(J. D. Ros & N. Prat, eds.). 1991. *Oecologia aquatica*, 10: 203-213

PROCESSES OCCURRING DURING FISH LARVAE STAGES AS DETERMINANTS OF YEAR-CLASS STRENGTH IN FISH POPULATIONS IN THE NORTH-WESTERN MEDITERRANEAN

ANA SABATÉS & JOSEP-MARIA GILI

Institut de Ciències del Mar (CSIC). Passeig Nacional s/n. 08039 Barcelona. Spain.

Received: April 1990.

SUMMARY

The spatial and temporal mesoscale distribution pattern of fish larvae on the Catalan coast is closely linked both to mesoscale hydrodynamic mechanisms in the area, and to the distribution patterns of the remainder of zooplankton, including their predators and potential prey. Spatial coincidence with their most likely prey and the non-coincidence in time with their predators or potential competitors for the same prey are considered to be the mechanisms that most contribute to the survival of fish larvae in the area studied. The set of processes described which occur during the larval fish stages on the Catalan coast is one of the factors that may explain the fact that the number of adults captured has remained constant over recent years, despite the fact that the fishing effort has suffered few variations, that fishing power has increased (a greater number of ships with more efficient techniques), and that fishing techniques have diversified (there is now a tendency to exploit a greater number of species).

KEY WORDS: Fish larvae, spatio-temporal distribution, potential prey and predators, North-Western Mediterranean.

INTRODUCTION

Over the last few decades, fish populations along the Catalan coast have been intensely exploited by the local fishing fleets. However, recent studies in which stocks are evaluated on the basis of hauls and of size distributions have led to the hypothesis that despite the high intensity of fishing activities, stocks have reached a state of equilibrium (MARTÍN, 1989). The representativity of those studies, taking into account the fishing statistics for a given area in order to evaluate the evolution of the actual fish populations, is a factor that has been discussed at length (CADDY & GARCÍA, 1983; GARCÍA, 1984). The two main aspects argued are that the studies concentrate on those species of greatest commercial interest, and that the catches should be considered as representative only during the period of the fish life cycle, when the individuals can be caught using fishing techniques. Nevertheless, other information on fish populations, different or complementary to that offered by fisheries, is scarce or inaccurate. In the Mediterranean especially, the fishery is multispecific: a considerable number of species are exploited and fishing techniques have become diversified. This has meant that information on the evaluation of stocks is very incomplete, which is an obstacle to the attainment of a global vision, a vision which today is available only for those species of greater commercial interest.

The fishing techniques used off the Catalan coast are very diversified, ranging from traditional fishing gear to others of greater impact on fish populations such as trawling and purse seining. This has led to a situation in which the different types of fishing techniques tend to select different species and different fractions of the same population (LLEONART, 1990). Despite these limitations to evaluate adult populations, the evolution of fisheries on the Catalan coast gives us a fairly accurate idea of how the populations of the commonest fish species in the area have evolved. If the intensity of fishing activities has varied little (especially trawling, although there has been an increase in traditional methods), the level of hauls has remained constant (even among the fish first-year class; MARTÍN, 1989) and, furthermore, immature specimens represent a major proportion of the total catch. There must, then, be mechanisms or phenomena within the life cycle of the fish, and specifically in the area studied, which keep the stocks constant. Many pelagic and some demersal species have a high fecundity, which means that the number of eggs and yolk-sack larvae in the sea will initially be very high; however, if there are no mechanisms at work to maximize the survival of the larvae until they reach the juvenile stage, only with great difficulty will these stocks of adults be maintained at a constant level.

Recently, a great number of authors seem to coincide in the description of the most general mechanisms that ensure that the larvae of a given species survive in sufficient numbers to guarantee the recruitment and development of the fish first-year class. These mechanisms can be summarized into two general theories which, despite an initial discrepancy as regards the importance that different authors attach to them, must be considered together, though at different scales of space and time.

In the first place, the need to have sufficient food available is essential for the development of any planktonic organism, such as fish larvae. These, like all plankton, are distributed in a wide three-dimensional space where they develop more or less together in groups or patches. The time and place of encounter between larvae and their prey is particularly crucial during the critical period (HJORT, 1926) when larvae come to depend on external resources once they have absorbed the yolk. When this moment is reached, the availability of sufficient and adequate prey is a limiting factor in larval survival, which led CUSHING (1975) to postulate his theory of match-mismatch. More recently, and gathering the opinions of other authors, BAILEY & HOUDE (1989) have placed predation on larvae by other planktonic and nektonic organisms at the same level of importance as the availability of food when it comes to guaranteeing success in the recruitment of a given species.

In the second place, the close relationship between hydrodynamic mechanisms and the dispersion-concentration of zooplankton organisms, led ILES & SINCLAIR (1982) to postulate their theory of hydrographic retention areas. These authors link the survival of larvae to the possibility of developing, in geographically limited areas, particular hydrodynamic features that ensure the integrity of larval populations. Subsequently, and with the idea of widening the scope of this theory, SINCLAIR (1988) renamed it the member-vagrant theory, in which it is considered to be more advantageous for larvae to be grouped together in a more or less delimitated area than to be wandering in the open sea as isolated individuals.

The aim of the present study is to describe the spatial and temporal distribution patterns of fish larvae on the Catalan coast in relation to the mesoscale hydrodynamic mechanisms that originate them, as well as to their potential predators and prey. The hypothesis we put forward here is that the set of mesoscale processes occurring during planktonic stages of fishes in the area contributes towards an increase in larval survival, and may be one of the factors which have greatest influence on the fact that the adult stocks of many species remain constant, at least in their first year class.

THE SPATIAL AND TEMPORAL MESOSCALE DISTRIBUTION PATTERN OF FISH LARVAE ON THE CATALAN COAST IN RELATION TO THE HYDROGRAPHICAL PATTERN

The mesoscale spatial distribution pattern of fish larvae on the Catalan coast follows two general tendencies. Within the overall pattern, however, the species present small variations related to the spatial distribution of the adults and their spawning areas and periods. Thus, for example, the fact that the structure of the Catalan continental shelf is very heterogeneous, and therefore the distribution of the types of bottoms as well (GILI *et al.*, 1987a), gives rise to a greater number of species where the shelf is wider than where it is narrower.

The first tendency observed is a greater abundance of larvae on the edge of the continental shelf, the result of spatial coincidence between larvae of mesopelagic and shelf species (Fig. 1; SABATÉS, 1990a). This concentration has been observed to be linked to the presence of a hydrographic shelf-slope front on the edge of the shelf, associated to the so-called Catalan current (FONT, 1987). Though the situation of this front is variable, it is always present and remains between the 200 and 1000 m isobaths (WANG *et al.*, 1988; FONT *et al.*, 1988). If this front is assumed to be a continuation of that of the Ligurian Sea with a similar hydrographic structure, then, according to BOUCHER *et al.* (1987), it presents a continuous series of convergence/divergence cells.

SABATÉS (1990a) and SABATÉS & MASÓ (1990) argue that this front could act as a barrier to the dispersal of the coastal and shelf species offshore and, at the same time, would favour the transport of oceanic and mesopelagic fish larvae over the shelf. The instability of the shelf-slope front gives rise to the penetration of slope waters onto the shelf, especially in the area to the north of the Ebro Delta (FONT *et al.*, in press) and of the Blanes canyon (MASÓ, 1989), due largely to the effect on the circulation of the structure of the continental shelf. With this, high concentrations of mesopelagic fish larvae, associated with waters related to the front, can be observed near the coast in certain zones and at certain periods of the year.

The second general tendency in the spatial distribution of larvae is related to the year-round thermal regime on the Catalan coast. The temperature of the water rises from north to south along the coast. This thermal gradient between the northern and southern parts of the area is especially marked in spring and autumn. This gives rise to the fact that in some species - e.g. *Cepola macrophthalma* (L.) or anchovy, *Engraulis encrasicolus* (L.) - the spawning begins in the southern zone, when temperature increases, and progressively extends northward (SABATÉS, 1988; PALOMERA & SABATÉS, 1990). Thus, in these species, the spawning is more protracted in the southern than in the northern zone. In contrast, in the species which reproduce at the beginning of autumn, in colder waters, the spawning begins in the northern zone and later spreads southwards. These thermal variations are less accentuated in areas further away from the coast than in nearer areas, where the greatest fluctuations in salinity and temperature have been observed (MASÓ & DUARTE, 1989).

From the seasonal point of view, it was observed that the concentration of larvae increases in mid-spring, reaching maximum densities in June and July (Fig. 2), coinciding with the spawning period of most of the species, anchovy being the dominant species (SABATÉS, 1988; PALOMERA, 1989). This seasonal phenomenon is observable in the whole of the Western Mediterranean (ABOUSSOUAN, 1964; MARINARO,

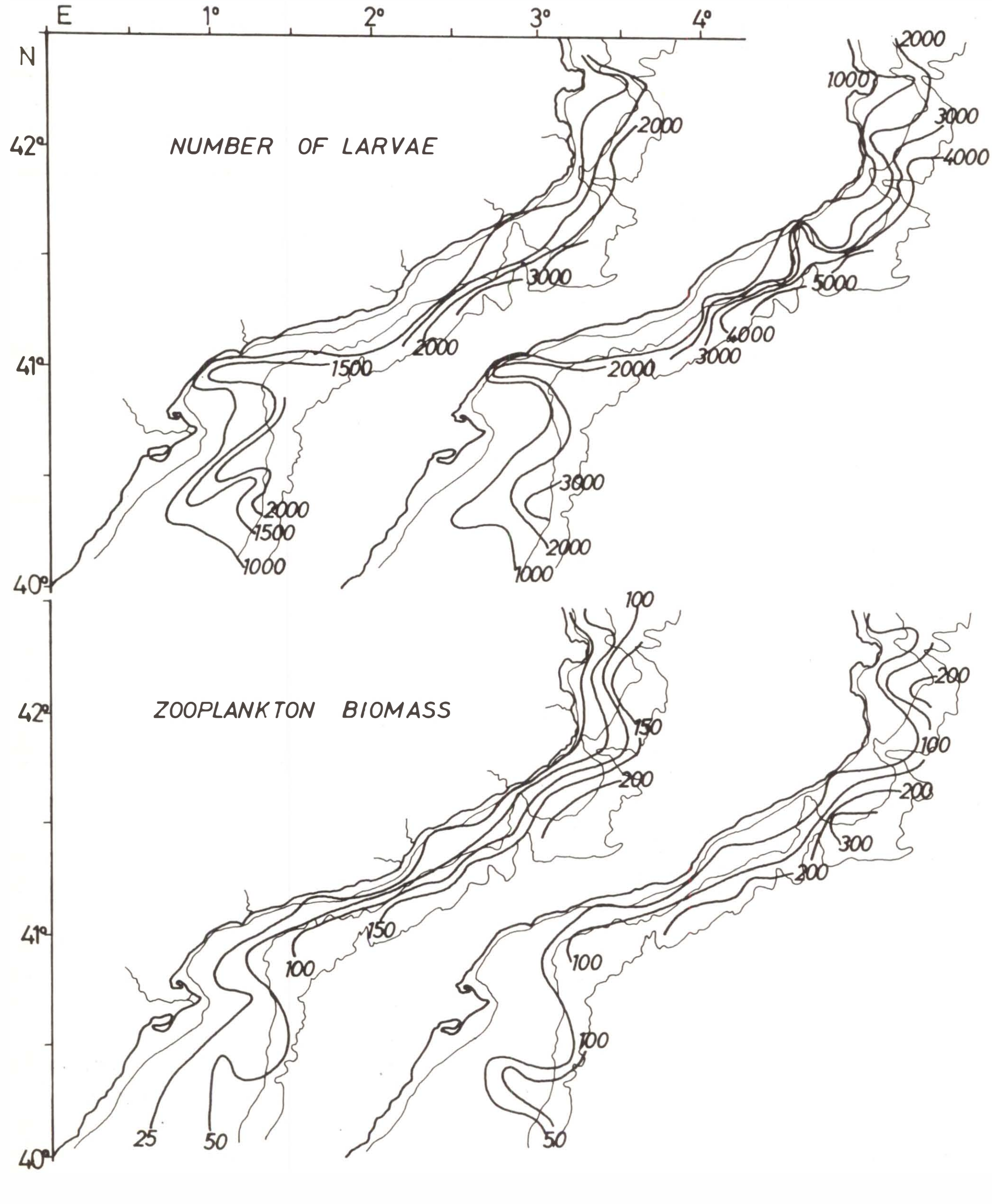

FIGURE 1. Spatial distribution of average number of larvae x 10 m^{-2} (left) and standard deviation (right), and zooplankton biomass (= displacement volume, ml 100 m^{-3}) along the Catalan coast. Data from SABATÉS (1990a) and SABATÉS *et al.* (1989).

1971), although the spawning lasts from one or few months in some species to several months in others. In the Western Mediterranean, as opposed to other geographical areas such as the North and South Atlantic, some mesopelagic fish species show a marked seasonality in their spawning (SABATÉS & OLIVAR, 1989) and, in many cases, this coincides with the aforementioned period of time.

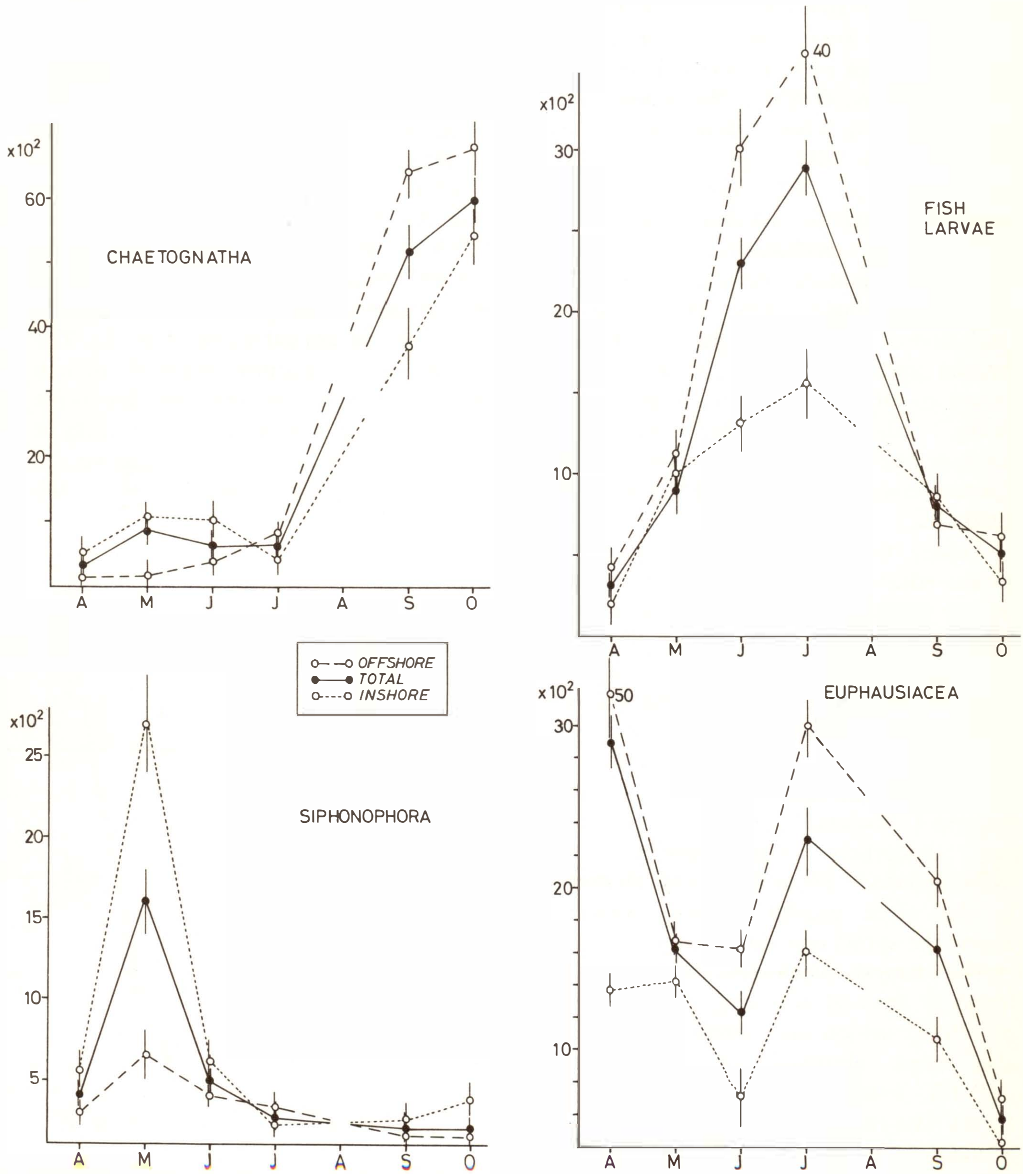

FIGURE 2. Seasonal distribution of fish larvae concentration and other zooplankton groups (especially main potential predators) along the Catalan coast. Vertical bars show standard error. Data from SABATÉS (1988).

THE SPATIAL AND TEMPORAL MESOSCALE DISTRIBUTION PATTERN OF POTENTIAL PREY AND PREDATORS OF FISH LARVAE ON THE CATALAN COAST

The general tendency observed in the distribution of fish larvae on the Catalan coast has also been observed in almost all the other groups of zooplankton in the area. Thus copepods, chaetognaths, euphausiids, amphipods and salpids show the greatest densities near the edge of the shelf (SABATÉS *et al.*, 1989). As was mentioned for the ichthyoplankton, the hydrodynamic mechanisms that describe this general pattern are the existence of waters associated with the persistent shelf-slope front and the north-south thermal gradient in the area. Overall, higher values are observed for the zooplanktonic biomass towards the edge and in the northern half of the continental shelf of the Catalan coast (Fig. 1; SABATÉS *et al.*, 1989).

Among the organisms that concentrate on the edge of the continental shelf, there are the chaetognaths, potential predators of fish larvae, and, at the same time and forming the majority, copepods, which in their nauplius and copepodite stages are the commonest potential prey for fish larvae. As opposed to the remainder of zooplankton groups in the area, other important potential fish larvae predators, the cnidarians (siphonophores and hydromedusae), are at their most numerous in the more coastal waters, especially during the spring and summer months.

The largest planktonic biomasses are found at the end of spring (SABATÉS *et al.*, 1989), which corresponds to what has also been observed in nearby areas (VIVES, 1966; RAZOULS & THIRIOT, 1968). The chaetognaths reach their peak of abundance in the late summer, while the cnidarians (and specifically the siphonophores) reach their peak in spring (Fig. 2). In the area of the Catalan coast a second peak of abundance was observed for cnidarians (siphonophores and medusae), although of lesser intensity, at the height of summer (RIERA *et al.*, 1986; GILI *et al.*, 1987b); a clear tendency was also observed to find the commonest species near the coast during this second abundance peak in the area (GILI *et al.*, 1987c).

The euphausiids are the only group whose peak of density coincides, temporally and spatially, with that of the fish larvae (Fig.2), though it is well known that they are predominantly herbivorous (RAYMONT, 1983).

On the basis of unpublished data by VIVES (1985), information has been obtained concerning the variation in the concentration of copepodites in the Catalan coast, over an annual cycle (Fig. 3). The densities of copepodites observed, though high, are lower than the real ones due to the fact that the hauls were made using nets of 200 μm mesh size, not adequate in retaining copepodites and nauplius, the

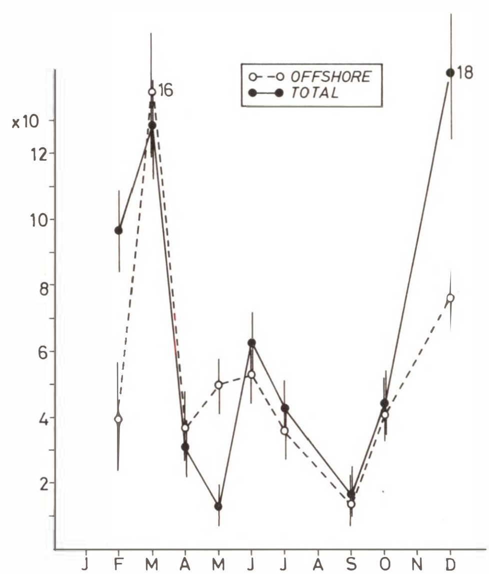

FIGURE 3. Temporal variation of copepodite concentration on the Catalan coast from unpublished data in VIVES (1985). Vertical bars show standard error.

common prey of fish larvae. Two peaks of maximum density of copepodites are observed at the beginning of spring and of autumn, besides a third peak of lower density at the end of the spring and beginning of the summer. As regards the data mentioned in VIVES (1985), if we consider only the stations furthest from the coast, the same pattern of seasonal variation may be observed and the concentrations are very similar to those of the coastal zone (Fig. 3).

THE MAINTENANCE OF FISH FIRST YEAR CLASS THANKS TO THE PROCESSES WHICH ENHANCE THE LARVAL SURVIVAL: A HYPOTHETICAL APPROACH

The mesoscale distribution patterns hitherto described for both fish larvae and zooplankton have a clear persistence. At the same time, the heterogeneity that the aforementioned hydrodynamic mechanisms are able to generate for the zooplanktonic populations can be understood only on this scale (MACKAS *et al*., 1985; HAURY & PIEPER, 1988), as consequence of a coupling between both biological and hydrodynamic processes in coastal areas (DENMAN & POWELL, 1984). Unusual hydrodynamic events that might take place on a smaller scale may affect the general patterns observed in the larval populations. In this respect SABATÉS (1990b) has observed that the effect of accidental phenomena, such as the unusually high outflow of continental waters, might affect the survival of larvae in a particular area, but after a time the mesoscale distribution pattern and concentration of individuals becomes quite similar to the initial pattern.

In the more coastal zones of the area studied, the level of environmental heterogeneity is greater than towards the edge of the shelf. Together with this hydrographic heterogeneity the phytoplanktonic biomass is much greater nearer the coast (MASÓ & DUARTE, 1989) and may generate a greater concentration of zooplankton (LEGENDRE & DEMERS, 1984). Nevertheless, it seems that such fluctuating environmental conditions do not favour the mesoscale persistence of zooplankton populations. As SABATÉS *et al.* (1989) reported for the mesozooplankton, the less fluctuating hydrographical conditions at the end of the shelf allow the development of denser and more permanent populations, thanks to their conservative-type strategy.

The first process that must occur to enhance fish larvae survival is the synchronization between the period of larval development and the maximum density of its potential resources (HJORT, 1914; CUSHING, 1972). In the area studied, if we consider the density of copepodites, which probably coincides with a high number of nauplius, when the fish larvae concentrations are highest, we can deduce that the resources are sufficient for the estimated larval population. Densities of copepodites such as those observed, especially in the stations situated on the edge of the continental shelf (Fig. 3), are more than sufficient if we consider the rates of capture and consumption of prey observed by different authors both in the laboratory (e.g. LASKER *et al*., 1970; HOUDE, 1975; FRANK & LEGGETT, 1986) and *in situ* (e.g. LASKER & ZWEIFEL, 1978; HUNTER, 1981; JENKINS, 1987). Furthermore, one of the commonest prey observed in some species of the area studied, together with the nauplius of copepods, are cladocerans (Fortuño, personal communication), organisms which are extraordinarily common in the area at the end of the spring and beginning of the summer in surface waters (VIVES, 1966).

Spatial coincidence of fish larvae and their potential prey, especially copepods, increases the probability of survival of the former. Frontal areas like those observed on the Catalan coast have been shown by several authors to be very productive (e.g. KIØRBOE & JOHANSEN, 1986), and also support important concentrations of fish eggs and larvae (e.g. NAKATA, 1989), thanks to the presence of high numbers of a potential food supply (KIØRBOE *et al.*, 1988; IWATSUKI *et al.*, 1989). Furthermore, on the Catalan coast the populations of fish larvae associated with waters of the density front are highly multispecific (SABATÉS, 1988). This could lead to a problem of denso-dependence between the different species when it comes to sharing the available resources. Furthermore, recent studies (e.g. KANE, 1984; FORTIER & HARRIS, 1989) have brought to light the fact that there are quite specific prey selection mechanisms between larvae of different species within the same population, which favours their coexistence. These trophic selection mechanisms involve both a selection of prey belonging to different species (e.g. JENKINS, 1987) and prey of different sizes of the same species (e.g. HEATH *et al.*, 1989).

While LEGGET (1986) points out that food supply is as important as predation in the survival of the larvae, BAILEY & HOUDE (1989) consider that the action of the predators is one of the most important mechanisms in the control of the recruitment of fish. Although a wide range of predators are known, some of these, such as chaetognaths and cnidarians, can at certain times produce a high death toll (e.g. BREWER *et al.*, 1984; PURCELL, 1985). Recently, some authors have considered that the relationship between fish larvae and their potential predators is established on the level of competition for the same prey rather than as direct predation upon the fish larvae (FORTIER & HARRIS, 1989; BAILEY & HOUDE, 1989). One of the mechanisms observed as being more effective in avoiding these predators or competitors is to minimize the temporal overlap of their maximum densities (e.g. BOLLENS *et al.*, 1989). A similar situation has been observed on the Catalan coast (Fig. 2). Both cnidarians (especially siphonophores) and chaetognaths show their blooms just before and after those of the larvae. Furthermore, the high concentrations of both groups of predators coincide with the blooms of copepodites in the area (Fig. 3). In this way, although the concentration of prey is lower during the period of maximum concentration of fish larvae, these can thus avoid their predators and the competition with them for the same prey. In any case, in multispecific populations in which there is always a dominant species (such as the anchovy on the Catalan coast), predation rates would be reduced since the dominant species saturate the predator field (FRANK & LEGGETT, 1983). According to these authors, this is a common situation in temperate and boreal regions. In the Catalan coast, PALOMERA & LLEONART (1989) observed that the mortality rate of anchovy larvae was highest during the period of maximal abundance of the species, although it coincided with important concentrations of their potential food.

FRANK & LEGGETT (1985), on observing the inverse correlations between fish larvae and their predators described by other authors, affirmed that they were due more to a spatial distribution of both collectives of organisms in different water masses than to direct action on the part of predators, which would drastically reduce the population of fish larvae. A similar situation may be observed on the Catalan coast, where the cnidarians, as potential predators or competitors, are distributed in the more coastal waters, even in those periods when the densities of larvae are high (GILI *et al.*, 1988).

In conclusion, observations made on the mesoscale spatial and temporal distribution pattern of fish larvae on the Catalan coast in terms of population, leads us to postulate a spatial and temporal synchronization between the populations of larvae and those of the remainder of zooplankton.

Meanwhile, the distribution of the whole range of zooplanktonic organisms depends upon the mesoscale hydrodynamic mechanisms in the area. Both phenomena together make possible a level of survival sufficient to determine the year-class strength of many species in the area, probably giving rise in turn to a level of recruitment of many species that would corroborate our initial hypothesis. The processes that occur during the larval stages of fishes on the Catalan coast may be one of the causes of the constancy of fishing stocks in the area.

REFERENCES

ABOUSSOUAN, A. 1964. Contribution à l'étude des oeufs et larves pélagiques des poissons téléostéens dans le golfe de Marseille. *Recl. Trav. Stn. mar. Endoume*, 32 (48): 87-171.

BAILEY, K.M. & HOUDE, E.D. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Adv. Mar. Biol.*, 25: 1-83.

BOLLENS, S.M., FROST, B.W. & SCHWANINGER, H.R. 1988. Seasonal abundance patterns in the ichthyoplankton and zooplankton of a temperate fjord, with a discussion of selective forces molding the timing of spawning in marine fishes. *ICES, 1988 Early Life History Symposium*, 23: 10.

BOUCHER, J., IBANEZ, F. & PRIEUR, L. 1987. Daily and seasonal variations in the spatial distribution of zooplankton populations in relation to the physical structure in the Ligurian Sea Front. *J. mar. Res.*, 45: 133-173.

BREWER, G.D., KLEPPEL, G.S. & DEMPSEY, M. 1984. Apparent predation on ichthyoplankton by zooplankton and fishes in nearshore waters of southern California. *Mar. Biol.*, 80: 17-28.

CADDY, J.F. & GARCÍA, S. 1983. Production modelling without long data series. *FAO Fish. Rep.*, 278 (Suppl.): 309-313.

CUSHING, D.H. 1972. The production cycle and numbers of marine fisheries. *Symp. Zool. Soc. London*, 29: 213-232.

CUSHING, D.H. 1975. *Marine ecology and fisheries*. Cambridge University Press. London.

DENMAN, K.L. & POWELL, T.M. 1984. Effects of physical processes on planktonic ecosystems in the coastal ocean. *Oceanogr. mar. Biol.*, 22: 125-168.

FONT, J. 1987. The path of the Levantine intermediate water to the Alborán Sea. *Deep-Sea Res.*, 10: 1745-1755.

FONT, J., SALAT, J. & TINTORÉ, J. 1988. Permanent features in the circulation of the Catalan Sea. In: *Oceanologica Acta*, Special issue, *Océanographie pelagique méditerranéenne*, (H.J. Minas & P. Nival, eds.), 9: 51-57.

FONT, J., SALAT, J. & JULIÀ, A. in press. Marine circulation along the Ebro continental margin. *Mar. Geol.*

FORTIER, L. & HARRIS, R.P. 1989. Optimal foraging and density-dependent competition in marine fish larvae. *Mar. Ecol. Progr. Ser.*, 51: 19-33.

FRANK, K.T. & LEGGETT, W.C. 1983. Multispecies larval fish associations: accident or adaptation? *Can. J. Fish. Aquat. Sci.*, 40: 754-762.

FRANK, K.T. & LEGGETT, W.C. 1985. Reciprocal oscillations in densities of larval fish and potential predators: a reflection of present or past predation? *Can. J. Fish. Aquat. Sci.*, 42: 1841-1849.

FRANK, K.T. & LEGGETT, W.C. 1986. Effect of prey abundance and size on the growth and survival of larval fish: an experimental study employing large volume enclosures. *Mar. Ecol. Progr. Ser.*, 34: 11-22.

GARCÍA, S. 1984. Un exemple d'utilisation des modèles de production composites en Meditérranée espagnole. *FAO Fish. Rep.*, 305: 97-105.

GILI, J.M., ROS, J.D. & PAGÈS, F. 1987a. Types of bottoms and benthic cnidaria from the trawling grounds (littoral and bathyal) off Catalonia (NE Spain). *Vie Milieu*, 37: 85-98.

GILI, J.M., PAGÈS, F. & VIVES, F. 1987b. Distribution and ecology of a population of planktonic cnidarians in the western Mediterranean. In: *Modern trends in the systematics, ecology, and evolution of hydroids and hydromedusas* (J. Bouillon, F. Boero, F. Cicogna & P.F.S. Cornelius, eds.): 157-170. Oxford University Press. Oxford.

GILI, J.M., PAGÈS, F. & RIERA, T. 1987c. Distribución de las especies más frecuentes de sifonóforos calicóforos en la zona norte del Mediterráneo occidental. *Inv. Pesq.*, 51: 323-338.

GILI, J.M., PAGÈS, F., SABATÉS, A. & ROS, J.D. 1988. Small-scale distribution of a cnidarian population in the Western Mediterranean. *J. Plankton Res.*, 10: 385-401.

HAURY, L.R. & PIEPER, R.E. 1988. Zooplankton: scales of biological and physical events. In: *Marine organisms as indicators* (D.F. Soule & G. S. Kleppel, eds.): 35-72. Springer. Berlin.

HEATH, M., LEAVER, M., MATTHEWS, A. & NICOLL, N. 1989. Dispersion and feeding of larval Herring (*Clupea harengus* L.) in the Moray Firth during September 1985. *Estuar. Coast. Shelf Sci.*, 28: 549-566.

HJORT, J. 1914. Fluctuations in the great fisheries of Northern Europe. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer.*, 20: 1-228.

HJORT, J. 1926. Fluctuations of the year-classes of important food fishes. *J. Cons. Int. Explor. Mer.*, 1: 1-38.

HOUDE, E.C. 1975. Effects of stocking density and food density on survival, growth and yield of laboratory-reared larvae of sea bream *Archosargus rhomboidalis* (L.) (Sparidae). *J. Fish. Biol.*, 7:

115-127.

HUNTER, J.R. 1981. Feeding ecology and predation of marine larvae. In: *Marine larvae. Morphology, ecology and relation to fisheries*. (R. Lasker, ed.): 33-77. University of Washington Press. Seattle.

ILES, T.D. & SINCLAIR, M. 1982. Atlantic herring: stock discreteness and abundance. *Science*, 215: 627-633.

IWATSUKI, Y., NAKATA, H. & HIRANO, R. 1989. The thermohaline front in relation to fish larvae. *Rapp. P.-v. Réun. Cons. int. Explor. Mer.*, 191: 119-126.

JENKINS, G.P. 1987. Comparative diets, prey selection, and predatory impact of co-occurring larvae of two flounder species. *J. Exp. Mar. Biol. Ecol.*, 110: 147-170.

KANE, J. 1984. The feeding habits of co-occurring cod and haddock larvae from Georges Bank. *Mar. Ecol. Progr. Ser.*, 16: 9-20.

KIØRBOE, T. & JOHANSEN, K. 1986. Studies of larval herring (*Clupea harengus* L.) patch in the Buchan area. IV. Zooplankton distribution and productivity in relation to hydrographic features. *Dana*, 6: 37-51.

KIØRBOE, T., MUNK, P., RICHARDSON, K., CHRISTENSEN, V. & PAULSEN, H. 1988. Plankton dynamics and larval herring growth, drift and survival in a frontal area. *Mar. Ecol. Progr. Ser.*, 44: 205-219.

LASKER, R., FEDER, H.M., THEILACKER, G.H. & MAY, R.C. 1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. *Mar. Biol.*, 5: 345-353.

LASKER, R. & ZWEIFEL, J.R. 1978. Growth and survival of first-feeding anchovy larvae (*Engraulis mordax*) in patches containing different proportions of large and small prey.In: *Spatial pattern in plankton communities*. (J.H. Steele, ed.): 329-354. Plenum. New York.

LEGENDRE, L. & DEMERS, S. 1984. Towards dynamic biological oceanography and limnology. *Can. J. Fish. Aquat. Sci.*, 41: 2-19.

LEGGETT, W.C. 1986. The dependence of fish larval survival on food and predator densities. In: *The Role of Freshwater Outflows in Coastal Marine Ecosystems*. (S. Skreslet, ed.): 117-137. Springer. Berlin.

LLEONART, J. 1990. *La pesquería de Cataluña: descripción global y planteamiento de las bases para su seguimiento*. Final Report of C.E.E. Program. General Direction XIV- B-1. Brussels (unpublished manuscript).

MACKAS, D.L., DENMAN, K.L. & ABBOT, M.R. 1985. Plankton patchiness: biology in the physical vernacular. *Bull. mar. Sci.*, 37: 652-674.

MARINARO, J.Y. 1971. Contribution à l'étude des oeufs et larves pélagiques de poissons méditérranéens. V Oeufs pélagiques de la baie d'Alger. *Pelagos*, 3 (1): 1-115.

MARTÍN, P. 1989. *Dinámica de la pesquería de arrastre en Cataluña*. Ph. D. Thesis. University of Barcelona.

MASÓ, M. 1989. *Variabilidad espacio-temporal de las características oceanográficas de la zona costera y su relación con el sistema planctónico*. Ph. D. Thesis. University of Barcelona.

MASÓ, M. & DUARTE, C. 1989. The spatial and temporal structure of hydrographic and phytoplankton biomass heterogeneity along the Catalan coast (NW Mediterranean). *J. mar. Res.*, 47: 813-827.

NAKATA, H. 1989. Transport and distribution of fish eggs and larvae in the vicinity of coastal fronts. *Rapp. P.-v. Réun. Cons. int. Explor. Mer.*, 191: 153-159.

PALOMERA, I. 1989. *Primeras fases del desarrollo de la anchoa (Engraulis encrasicolus) en la costa catalana*. Ph.D. Thesis. University of Barcelona.

PALOMERA, I. & LLEONART, J. 1989. Field mortality estimates of anchovy larvae, *Engraulis encrasicolus*, in the western Mediterranean. *J. Fish. Biol.*, 35 (Supplement A): 133-138.

PALOMERA, I. & SABATÉS, A. 1990. Co-occurrence of *Engraulis encrasicolus* and *Sardinella aurita* eggs and larvae in the Northwestern Mediterranean. *Scient. Mar.*, 54 (1): 61-67.

PURCELL, J.E. 1985. Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. *Bull. mar. Sci.*, 37: 739-755.

RAYMONT, J.E.G. 1983. *Plankton and productivity in the oceans. 2. Zooplankton*. Pergamon. Oxford.

RAZOULS, S. & THIRIOT, A. 1968. Le macrozooplancton de la région de Banyuls-sur-Mer (Golfe du Lion). *Vie Milieu*, 19: 133-184.

RIERA, T., GILI, J.M. & PAGÈS, F. 1986. Estudio cuantitativo y estacional de dos poblaciones de cnidarios planctónicos frente a las costas de Barcelona (Mediterráneo occidental): ciclos entre 1966-67 y 1982-83. *Misc. Zool.*, 10:23-32.

SABATÉS, A. 1988. *Sistemática y distribución espacio-temporal del ictioplancton en la costa Catalana*. Ph.D. Thesis. University of Barcelona.

SABATÉS, A. 1990a. Distribution pattern of larval fish populations in the Northwestern Mediterranean. *Mar. Ecol. Prog. Ser.*, 59: 75-82.

SABATÉS, A. 1990b. Changes in the heterogeneity of mesoscale distribution patterns of larval fish associated with a shallow coastal haline front. *Estuar. Coast. Shelf Sci.*, 30: 131-140.

SABATÉS, A., GILI, J.M. & PAGÈS, F. 1989. Relationship between zooplankton distribution, geographic characteristicsand hydrographic patterns off the Catalan coast (Western Mediterranean). *Mar. Biol.*, 103: 153-159.

SABATÉS, A. & MASÓ, M. 1990. Effect of a shelf-slope front on the spatial distribution of mesopelagic fish larvae in the Western Mediterranean. *Deep-Sea Res.*, 37: 1085-1098

SABATÉS, A. & OLIVAR, M.P. 1989. Comparative spawning strategies of mesopelagic fishes in two marine systems with different productivity. *Rapp. P.-v. Réun. Cons. int. Explor. Mer.*, 191: 27-33.

SINCLAIR, M. 1988. *Marine populations: an essay on population regulation and speciation in the oceans*. Sea Grant/University of Washington, Seattle (unpublished manuscript).

VIVES, F. 1966. Zooplancton nerítico de las aguas de Castellón (Mediterráneao occidental). *Inv. Pesq.*, 30: 49-166.

VIVES, F. 1985. *El ecosistema pelágico y bentónico de la costa NE española (Cataluña) en relación*

con la hidrografía local. Final Report C.A.I.C.Y.T. Madrid (unpublished manuscript).
WANG, D. P., VIEIRA, M., SALAT, J., TINTORÉ, J. & LA VIOLETTE,P.E. 1988. A shelf-slope front filament off Northeast Spanish coast. *J. mar. Res.*, 46: 321-332.