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Analysis of the early life history stages of mackerel. 1989 North East Atlantic

by

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Abstract

In this paper we describe the distributions of 5 different early stages of mackerel, from newly spawned eggs to larvae between 6 mm and 12 mm (the maturation takes about 5 weeks). Samples were obtained from the 1989 ICES mackerel and horse mackerel triennal egg survey. We have been using individual based statistics and geostatistics (Bez et al, 1996), using in particular centers of gravity and inertia of the different variables (location, density of eggs and larvae, sea surface temperature, bathymetry). The main results are as follows:

- A mean long term (1 month) transport of the eggs is estimated towards the North West at about 10 cm/s.
- The global productions estimated for each stage during the whole spawning season indicate a total mortality (natural + predation) of 99.75 % : 10 000 eggs give, on average, 25 larvae between 6 mm and 12 mm.
- At a given time in the spawning season, the mean sea surface temperature per individual is the same whatever the stage. It is about $12°C$ at the end of April and $13.8°C$ in mid June. Nevertheless, larvae temperatures are less dispersed around this mean than eggs (stageI) temperatures.
- At short distance, the spatial structures (covariograms) of the different stages of development get a sharp drop. This discontinuity increases from the stage I eggs to the stage I larvae. The drop indicates highly irregular distributions of the early life stages of mackerel with an increasing level of aggregation despite the enormous mortality and despite a probable transport of 10 cm/s. At larger distance, the spatial structures are also similar, except along the shelf edge where it extends to 350 n.m. for larvae stage I and up to 500 n.m. for eggs stage I.

Keywords: eggs and larvae, mackerel, individual based statistics, covariogram

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1 Introduction

As a by-product of the triennal surveys co-ordinated by the International Council for the Exploration of the Sea (ICES) for the mackerel and horse mackerel egg production assessments, we get, for 1989, densities of different stages of development from newly spawned eggs to old larvae, just before they become juveniles. Then it is of great interest to compare the distributions, the abundances and the survival rates of some early life history stages in order to describe and also to quantify the impact of some hydrographycal parameters like the temperature and the bathymetry.

We have here the opportunity to study some fundamental elements of the pre-recrutment of the mackerel. As a matter of fact the distributions and the abundance of eggs and fish larvae are often analysed separately in relation to variations in the associated biotic and abiotic environment (Horstman and Fives, 1994; O'Brien and Fives, 1995; Bez *et al.*, 1995). The comparison of the different early life stages should strengthen the biological interpretations.

The analysis are done by using simple descriptors based on the use of individual based statistics and individual based geostatistics (Bez *et al.*, CM 1996/S:23).

2 Material and method

2.1 Material

The present data set corresponds to the ICES triennal "mackerel and horse mackerel egg production" surveys that took place in 1989 in the North East Atlantic (Bay of Biscay, Celtic Sea and Irish Sea). Surveys are designed to assess the mackerel egg production. They are then not completely oriented towards the analysis of larvae distributions and also not focussed on the analysis of the link between early development stages and some environmental parameters. In that respect, this analysis (larvae and environmental impact) has to be considered as by-products of the egg surveys.

The sampling, which tries to cover in space and time the whole spawning season, is divided into 5 sampling periods (date, participants, latitudinal extension of the sampling and number of samples collected during each period are presented in Table 1). As recommended the sampling is based on a regular grid (0.5° of longitude by 0.5° of latitude). But some additional samples taken in the a priori rich areas of egg productions, some difficulties at sea and some other reasons induce irregularities in the final sampling (several samples per square and duplicates coming from the geographical overlap of 2 cruises that take place at different moments). During the first period, samples are located on the shelf edge only with no respect to the scheduled regular sampling grid. This is mainly why this period has been removed from the analysis. The remaining periods are re-numbered from 1 to 4.

period	time period	mean date (julian day)	countries*	area coverage (latitude)	number of samples
1	23/4 - 14/5	124	2 + 3	44°30'N - 56°00'N	136
2	21/5 - 6/6	151	4 + 6 + 5	44°30'N - 56°00'N	306
3	7/6 - 24/6	166	6 + 2 + 7 + 3	44°30'N - 56°00'N	292
4	4/7 - 19/7	191	7	45°00'N - 53°00'N	85

Table 1: Description of the sampling periods. (*) country codes : 1 = Germany - 2 = Scotland - 3 = Spain - 4 = England - 5 = Ireland - 6 = France - 7 = Netherlands

All samplers were fitted with flowmeters to determine the volume of water filtered (which often exceeds 300 tonnes). Samples corresponds to oblique hauls at 5 knots from the surface to a certain depth and then back to the surface (Lockwood *et al.*, 1981); maximum sampling depth is to the bottom or to 200m depth or to 20 m below the thermocline when it is greater than

2.5°C in 10 m depth. Each sample is fixed with a 4% solution of formaldehyde and analysed on shore.

All larvae and when possible (i.e. for small quantities) all the eggs are identified, counted, and staged. A sub-sampling might be done to estimate the abundance of eggs. Knowing the volume of water filtered and the depth reached by the trawler, abundances are turned into densities expressed in number of individual per meter square (ind/m^2). Mackerel eggs are classified into 5 morphological stages (Lockwood *et al.*, 1981). Comparison of egg staging has been experienced under the co-ordination of ICES on 10 samples of 50 mackerel eggs each read by 5 countries. It has been shown (Anon., 1993) that the variation between the counts by different countries was less for the first and the last stage than for the intermediate ones. In this study, we will then only consider the stages I and V eggs respectively noted E1 and E5 (Tabl. 2). The larvae are grouped into 3 length groups named L1, L2 and L3 (Tabl. 2). Data on larvae are only available between latitude 48°00'N and 55°00'N.

stage	level	code	designation	duration at 12°C	time from fertilization
eggs	I	E1	from fertilization to blastodisc as a 'signet ring'	1 day+20 hours	44 hours
eggs	II to IV	—	————————	80 hours	124 hours
eggs	V	E5	growth of the embryo until the tail is past the head	18 hours	6 days
larvae	I	L1	from 2.5 mm to 3.9 mm	5 days	11 days
larvae	II	L2	from 4 mm to 6 mm	10 days	3 weeks
larvae	III	L3	from 6 mm to 13 mm	15 days	5 weeks

Table 2: Designation and duration of the stages of eggs and larvae.

As the duration of the development stages are different, the comparison between stages has to deal with rates of productions rather than densities. Knowing the stage durations, density values are converted into daily production expressed in number of individual per meter square and per day (ind/m^2/day). Durations of the egg stages are given by a function of the sea surface temperature (Lockwood *et al.*, 1981). Durations of the larvae stages are said to be also sea surface temperature dependent, but this dependency has not been quantified. We took constant durations independent of the temperature, according to the bibliography (Tabl. 2).

Sea surface temperature (SST) are measured at the beginning of each tow. Bathymetry comes from physical oceanographic surveys.

2.2 Method

First of all, for each period, sample values are averaged over 0.5° of latitude by 0.5° of longitude rectangles centered on each node of the intended regular sampling grid.

Then analyses call upon individual based statistics (Bez *et al.*, 1996). For each of the 5 development stages we estimate the center of gravity and the inertia of the available characteristics per individual : the location, the density, the sea surface temperature and the bathymetry. They correspond to the mean and variance of the characteristics of an individual taken at random in the whole population. In case of regular sampling, they are estimated directly by a discrete sum of sample values, discretizing the exact formulae expressed with integrals. In the same manner, total abundances of each stage are estimated by the sum of sample values times the surface of the grid mesh which is known to be an unbiased estimator of the real abundance.

We summarise the 20 experimental distributions (5 stages during 4 periods) with 5 figures representing the centers of gravity of the location of each stage together with their inertia splitted into two principal axes given by a weighted principal component analysis of the coordinates. Prior to computations, the longitudes are converted into distances from the 200 meters depth isobathe. A reverse transformation is done for plotting the centers of gravity. We also represent the mean locations of the samples of each period to support the interpretations.

To estimate the production of each stage over the whole spawning season, we integrate the experimental curves of the daily production against the mean cruise date (expressed in julian day). The start date for spawning was assumed to be 21 March and the end of spawning was taken as the last day on which stage I eggs were found, that is 19 July (Anon., 1990). Productions curves are plotted in raw scale and in decimal logarithm scales.

Shifts are estimated by the distance, expressed in nautical miles (n.m.), between the centers of gravity of the various stages. According to the durations of the eggs and larval developments (Tabl. 1) and to the duration of the sampling periods (Tabl. 2), the center of gravity of L3 of a given period is associated to the one of E1 of the previous period in order to estimate long term shifts (around 5 weeks). A transport velocity is estimated by dividing this distance by the time lag between the mean date of each sampling period.

For the geostatistical part of the analysis, we looked at the spatial structure of each stage within each sampling period by computing covariograms (Matheron, 1971; Bez *et al.*, 1996). Relatively to the square abundance, the covariogram is a function of the distance which gives, for a given distance h, the probability for two individuals taken independently at random to be effectively h apart (covariograms are given in inversed square nautical miles). Their behavior near the origin (discontinuity or slope) quantifies the more or less spatial continuity of the density under study. As covariograms are about the same whatever the period, we computed a mean seasonnal spatial structure by averaging the covariograms of the 4 periods.

Taken as an experimental tool, the covariogram gives the opportunity to summarise and to describe spatial structures. When modelised with an appropriate function, it can be used to do mapping (external kriging) and to compute estimation variance for global estimation.

3 Results

3.1 Mean location of stages and transports

For each development stage, the mean location of an individual shifts to the NortWest during the spawning season (Fig. 1). For instance, the center of gravity of the spawning (i.e. stage I eggs) derives to the North West of about 150 n.m. from period 1 to period 2 (Fig. 1(a)). It moves back to the South East from period 3 to period 4. There is no equivalent shift in the mean location of samples per period (Fig. 1(f)). The dispersion (inertia) of the location of individuals decreases from stage I eggs to stage III larvae. The direction which explains most of the dispersion of individuals is always more or less parallel to the shelf edge.

From period 1 to 2 and from period 2 to 3, shifts between the centers of gravity of stages I eggs and a stage III larvae are directed to the North along the shelf edge (Fig. 2). The corresponding transports get a velocity equal to 10 cm/s or 11 cm/s. It is also noticable that eggs released during the second period are located on average at the same location than the stage III larvae.

3.2 Production curves, total mortality and mean densities

The peak of production occurs at the end of May (julian day = 150) where about 2.4 10^{13} eggs are released each day (Fig. 3(a)). In the meantime there are about 8 10^{10} stage III larvae produced per day. The total quantities of stage I egg and stage III larvae are respectively 1.4 10^{15} eggs and 3.6 10^{12} larvae which leads to a total mortality of 99.75%. This means that, on average over the spawning season, 10 000 fertilized eggs gives 25 pre-juvenile mackerels. Moreover the mortality rate increases with the level of development:

- the abundance of E5 represents 50% of the abundance of E1
- the abundance of L1 represents 22% of the abundance of E5
- the abundance of L2 represents 22% of the abundance of L1

- the abundance of L3 represents 9% of the abundance of L2

With decimal logarithm scale (Fig. 3(b)), the daily productions of every stage, except stage I eggs, appear to have the same seasonal evolution eventhough the order of magnitude of the abundance is 5 times lower from one stage to the next one. In mid June the daily production of larvae ended more rapidly than the production of eggs.

Mean density per period and per stage is bell shaped. By the end of May there are on average : 300 stage I eggs/m^2/day and 1 stage III larvae/m^2/day. The mean density of stage V egg is smaller than the one of stage I egg before the peak of spawning and approximatively the same after.

3.3 Sea surface temperature and bathymetry

Mean sea surface temperature per individual is the same whatever the development stage (Fig. 4(a)). It increases slowly from $12°C$ at the end of April to $13.8°C$ in mid June. In mid July it is equal to $17°C$. Nevertheless, stage I egg temperatures are the more dispersed compared to the other stages, especially during the first two periods where the inertia of a stage I egg SST is twice the inertia of a stage V egg (Fig 4(b)).

The bathymetry of a stage I egg decreases on average through the spawning season from 1200 m depth to 175 m depth (Fig. 4(c)). The associated inertia decreases. In period 1 the others stages get the same centers of gravity and the same inertia. But during the season, the mean bathymetry per individual and its inertia are smaller for older and older stages.

3.4 Covariograms

At short distances, relative covariograms get large drops (nugget effects) near the origin whatever the stage (Fig. 5). This means that the spatial structure of any of the early stages is deeply irregular. A careful observation of the covariograms shows that the dropss are different. This is mainly due to the value of the covariograms at null distance which indicates the probability for 2 individuals to be at the same location. So this can measure the level of aggregation. The one of E5 is about twice the one of E1. And the one of L1 is also about twice the one of E5. This means that, relatively to the total abundance, the stage I larvae are more aggregated than the stage V eggs, also more aggregated than the newly spawn eggs.

At larger distances we can see that the mean probability distance are the same in 3 directions (North, North-East and East) where covariogram is zero for distances larger than 200 or 250 n.m. In fact the difference between the 5 stages is mainly due to the spatial structure in the North-West direction. The range (i.e. maximum distance for positive covariogram) decreases from 500 n.m. to 400 n.m. for the stage I egg and the stage I larvae.

4 Elements of discussion

Transport

Due to difference in the sampling, the estimations of transport (10 cm/s) have to be used cautiously. As a matter of fact, the center of gravity of the eggs is pulled to the South because of large densities observed in the Bay of Biscay. In the mean time, we do not have larvae data south to 48°00'N (Fig. 2). So the difference between the centers of gravity might come from the fact that they are computed on different populations.

Conditioning?

We have seen that the different development stages get the same mean sea surface temperature but a different inertia of temperature per individual. In particular the inertia decreases from the egg stages to the larvae stages. This can be partly explained by the reduction of the spatial extension of the different stages as observed on the covariograms (decrease of range). Assuming that the temperature is regular (smooth) in space, the elimination of the borders should reduce the dispersion of temperature where individual are present and though the inertia.

This might also be due to the fact that the survival eggs and larvae are more and more concentrated in areas with favorable temperatures (passively or actively). We know from the covariograms that the individual tends to be more and more agregated as they grow from the stage I egg to the stage I larvae. So we do not know simply by interpreting the mean and variance of temperature per individual, if temperature is conditioning the distribution of the eggs and larvae.

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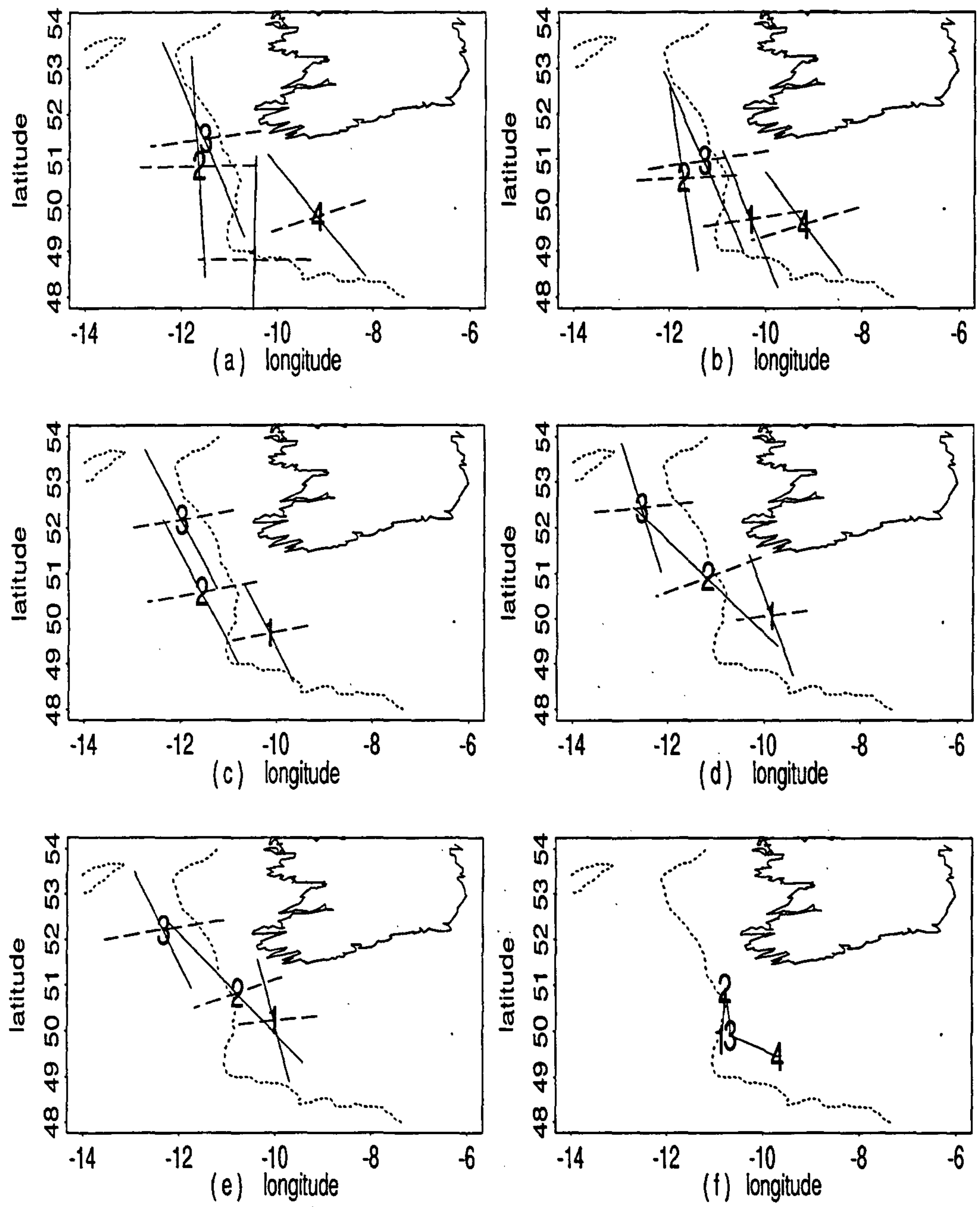

Figure 1: Centers of gravity and inertia of location of (a) stage I eggs, (b) stage V eggs, (c) stage I larvae, (d) stage II larvae, (e) stage III larvae, (f) eggs samples per period and per stage. Digits, giving the number of the periods, are located at centers of gravity. The first principal axis of inertia is the continuous line. The second axis is represented in dashed line. The dotted line represents the 200 m depth.

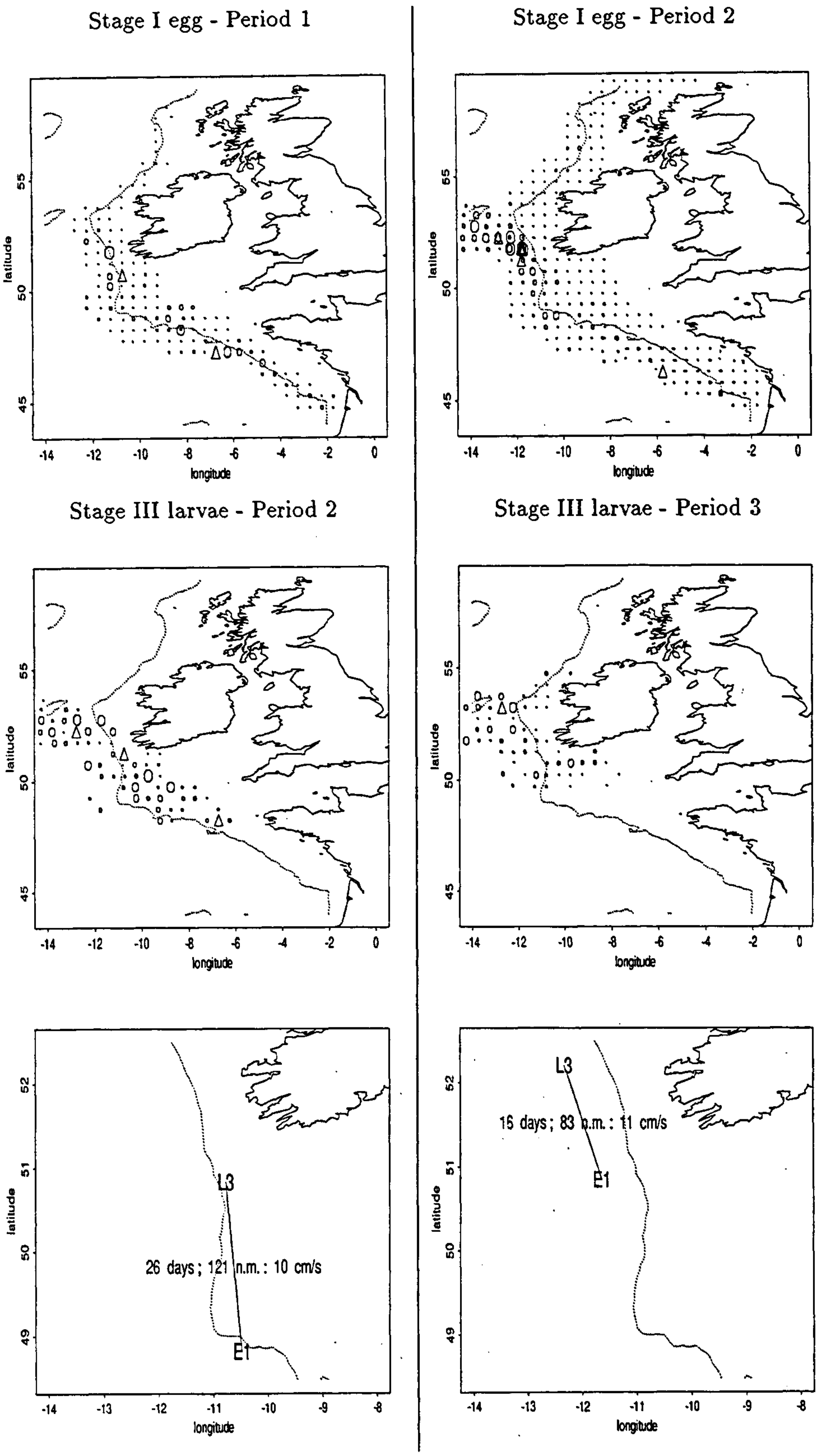

Figure 2: Shifts in the mean location of a stage I egg and a stage III larvae for consecutive periods. Proportional representations with circles of the daily productions. Data higher than 500 eggs/m^2/day and 2 larvae/m^2/day are represented by a triangle. Estimation of transport.

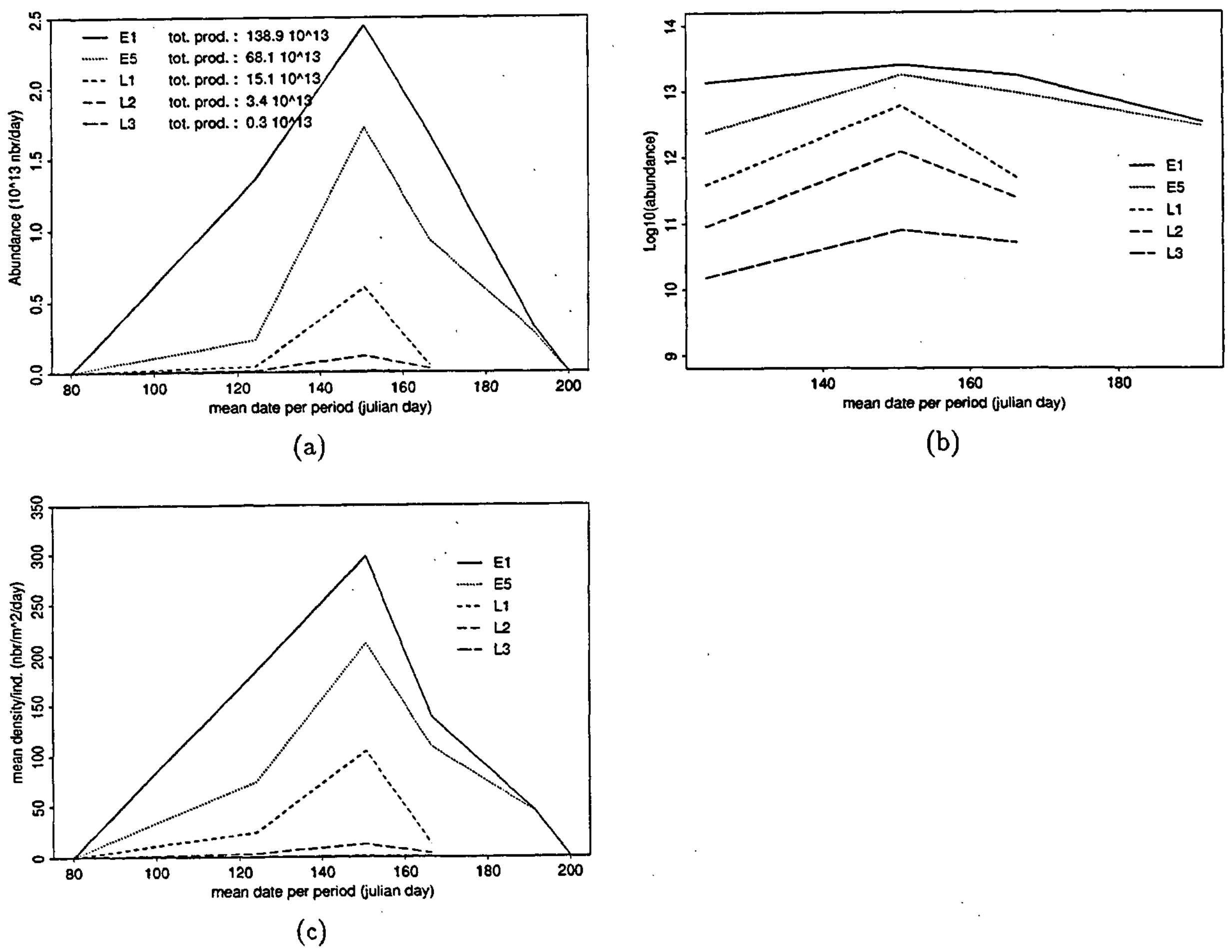

Figure 3: Daily production (a,b) and mean density per individual (c) versus the mean date of sampling period.

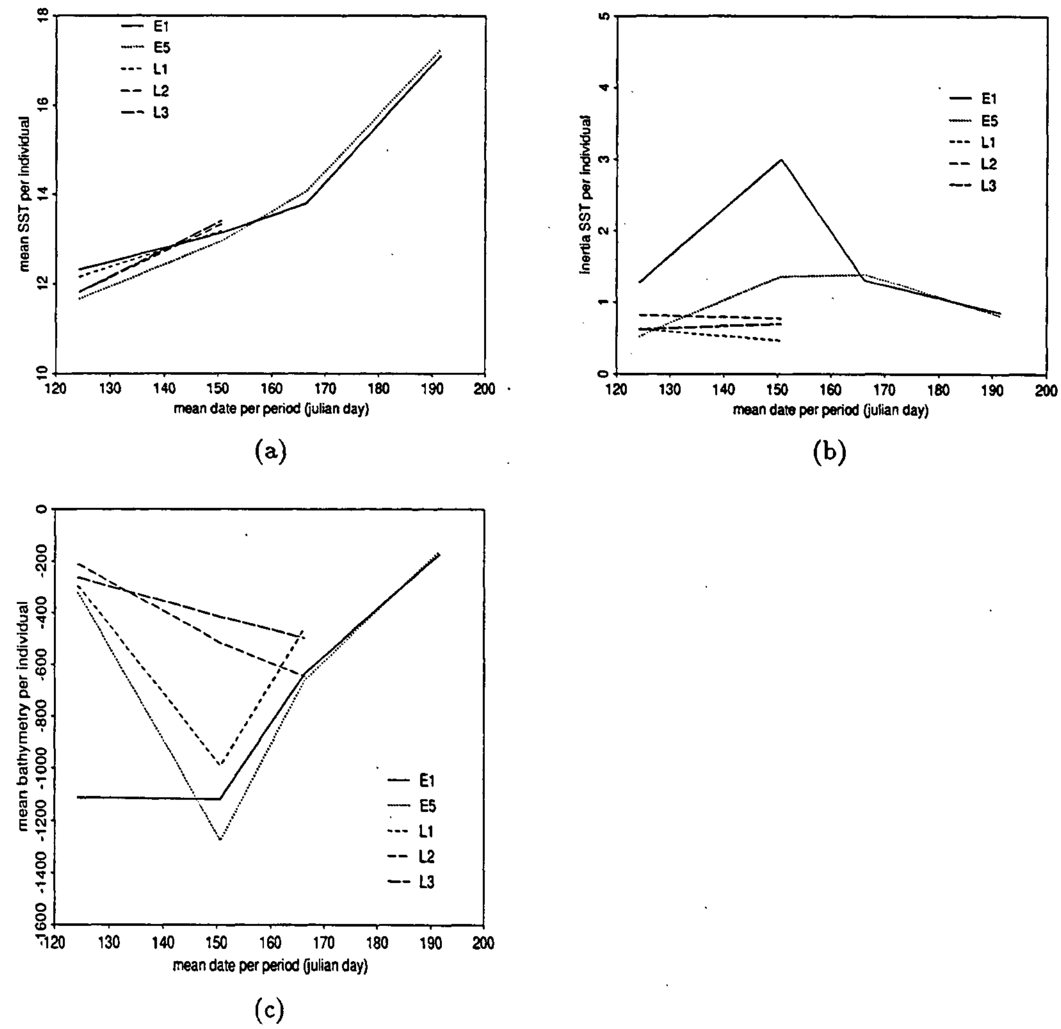

Figure 4: For each stage, center of gravity of the SST (a) and the bathymetry (c) per individual. Inertia of the sea surface temperature per individual (b).

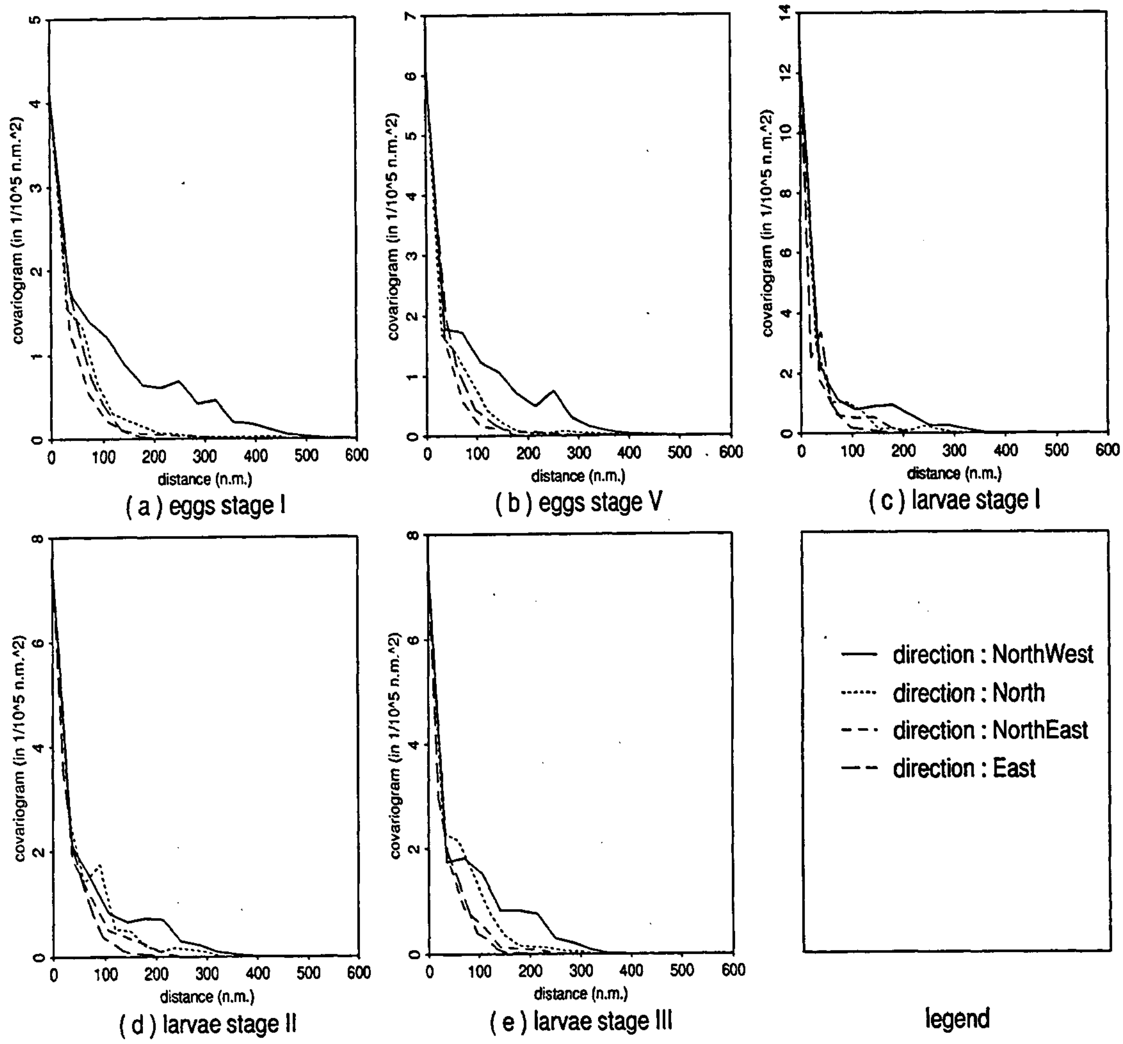

Figure 5: Mean annual spatial structure per development stage. Experimental covariogram in 4 directions : North-West, North, Nort-East and East.