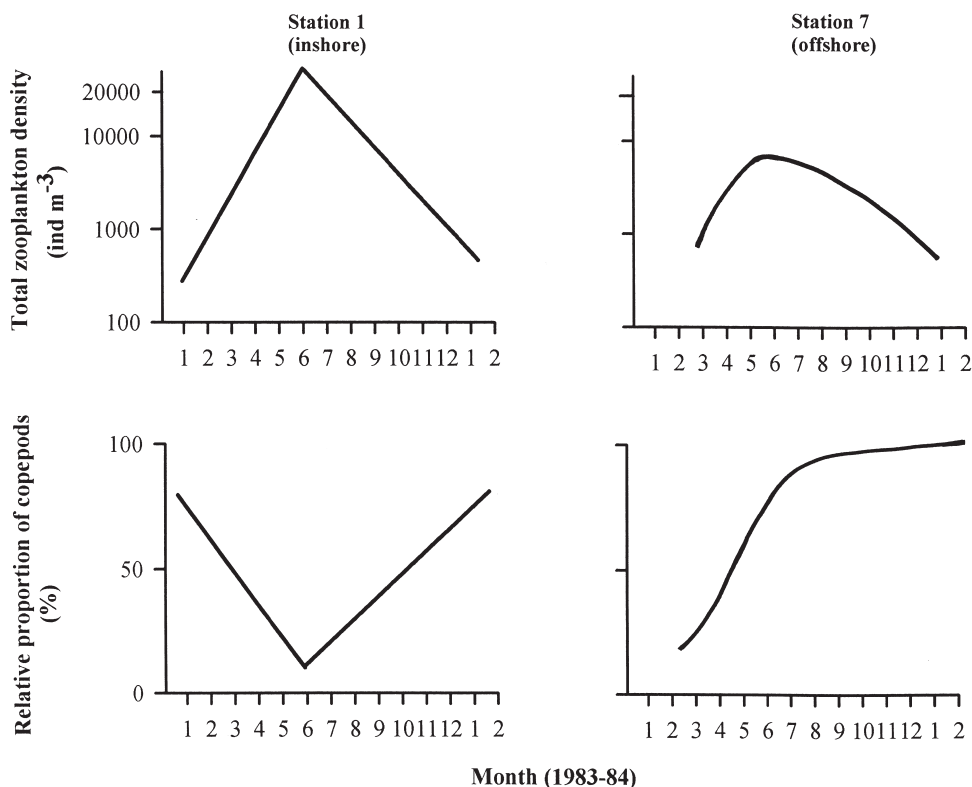

FIG. 7. – Seasonal changes of zooplankton biomass and proportions of copepods inshore (Station 1) and offshore (Station 7) the Gironde Estuary during 1983-84 (from D'Elbée and Castel, 1991).

ous in oceanic, shelf and estuarine habitats, depending on taxa (e.g. Beaudouin, 1971; Mathivat-Lallier and Cazaux, 1990) or correspond to macrozooplankton species existing in more oceanic and deeper waters (see Tesch, 1946; 1949; Kramp, 1959; Reyssac, 1963; Casanova, 1971 for details). Moreover, these organisms are extremely patchy; and as such, some of them may be dense food stocks at specific depths, locations and seasons when they occur.

Further information about the species composition of zooplankton are available for the northern (e.g. Moal *et al.*, 1985) and southern (e.g. Valdès *et al.*, 1990; 1991; 1992) regions of the Bay of Biscay.

The seasonal variations in zooplankton composition have been studied in detail by a limited number of authors (e.g. Beaudouin, 1971; 1975; Moal *et al.*, 1985; D'Elbée and Castel, 1991; Valdès *et al.*, 1992). This information is summarised in Figure 7, which shows variations of the total number of zooplankters per volume and the relative proportion of copepods in the southern Bay of Biscay (D'Elbée and Castel, 1991). These measurements were made in 1983-84 at stations close to the French coast of the Gironde Estuary (Stat. 1) and on the shelf-break (stat. 7), respectively. Similar patterns have been observed elsewhere in the Bay (Moal *et al.*, 1985; Valdès *et al.*, 1992). Total zooplankton density and the proportion of copepods vary in opposite direction at stations close to shore (Fig. 7: stat. 1), suggesting that zooplankton blooms are related to mero-

TABLE 4. – List of copepod species occurring during summer and fall in the Galician continental shelf (Data on the relative proportion (%), and total density of zooplankton (ind. m^{-3}) are from Valdès *et al.*, 1990). Bold stars correspond to the dominant species

Copepod species (%)	SUMMER (June)	FALL (September)
Calanus helgolandicus	**6**	**1.63**
Calanus tenuicornis	0.16	0.16
Calanoides carinatus	0.81	1.79
Eucalanus spp.	0.16	0.36
Paracalanus parvus	**8**	**27.52**
Calocalanus styliremis	0.65	0.28
Calocalanus tenuis	-	0.28
Mecynocera clausi	-	0.04
Pseudocalanus elongatus	**6.06**	**3.62**
Clausocalanus spp.	**0.98**	**2.81**
Ctenocalanus vanus	1.63	0.56
Aetideus armatus	0.16	0.08
Gaetanus minor	-	0.04
Euchaeta hebes	0.48	0.36
Scolecithricella dentata	0.16	0.12
Diaxis durani	-	0.08
Temora longicornis	**10.32**	**10.92**
Metridia lucens	0.81	0.24
Pleuromamma gracilis	-	0.08
Centropages typicus	**0.48**	**2.24**
Centropages chierchiae	0.98	0.36
Isias clavipes	0.48	0.12
Candacia armata	0.81	0.16
Anomalocera patersoni	-	0.04
Acartia clausi	**50.65**	**41.84**
Oithona plumifera	**3.44**	**2**
Oithona helgolandica	**5.4**	**1.38**
Oithona nana	-	0.61
Oncaea spp.	**0.98**	**9.17**
Corycaeus anglicus	0.48	0.2
Corycaeus furcifer	0.16	0.04
Corycaeus typicus	-	0.12
Corycaeus spp.	-	0.12
Euterpina acutifrons	0.48	0.16
Microsetella norvegica	0.16	0.04
Clytemenestra rostrata	0.32	0.08
Total (ind.m^{-3})	610	2452

TABLE 3. – Seasonal variations of the relative proportions (%) of zooplankton belonging to the major taxa found in the southern region of the Bay (i.e. Galician continental shelf ; Valdés *et al.*, 1992). Bold numbers correspond to the most abundant categories.

ZOOPLANKTON TAXA	1984 FALL	SUMMER	1986 SPRING
Foraminifera	0.2	0.25	0.52
Radiolairian	-	-	0.12
Tintinids	0.4	0.6	0.64
Rotifers	-	-	1.12
Cnidaria	-	1.7	-
L. Gasteropods	0.3	0.8	0.25
L. Lamelibranches	9.4	**16.4**	3.4
L. Polychets	0.1	1.6	0.3
Cladocerans	0.1	1.4	0.04
Nauplii (cop.)	**49**	41	**87.56**
Copepodites	**17.5**	9.4	6.68
Cyclopoida	**14**	**10**	0.96
Harpacticoida	2.9	2.2	0.5
L. Cirripedia	0.8	3.3	0.08
L. Decapoda	0.1	0.15	-
L. Bryozoan	0.2	0.3	0.44
L . Echinodermata	-	3.65	0.08
Appendicularian	-	**20.8**	0.16

L. = larvae

plankton in neritic, estuarine habitats. In contrast, total zooplankton density and proportion of copepods show parallel seasonal variations at stations located on the continental shelf and shelf-edge (Fig. 7: stat. 7). It means that in such habitats copepods are the dominant secondary producers among micro- and mesozooplankton. Valdés *et al.* (1991) have observed almost similar patterns at stations located on the Galician continental shelf (Table 3). As expected, the proportion of each taxa varies with time. At all seasons, copepods are generally the most abundant and most frequent members of these zooplankton communities. This is also true in some eastern and northern regions of the Bay (e.g. Moal *et al.*, 1985; D'Elbée and Castel, 1991); but several exceptions have been mentioned (see Fig. 7).

A list of copepod species is given in Table 4, representative of the north coast of Spain (Valdés *et al.*, 1990), although more reduced than the one pro-

Rank	Species of copepods	(%)
1	*Acartia clausi*	46
2	*Paracalanus parvus*	18
3	*Temora longicornis*	11
4	*Oncaea* spp.	5
5	*Pseudocalanus elongatus*	5
6	*Calanus helgolandicus*	4
7	*Oithona helgolandica*	3
8	*Oithona plumifera*	3
9	*Clausocalanus* spp.	2
10	*Centropages typicus*	1

duced by D'Elbée and Castel (1992) for the Gironde Estuary (See Table 2), it suggests that species diversity in neritic-estuarine environments is higher. Among the 36 species identified on average for the Galician continental shelf, copepods belong to the mesozooplankton group during the adult phase (i.e. size range: 0.2 - 2 mm; see Fig. 1- A and B) and to the microzooplankton group during their larval-juvenile phases of life (i.e. size range: 0.08 - 0.2 mm; see Fig. 1 A and B). Among these two groups, 68% of copepods belong, on average, to Calanoids, whereas 18% and 11% are Cyclopoids and Harpacticoids, respectively (Valdés *et al.*, 1991). The 10 most abundant and frequent species of copepods are listed in Table 5.

The biological and ecological characteristics of these species are still not well known (ca. life cycle, feeding, growth and reproduction, seasonal and spatial variations), especially in the Bay of Biscay. However, in the case of the most frequent ones (see Table 6), the information can be extrapolated from the literature for same species or genus occurring in other environments. New observations on the feeding of larvae and adult anchovy will indicate which taxa and size group of zooplankton are relevant to anchovy.

GROWTH RATES AND SECONDARY PRODUCTION PATTERNS IN COPEPODS

Information on the growth rate and secondary production of zooplankton in the Bay is scarce (see López-Jamar *et al.*, 1991; Bautista *et al.*, 1994). Focusing this last section on copepods is legitimate, since they often constitute the majority of mesozooplankton and nothing is known about the two other components, i.e.- micro- and macrozooplankton.

Moreover, field estimates of productivity is now requested to identify areas offering satisfactory food stocks to intensively feeding and fast growing anchovies.

Direct measurements of growth and secondary production at sea are difficult, because of methodological limitations. However, this point is now partly solved in copepods, considering that the "egg incubation method" calibrated by Laabir *et al.* (1995) for *Calanus helgolandicus* and reviewed by Poulet *et al.* (1995) is a practical approach allowing direct measurements of production in the field. One advantage of this method is its site- and time specificity, reflecting the instantaneous functional responses of copepods to their food environment (Kiørboe, 1993). Growth and production rules in copepods are governed both by temperature and food. The ranges for temperature and chlorophyll *a* concentration (used as an index of food concentration for copepods) measured in the Bay of Biscay are 10-21 °C and 0.1-20 μg Chlo *a*.l^{-1}, respectively (see Koutsikopoulos and Le Cann, this volume; Holligan *et al.*, 1984; Moal *et al.*, 1985; Maddock *et al.*, 1989; Lopez-Jamar *et al.*, 1991). Methods to estimate production of micro- and macrozooplankton do not exist.

The growth rate rules

Growth of omnivorous copepods is both temperature and food dependent and follows few basic rules. Under saturated food conditions (C_{max}: above which growth rate is maximal), growth rate (Y) is linked directly to temperature (e.g. Miller *et al.*, 1977). At food concentration below saturation level (C_{min}: where assimilation balances respiration) growth is rather food dependent; and thus, it follows a classic Michaelis-Menten function, given by the equation: $Y = W_o.I^{C.k}$; where Wo is the initial weight, I is ingestion rate and k a constant related to assimilation. In most cases, copepods are acclimated to their ambient temperature, while food is often limiting (see below). Thus, one can safely assume that zooplankton growth is first controlled by food concentration, rather than by temperature. This rules should apply to the Bay of Biscay where the maximum amplitude of temperature coincides with the lower and upper limits of copepod specific growth rates Gmax (d^{-1}) known in the literature and illustrated in Figure 8 (e.g. Vidal, 1980; Huntley and Boyd, 1984). Extrapolation from these data predicts that maximum daily growth rate of most copepods
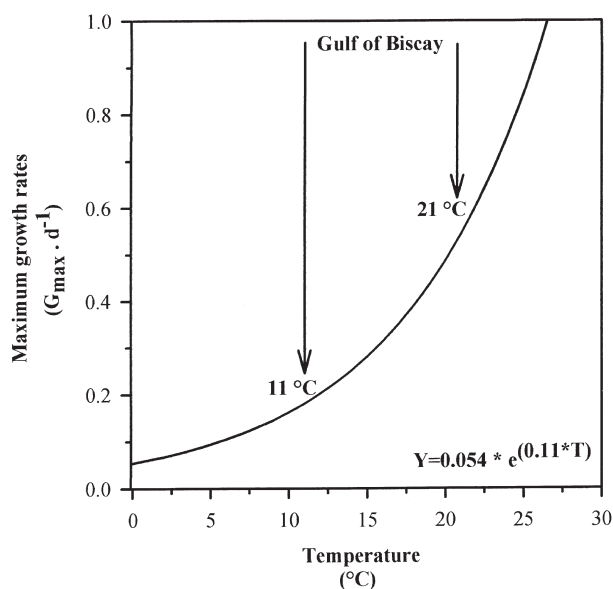
FIG. 8. – Relationship between temperature and the specific maximum growth rate of copepods. Arrows show the *in situ* temperature range for the Bay of Biscay (modified after Huntley and Boyd, 1984).

in the Bay of Biscay may vary between 0.15 and 0.6, assuming that copepods are not food limited. This growth / temperature exponential function is best fitted (r = 0.86) by: $Y = 0.0542.e^{0.11.T}$. It applies to *Calanus, Acartia, Pseudocalanus, Eurytemora,* and
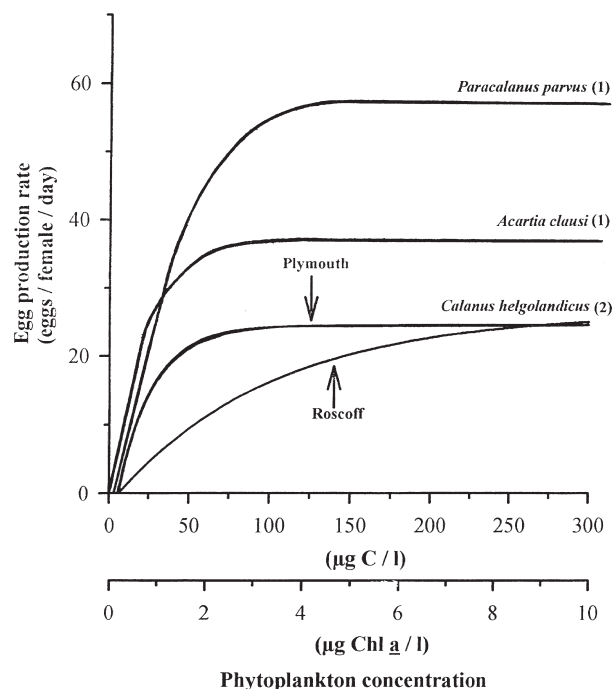

FIG. 9. – Functional responses of zooplankton to food conditions. Comparison of secondary production between 3 copepod species and two types of water conditions (Western English Channel- permanent well-mixed : Roscoff ; seasonally stratified: Plymouth). Data are from : (1) Ambler (1985) and (2): Laabir *et al.* (submitted).

Temora species (see review by Huntley and Boyd, 1984). However, this relationship does not hold when copepods are food limited, or starving. The question is: how often, where and when are copepods food limited in the Bay of Biscay? The point is that copepods are close or just above starvation conditions in most of the environments, except during phytoplankton blooms (Laabir *et al.*, submitted, see Fig. 10 below).

The food limitation problem

Using egg production as an indicator of growth of adult females, the threshold of food concentration below which secondary production is food limited is given in Figure 9.

The production of 3 copepods in responses to the range of phytoplankton concentrations, are shown in Figure 9. Egg production rates fit a non-linear relation versus Chlo *a*, the values of which are species dependent. However, egg production of most copepods is exponential below a lower threshold of phytoplankton density (≤ 1.5 μg Chlo *a* l[-1]). Above the concentration threshold, (ca. Chlo *a* $\geq$ 2-3 μg. l[-1]), corresponding to food saturation levels, production reaches a plateau. Maximum daily egg production of copepods fed *ad libitum* under laboratory food conditions (i.e. $\geq$ 5-10 μg Chlo *a* l[-1]) are given in Table 6. Egg production varies between 3 to 230 eggs per female, depending on species (see review by Ambler, 1985; Ianora *et al.*, 1995). Maximum values are close to 50-60 eggs .female[-1].day[-1] for most species, and are much less in species carrying egg sacs. Among copepods, spawning lasts between 10 to 30 days or more in *Calanus* spp., after mating. Optimum production responses are likely not to achieved in many habitats, because spawning duration and egg production, may be reduced by predation pressure on adults, natural mortality as well as food limitation.

In nature, a decrease in production due to food limitation is illustrated in Figure 10, assuming optimum fecundity in *Calanus helgolandicus* of 60 eggs.female[-1].day[-1]. Results obtained in 1994 indicate that estimates of *in situ* egg production by *Calanus helgolandicus* was below 30 eggs.female[-1] .day[-1] in well-mixed water conditions offshore of Roscoff (English Channel, France), even during spring-summer phytoplankton blooms which are generally $\leq$ 4 μg Chlo *a*. l[-1]. However, in April or October, when females reach minimum fecundity because food is limiting (Chlo *a* $\leq$ 0.5 μg.l^{-1}),
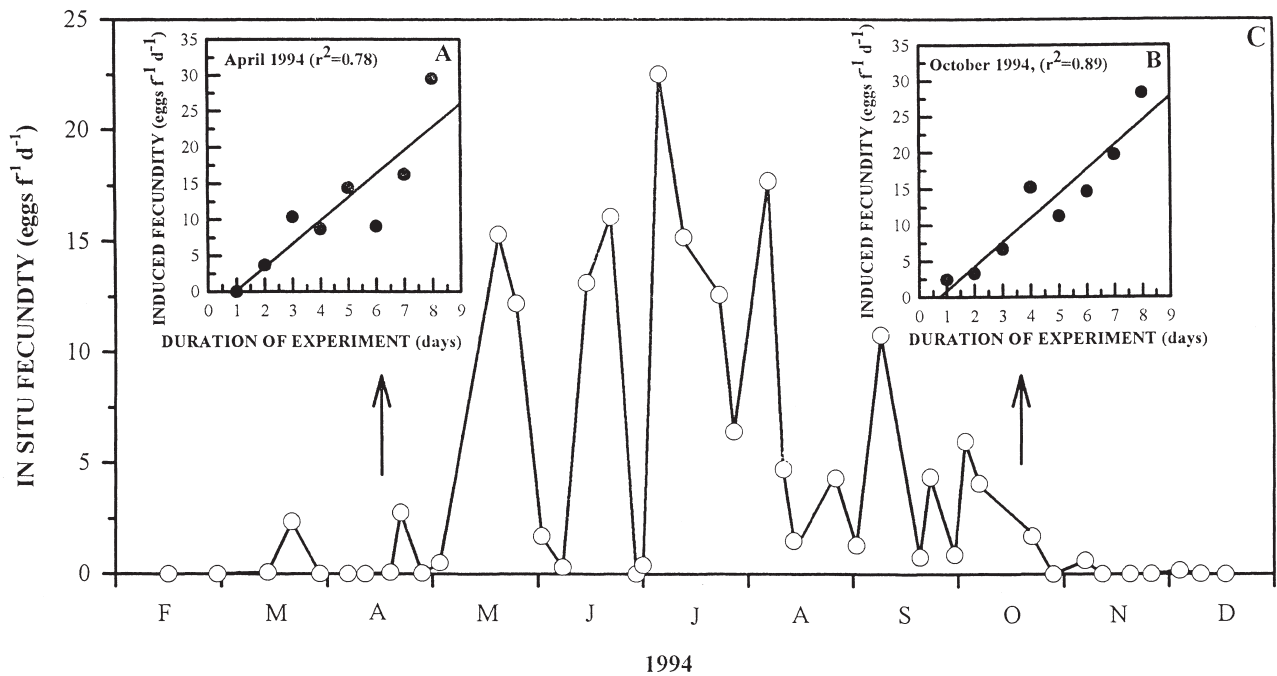
FIG. 10. – Seasonal changes of the fecundity of *Calanus helgolandicus*, estimated in the field, off Roscoff, in 1994 (Western English Channel), showing that optimum physiological production is not reached in this region. A and B correspond to production pulses induced under laboratory conditions at two different periods of the year, when phytoplankton standing stock and fecundity were both low (Laabir *et al.*, submitted).

increases in egg production could be induced in the laboratory simply by adding algal cultures and feeding the females for a week (Fig. 9-A an B). These observations show that below 2-3 μg Chlo *a*. l^{-1}, copepods are food limited. Production rate is reduced twice below physiological maximum values, even during phytoplankton blooms occurring in the field during spring-summer (Fig. 10). We suspect that the same rules apply to the Bay of Biscay, where estimates of egg production rates (e.g. *Calanus helgolandicus, Temora longicornis, Acartia clausi, Paracalanus + Pseudocalanus + Clausocalanus*), were between 4 and 40 eggs.female^{-1}.day^{-1} (Lopez-Jamar *et al.*, 1991; Bautista *et al.*, 1994), and hence below the optimum reproduction capacity of these copepods species (Table 6).

Relationship between water conditions and secondary production

The link between physical oceanography conditions, phytoplankton characteristics and the functional response of zooplankton production has been documented by several authors for short time periods associated with wind stress, storms and turbulence (e.g. see Kiørboe, 1993) and in relation to fisheries for longer periods (decadal changes: see Cushing, 1995). We are just beginning to understand and mea-

sure the functional responses of copepods to shifts of phytoplankton biomass and species (Poulet *et al.*, 1995; Fig. 10) induced by physical events occurring at small and large scales. An example of this type of physical-biological relationship is given in Figure 9-(2). Field estimates of *Calanus helgolandicus* fecundity were made in 1993-94, simultaneously offshore Roscoff (i.e. permanent well-mixed water conditions; *in situ* Chlo *a* range: 0.2 - 4 μg.l^{-1}) and Plymouth (i.e. seasonally stratified water conditions ; *in situ* Chlo *a* range: 0.2 - 10 μg.l^{-1}) ; located on each side of the English Channel. Results show that fecundity was below the maximum physiological ability in both areas (Laabir *et al.*, submitted). They also show that production values were higher on the Plymouth

TABLE 6. – Range of maximum values related to fecundity of the major species of copepods also occurring in the Bay (data from- 1: Ambler, 1985 ; 2 : Ianora *et al.*, 1995).

COPEPOD SPECIES	MAXIMUM RANGE OF FECUNDITY (egg / female / day)			Reference
Acartia clausi	20	-	70	1 & 2
Acartia tonsa	22	-	60	1 & 2
Paracalanus parvus			82	
Pseudocalanus elongatus	1	-	3	1
Centropages typicus	80	-	230	1 & 2
Temora stylifera	30	-	100	1 & 2
Calanus helgolandicus	30	-	60	1 & 2

side as compared to Roscoff, suggesting that stratified water conditions were likely more favourable for *C. helgolandicus*.

The gross efficiency of egg production

The gross efficiency of egg production is given by the ratio $K_{1(B)} = B / (I_p + I_e)$ (e.g. Checkley, 1980, for *Paracalanus parvus)*, corresponding to the ratio between rate of egg production (B) and rates of ingestion (I_e) and phytoplankton concentration (I_p), expressed in carbon or nitrogen units. It is an hyperbolic function of the C: N ratio of food. Checkley (1980) found in *Paracalanus parvus* that $K_{1(B)}$ (given in carbon units) varies between 0.1 and 0.6, while values for C: N in algal food varies between 4 and 12.

In the Bay of Biscay, the C: N ratio, considered as potential food for copepods, ranges between 7.7 and 10.3 (Holligan *et al.*, 1984). Extrapolating Checkley's data to the Bay and to other copepods, suggests that gross efficiency of egg production in copepods might be ≤ 0.2, which is 1/3 less than the optimum. Thus, whatever the units (e.g. Chlo *a* concentration, or C: N ratio of POC), it seems that average food conditions occurring in the Bay might induce much lower production responses than expected, except during phytoplankton blooms.

CONCLUSION

The Bay of Biscay is characterised by a high diversity of physical events, occurring at various scales in time and space (see Koutsikopoulos and Le Cann, 1996). Similarly, zooplankton communities are extremely variable and diverse (ca. 300 species: Thiriot, 1976). The patterns of copepods in these communities ressemble those described in other planktonic ecosystems of mixed and stratified waters, characterizing the European shelf seas (Williams *et al.*, 1994).

Before the seventies, the majority of the work on zooplankton has been almost exclusively related to qualitative and taxonomic studies (see review in Thiriot, 1976).

From the seventies onward, studies have shifted to more quantitative and ecological approaches. Coverage of mesozooplankton was fairly good, whereas investigations related to micro- and macrozooplankton were still scarce. Also, during this period, few attempts were made to estimate secondary production in the field.

Beyond the nineties, the scope and type of future studies will have to be re-examined in relation to physical oceanography, and to anchovy habitats, including feeding behaviour, and food requirements of the fast growing larvae and juveniles. In particular, information relevant to patchiness, biomass, production rates and chemical nutritional values of the three components of zooplankton (see Martin-Jézéquel *et al.*, 1989; Poulet and Williams, 1991) will probably require deeper investigations. It should be kept in mind that anchovies modify their selectivity for food during ontogenic development ; preying upon zooplankton and filtering phytoplankton (e.g. James, 1988; James and Findlay, 1989) during the first year of life. Knowing that anchovies need large amounts of zooplanktonic food during larval growth and reproduction of adults in spring and early summer, areas offering both the highest standing stock and production of copepods will be most favourable to fish recruitment. In the Bay, these areas are located near the coast, on the shelf or shelf break, where estuarine plumes, river discharges, fronts and upwellings are observed.

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