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THE STABILITY OF THE SPATIAL DISTRIBUTION OF THE PELAGIC STAGES OF SOLE AS EXPLAINED BY THE TRAJECTORIES OF "ARGOS" SATELLITE TRACKED BUOYS

by

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Résumé

Les études sur les stades pélagiques de la Sole (*Solea vulgaris*, Quensel dans la partie nord du Golfe de Gascogne montrent de faibles différences dans la répartition spatiale durant le développement embryonnaire et larvaire. La circulation des masses d'eau dans le secteur de la frayère a été étudiée à l'aide de balises "Argos", suivies par satellite. Les résultats obtenus en 1986 ont été validés par les opérations réalisées en 1987. Les différences de trajectoire observées entre les drogues de 7 et de 34 m sont expliquées par la stratification de la colonne d'eau. Après 40 jours de conditions météorologiques variables, la balise ancrée à 34 m était à 10 milles du point de départ. Ces résultats suggèrent que la stabilité spatiale des stades pélagiques peut être expliquée par un comportement passif des oeufs et des jeunes larves et l'apparition de préférences concernant la distribution verticale avec l'âge.

Summary

The studies on the early life stages of Sole (*Solea vulgaris*, Quensel) in the northern part of the Bay of Biscay show that there are little changes in the spatial distribution during the embryonic and larval development. Studies on the water masses circulation in the spawning area have been realized with the deployment of "Argos" satellite tracked drifters. The results obtained in 1986 were validated by the operations realized in 1987. The differences observed between the trajectories of the drifters anchored at 7 and 34 m are explained by the stratification of the water column. After 40 days of variable environmental conditions, the 34 m drifter was at 10 miles from the starting point. These results suggest that the spatial stability of the pelagic stages could be explained by a passive behaviour of eggs and early larvae and the appearance of preferences concerning the vertical distribution with increasing age.

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INTRODUCTION

It is generally admitted that recruitment may be related to the survival of the early life stages (one could say at least that this hypothesis is not clearly rejected). Meteorologic and oceanographic factors modify the biotic and abiotic environment during the embryonic and larval development. In some cases a good correlation between environmental conditions and year-class strength is detected, but the robustness of these models remains low and causality is not clearly demonstrated.

In early 70's, many scientists suggest the preponderance of biotic factors (food availability, predation) for the survival of fish eggs and larvae. The match-mismatch theory (Cushing, 1975) is an elegant development of these concepts. In spite of several recent fields tests of the match-mismatch theory that undermine its validity (Methot, 1983) these concepts are still valid.

More recently the regulation of fish populations was related to the spatial constraints in the distribution of the early life stages. The importance of physical processes is now well argued (Sinclair, in press and other references herein). Many studies are devoted to establish the relationship between the year class strength and the variations of physical forcings, that is deviations of oceanographic features from their mean level could explain an important part of recruitment variations.

This paper presents the development of the studies concerning the oceanic circulation and their linkage with the evolution of the early life stages of the Sole in the Bay of Biscay.

The comparison of the satellite tracked drifters trajectories and the evolution of the pattern of the eggs and larvae distribution suggests a passive behaviour of eggs and early larvae and the appearance of preferences concerning the vertical distribution with increasing age.

The strength of these conclusions will permit to focus the future studies at levels of the early life cycle that show important variations. Therefore the deviations of the recruitment from its normal level will be related to a restrained number of logically significant parameters.

In that perspective, the strategy deployed in spring 1987 with the participation of a Canadian team (Institut Maurice Lamontagne and University Laval, Québec), physical oceanographers (University of Brest) and Biologists (IFREMER, CNRS) is briefly described.

The exposed experiences are a part of the French program on the recruitment studies (Programme National sur le Déterminisme du Recrutement). The main objectives and the strategy of the studies realized in spring 1987 was influenced by the present results. Thus, they are rapidly exposed and must be considered like a step in the overall evolution.

THE STUDY (Methods and data)

The results of the 1985 surveys in the most important spawning ground of the Bay of Biscay were used to define the spatial and temporal windows for the study of the evolution of the pelagic stages of the Sole (*Solea vulgaris*, Quensel).

Five surveys have been realized during the 1986 studies and three in 1987 in the sector presented in figure 1. During the first 1986 survey, three "Argos" satellite tracked buoys "moored" at different depths (7, 22 and 34 m) have been released in the middle of the eggs patch. The evolution of the drifters position will be compared with the modification of the eggs and larvae pattern distribution.

Before this comparison, we will evaluate in which measure the results of one drifter may be considered as relevant of the water masses circulation. For this, we will examine the trajectories obtained in the same sector in 1987 when 9 drifters have been released during the first cruise at different depths (3 at 6.5 m, 3 at 26.5 m and 1 at 39, 49 and 59 m). All the positions will be defined as onshore and alongshore distance (km) from a given point presented in figure 1.

The evolution of the spatial distribution of the pelagic stages with age is represented by the distribution of the first eggs stage during the first survey and the resultant distribution of the corresponding stages at the time of subsequent cruises. For the definition of this "cohort" the Riley's relation (1974) between temperature and duration of the development was used.

For each survey, the mean temperature and its standard deviation (measurements realized in the entire sector at different depths) have been considered, because there was, at the time of the study, no precise idea of the fine scale vertical distribution of the pelagic stages.

Finally to summarize the pattern distribution of the pelagic stages we have calculated for five selected stages and for each cruise the center of gravity of the spatial distribution and its variance on the onshore and alongshore axes. Details on these calculations are presented in legend of the table 1.

RESULTS

Trajectories of the drifters related to the stratification of the water column

The displacement of two drifters (7 m and 34 m) during the 1986 surveys is presented in the figure 2. There is a great difference between the circulation at these two levels. The evolution of the alongshore and onshore displacement with time is presented in figure 3. The drifter moored in the surface layer leaves after 8 days the sector of the survey. Its trajectory is related to the wind. The 34 m drifter stays close to its departure point for about 40 days.

The results of the 1987 "Argos" experience show that for a given depth the displacement of the buoys was very similar (fig. 4). Therefore, we can consider that the trajectory of one drifter is a quite good indication of the water masses displacement. It is clear (and well known) that the response of the water masses to particular wind forcings depends on depth. But the circulation at a given depth depends also on the vertical stratification of the water column (fig. 5). The differences in the "activity" (see legend) of the drifters at different depths are explained by the pronounced stratification observed during the 1986 surveys. There are no differences for the drifters anchored at depths varying from 6.5 to 59 meters in the homogeneous water column observed during the 1987 surveys.

Evolution of the spatial distribution of the early life stages

The evolution of the pattern distribution of a "cohort" from survey to survey shows an important spatial stability (fig. 6). The pelagic stages stay in the spawning area during the 36 days of the successive surveys. The calculated center of gravity of the distributions of different stages for the five surveys confirm these results (table 1).

These elements suggest that a particular vertical distribution of eggs and larvae with a preference for a water masse showing a low residual circulation (as the 34 m drifter suggests) could explain the stability of the spatial distribution of the pelagic stages of Sole.

These observations suggest that the transport from the spawning area to the estuarine nursery grounds must be realized during the old post-larval stages. This displacement should be controlled by an active behaviour, because no elements indicate an important onshore oriented residual circulation.

SOME IMPORTANT POINTS

- Can we consider the fish eggs and larvae as passive contaminants or is their distribution controlled by an active behaviour ? This is the most important question for the study of the effects of the oceanic and coastal circulation on recruitment and year-class strength.

  The active behaviour concerns principally modifications in the vertical distribution. Ontogenic components control this vertical distribution. But in order to understand the relation between Lagrangian circulation (that is the most suitable for biological studies) and the evolution of the spatial distribution of larval fish, we have to study the reaction of the organisms to particular hydrographic features.

- If the pattern distribution of the early life stages is really related to the year-class strength, it is important to identify the environmental processes and parameters that modify the water masses circulation. In this way, we could pass from empirical to causal relationships and from a practical point of view, we will decrease the number of parameters (decrease the effort) explaining a big part of the recruitment variance.

  The robustness of the conclusions of the process-oriented studies is obviously the most important point. The year to year verification of the proposed hypothesis is the normal, but slow and expensive way to evaluate the robustness. An interesting alternative concerning the studies of linkage between physical process, fine scale (horizontal and vertical) distribution and the overall spatial distribution of the pelagic stages is the interspecific comparison. For species with similar morphology and comparable spawning grounds differences in vertical distribution and behaviour must be traduced by spatial discriminations.

THE FUTURE FIELDS EXPERIMENTS

An operation named CIRESOL (Circulation et Recrutement de la Sole) was realized this year. This project was developed with V. MARIETTE and B. LE CANN from the Laboratory of Physical Oceanography of the University of Brest, L. FORTIER from the Department of Biology (University Laval, Québec) and J. GAGNE from the Institute Maurice Lamontagne, Québec.

Only the results of the satellite tracked drifters were used in the present paper to validate the results of a similar experience realized in 1986. Intensive sampling techniques were deployed. The results are not yet available. The main objectives and the strategy of this operation will be presented.

The objectives of the studies realized in spring 1987 are mentioned above. For the study of the influence of local forcings (wind and density-driven) on the residual circulation long duration measurements of currents and pressure in the area of the principal spawning ground have been realized with 7 moorings. These measures are necessary for the development of numerical models. More precisely they serve to test the following hypothesis :

the spatial scale of the variations on the alongshore axis is about an order of magnitude higher than on the onshore direction (most rapid variation of the phenomena on the onshore direction).

The points are of crucial importance to elucidate the transport mechanism of the post-larvae form the spawning ground to the estuarine nursery areas.

In parallel, the fine and large scale distribution of the early life stages of Sole was studied. Three surveys on the sector have been realized. For the study of the fine scale horizontal distribution of the pelagic stages of Sole, a continue sampling with a 1 m^2 sampler in a transect across (onshore direction) the spawning ground was realized. We hope in this way define the scale at which local phenomena become important. All these elements will be used to evaluate the relative importance of the advective and diffusive processes occurring in this area.

For the fine scale vertical distribution two approaches were adopted :

- a time series (72 hours, 2 h lag) at a point near a mooring ;

- three transects across the spawning area with profiles realized every 5 miles.

For these operations, the vertical resolution of the samples was 5-10 m and T° S‰ measurements have realized simultaneously (a BIONESS 1 m^2 and a V-FIN were used).

The first operation will give informations on the periodic variations (diel, tidal) variations of the vertical distribution. Variations due to the Eulerian flow at this point will be related to results of the close situated arrays of current meters.

The second operation has been realized for the study of the influence of hydrographic and topographic features on the fine scale vertical distribution of the early life stages.

These informations will be used as an indication of the larval response to particular environmental situations.

For these fine scale studies, the distribution of the larvae of all the fish species will be identified, thus interspecific comparisons will permit to evaluate the robustness of the conclusions.

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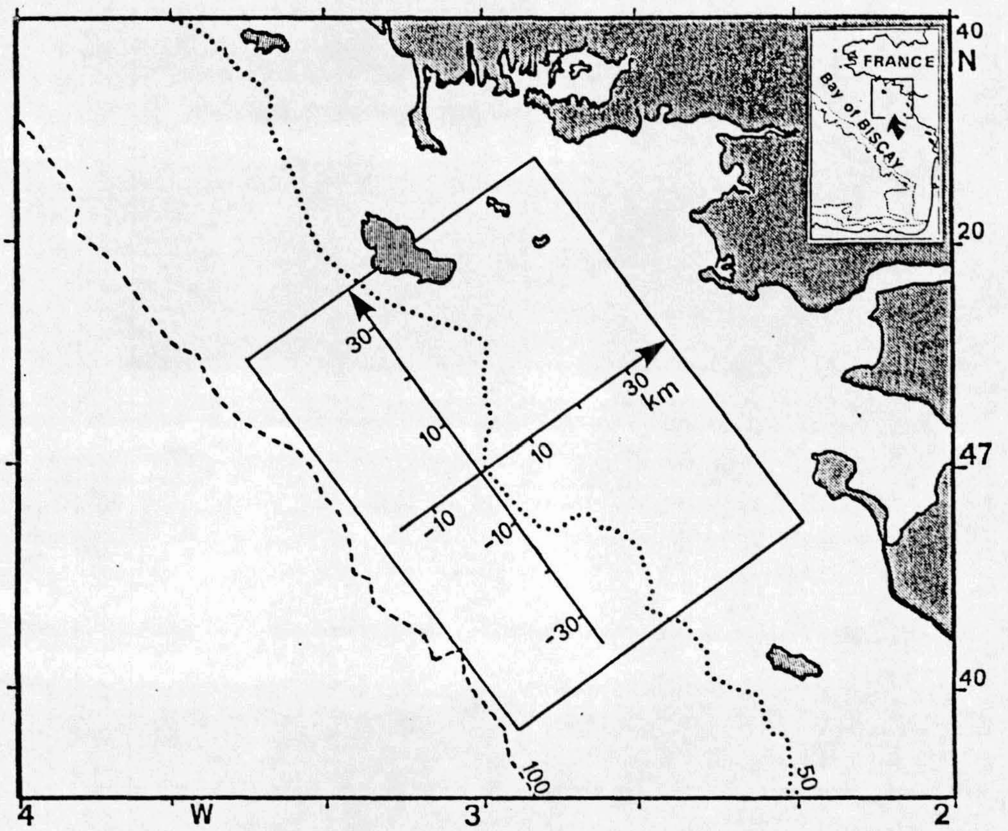


Fig. 1 - The region of the surveys concerning the early life stages of Sole. In the paper, all the positions and displacements are referenced to axes aligned with 325° (alongshore) and 35° (onshore).

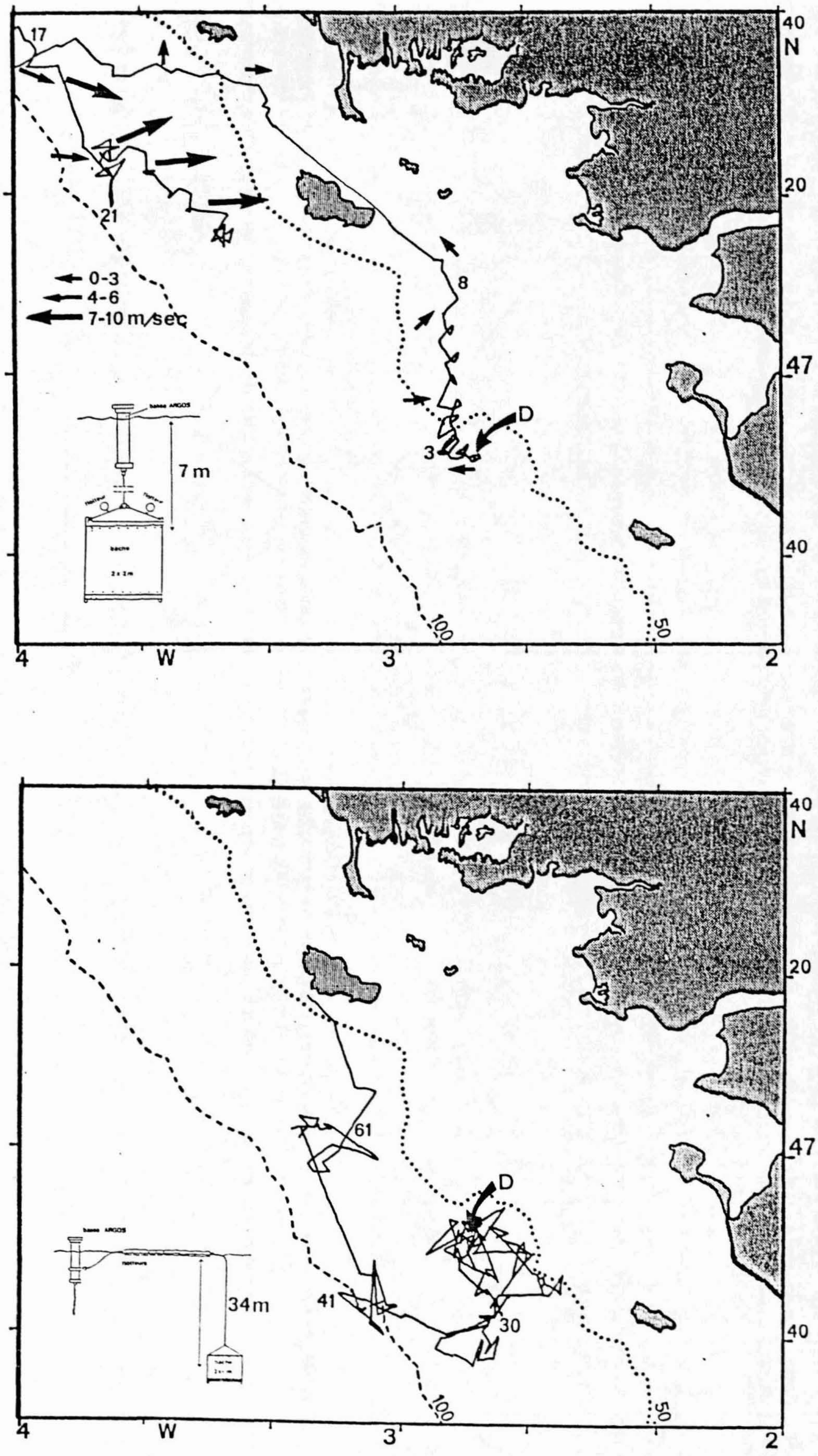
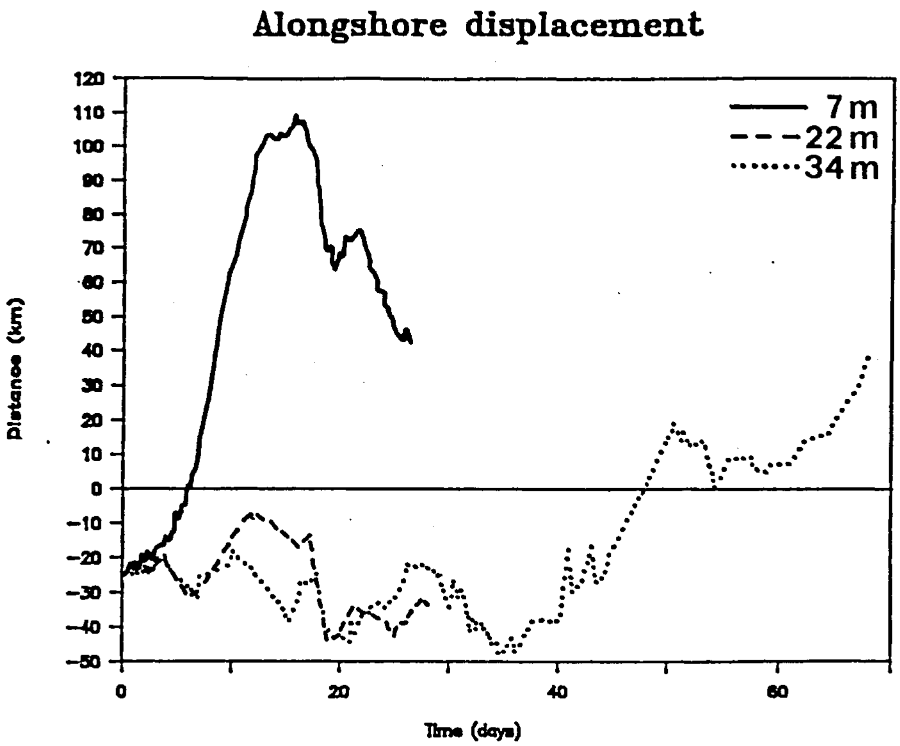


Fig. 2 - Trajectories of drifters deployed on March 6, 1986. The time labels correspond to the number of days from the begining of the experience. Mean wind vectors are also indicated.



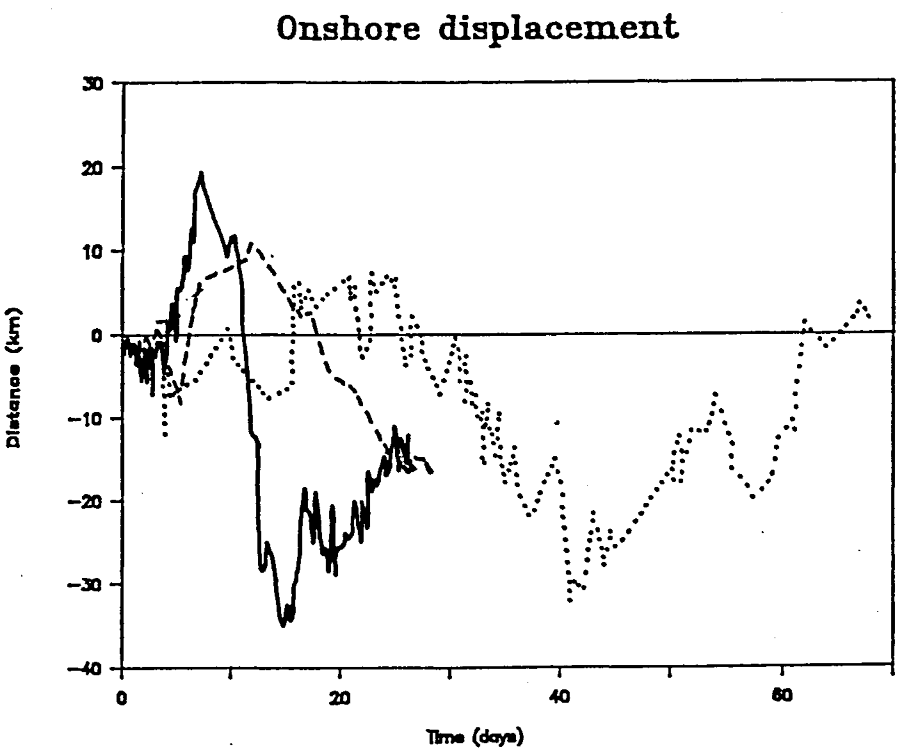


Fig. 3 - Evolution of the drifters position with time, during the 1986 experiments.

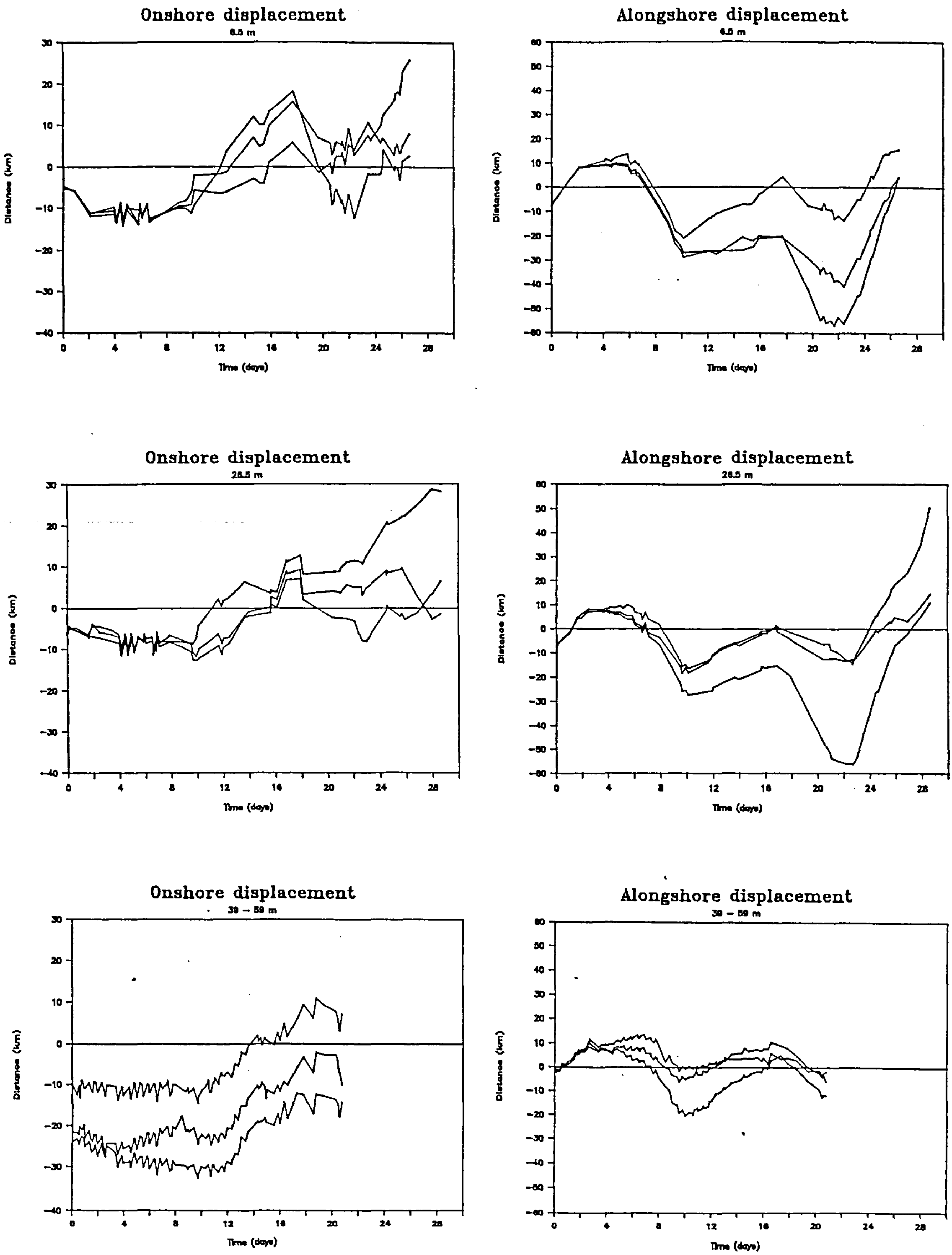


Fig. 4 - Evolution of the drifters position with time during the 1987 experiments. For each group of drifters only the positions at time t±20 minutes have been retained to avoid problems with displacements related to the tidal cycle. The differences in the released position for the drifters at 39, 49 and 59 m are explained by a voluntary deployment of the drifters on a depth gradient.

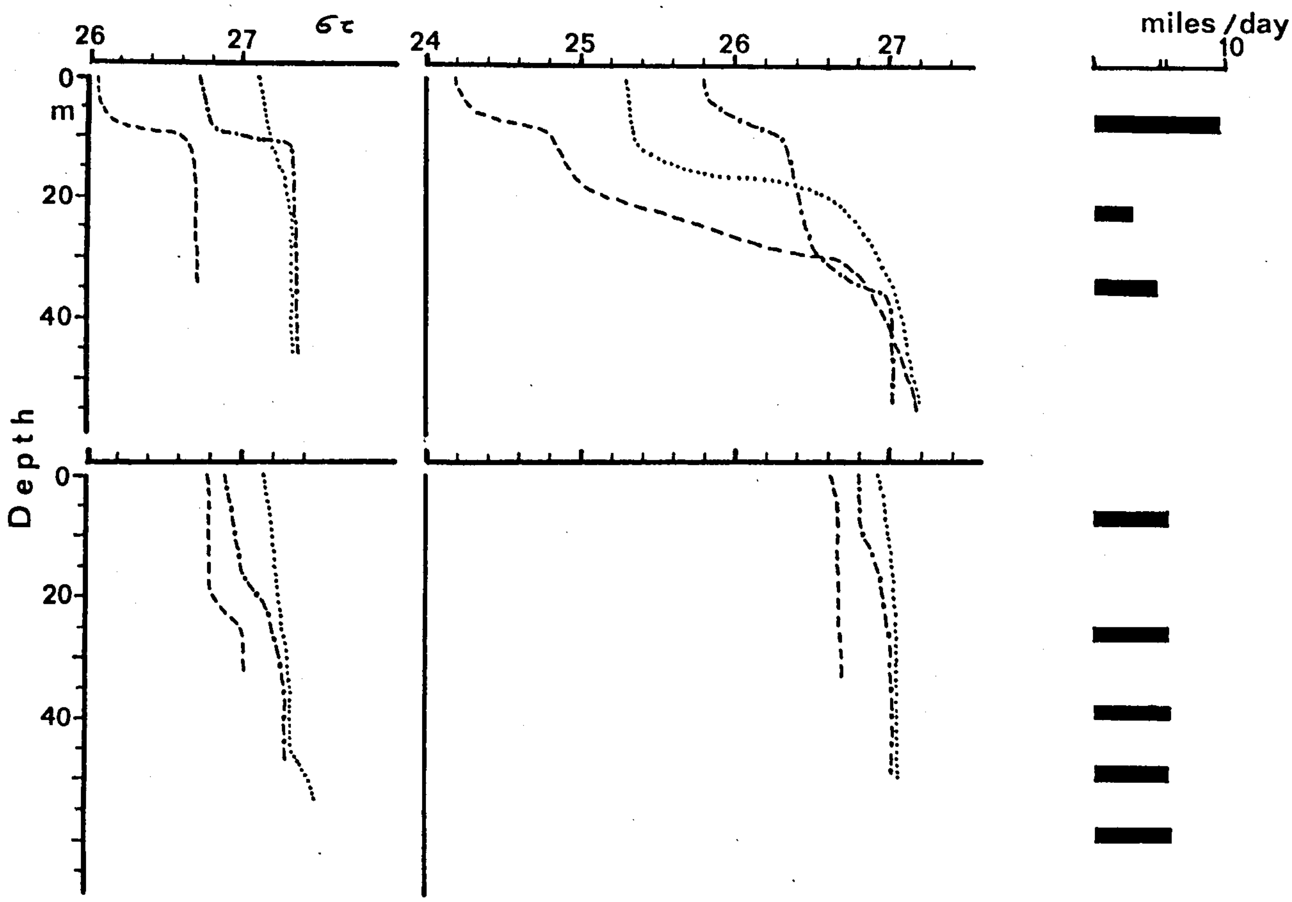
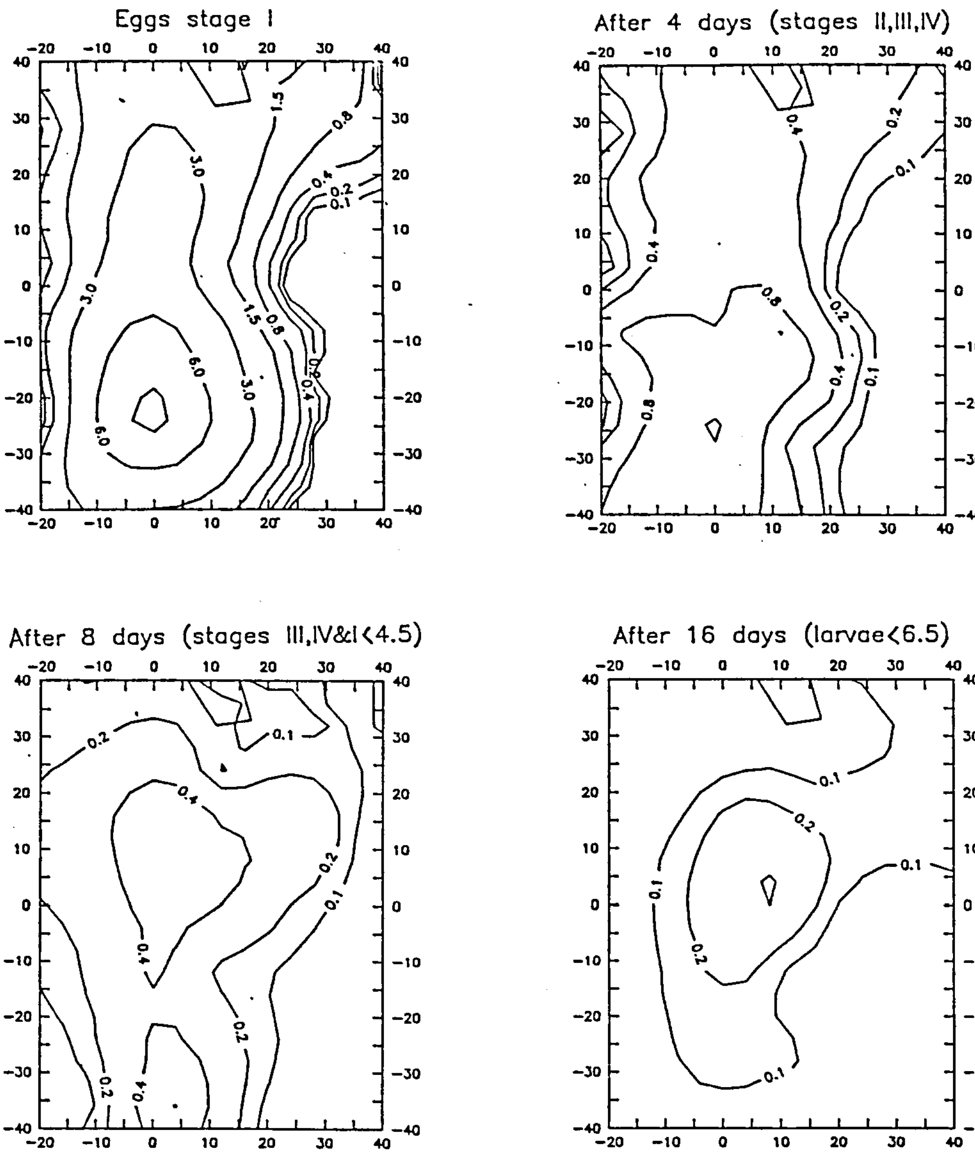


Fig. 5 - Water density profiles and indices of "activity" of the drifters at different depths. The index of "activity" corresponds to the mean velocity of the drifter. It is computed as the total distance covered (the sum of the vectors defined by two successive positions) divided by the duration of experiment for the given drifter (sum of time intervals between successive positions). The profiles at three different points on a depth gradient around the center of the area are presented.



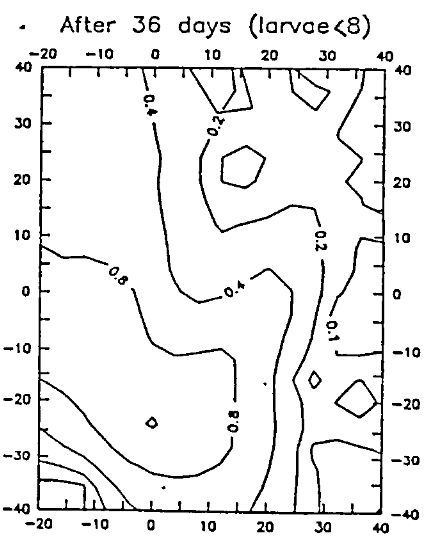


Fig. 6 - The evolution of the spatial distribution with time for a "cohort". The definition of this "cohort" is presented in The Study (Methods and data).

March 2-5, 1986	mx	s_x^2	my	s_y^2	rm
eggs stage IB	.50	60.66	-10.80	383.61	18.18
eggs stage IV	3.03	37.52	-22.39	310.15	14.00
larvae < 4.5 mm	3.00	78.21	-21.91	204.59	13.29
4.5 < l < 6.5 mm	13.66	41.97	-18.44	207.60	12.54
6.5 < l < 8.5 mm	-	-	-	-	-
larvae > 8.5 mm	-	-	-	-	-

March 10-13, 1986	mx	s_x^2	my	s_y^2	rm
eggs stage IB	-2.63	89.31	-6.74	450.10	20.88
Eggs stage IV	2.92	153.84	-3.90	423.31	22.34
larvae < 4.5 mm	6.72	114.23	-5.83	371.93	20.26
4.5 < l < 6.5 mm	8.01	50.87	-11.97	423.85	19.41
6.5 < l < 8.5 mm	7.89	34.89	-19.10	61.62	9.79
larvae > 8.5 mm	-	-	-	-	-

April 7-10, 1986	mx	s_x^2	my	s_y^2	rm
eggs stage IB	16.07	251.58	-2.48	288.92	21.24
eggs stage IV	3.40	135.59	-12.67	323.48	19.31
larvae < 4.5 mm	-.10	217.83	-12.69	283.04	20.33
4.5 < l < 6.5 mm	3.24	191.11	-5.45	292.47	20.06
6.5 < l < 8.5 mm	-2.77	175.85	-1.73	451.01	23.53
larvae > 8.5 mm	.04	132.73	-.66	368.07	20.86

March 6-9, 1986	mx	s_x^2	my	s_y^2	rm
eggs stage IB	-.03	88.47	-10.24	286.32	16.89
eggs stage IV	3.79	95.62	-5.57	419.33	20.22
larvae < 4.5 mm	5.33	114.90	-18.91	344.06	18.58
4.5 < l < 6.5 mm	11.70	15.27	-.13	460.26	18.04
6.5 < l < 8.5 mm	-	-	-	-	-
larvae > 8.5 mm	-	-	-	-	-

March 18-22, 1986	mx	s_x^2	my	s_y^2	rm
eggs stage IB	-.92	157.94	-4.69	350.60	20.70
eggs stage IV	-1.71	176.25	-3.07	256.06	17.87
larvae < 4.5 mm	10.06	244.66	3.14	252.77	19.28
4.5 < l < 6.5 mm	3.37	111.71	-5.70	390.96	19.72
6.5 < l < 8.5 mm	12.00	164.16	-8.96	330.68	20.21
larvae > 8.5 mm	2.05	0	-10.26	0	0

Table 1 - The evolution of the spatial distribution of the early life stages of Sole from survey to survey.
n, number of samples realized during each survey.
i, a sample realized at a point with coordinates dx_i and dy_i on the onshore and alongshore axes respectively.
P_i, the density (Nb/10 m³) of a particular stage for the sample i.
m_x, m_y, the coordinates of the center of gravity of the distribution.
s_x, s_y, an index of the dispersion on the onshore and alongshore axes of a particular stage around its center of gravity.
r_m, an index of the dispersion of a particular stage around its center of gravity. It corresponds to the mean distance from this center.

$$m_x = \frac{\sum_{i=1}^{n} P_i \times dx_i}{\sum_{i=1}^{n} P_i} \qquad s_x^2 = \frac{\sum_{i=1}^{n} P_i \times dx_i^2 - \left(\sum_{i=1}^{n} P_i \times dx_i\right)^2 / \sum_{i=1}^{n} P_i}{\sum_{i=1}^{n} P_i}$$

$$m_y = \frac{\sum_{i=1}^{n} P_i \times dy_i}{\sum_{i=1}^{n} P_i} \qquad s_y^2 = \frac{\sum_{i=1}^{n} P_i \times dy_i^2 - \left(\sum_{i=1}^{n} P_i \times dy_i\right)^2 / \sum_{i=1}^{n} P_i}{\sum_{i=1}^{n} P_i}$$

$$r_m = \frac{\sum_{i=1}^{n} \sqrt{(dx_i - m_x)^2 + (dy_i - m_y)^2} \times P_i}{\sum_{i=1}^{n} P_i}$$