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(de l'exercice des années de 1990 et 1991)

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Les membres de la Société peuvent publier 7 pages imprimées sans frais d'impression dans la mesure à leur manuscrit qui ne demande pas de frais d'impression excessifs (pour des photos couleurs, par exemple). Dans les autres cas, y compris la présentation d'un non-membre, tous les frais seront à la charge de l'auteur.

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Proceedings of the FRANCE-JAPAN Symposium
on
Determination of Biological Recruitment in the Sea

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13-14 November 1990

La mer 28 : 163-164, 1990
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FOREWORD

Hubert J. CECCALDI

The study of the determinism of recruitment represents actually one of the main theme of interest in marine biology and biological oceanography. Its final aim is to understand and to try to master the variations of living resources of the ocean. For many species, the mechanism playing a role in the survival of eggs and larvae, including physical and chemical processes, nutritional, physiological and biochemical characteristics, are poorly understood.

But these general themes have shown a great deal of interest recently, in different countries. Canada, Denmark, France, Japan, Netherlands, Norway, Scotland, USSR and USA for instance have developed several scientific programs on different aspects of this field of marine research.

In France, since 1986, a National Program on Recruitment Déterminism (Program National sur le Determinisme du Recruitement=PNDR) have been created, integrating the efforts of different laboratories belonging to Universities, to Institut français pour l'Exploitation de la Mer, (IFREMER), to Centre national de la Recherche Scientifique (CNRS), Museum national d'Histoire naturelle, Institut Français de Recherche Scientifique pour le Dévelóppment en Coopération (formely: Office de Recherch Scientifique et Technique Outre-Mer=ORSTOM), Ecole Pratique des Hautes Etudes (EPHE), between the most important scientific bodies involved in these scientific researches.

Activities of PNDR are coordinated by a Committee (Comité Directeur) of seven members belonging the main research organisms (IFREMER, CNRS, ORSTOM, University). The scientific activities are coordinated by another committee (Comité scientifique) of fifteen members, who propose its own recommendations on research programs select the best themes who are proposed by research teams, evaluate results of researches, suggest meeting and round tables, select budgets to adcquire large size research apparatus or of high price. The president is Mr. Paul NIVAL, Professor of Université Pierre et Marie Curie, Université Paris VI.

These organizations play the role of national coordinating system, which is also multidisciplinary and gathers the efforts of the scientists working in the same field in France and overseas Departments and Territories.

In Japan, such a national structure does not exist. Nevertheless, several laboratories and numerous scientists are working in the field of recruitment. In France, the necessity of a pluriannual programs and of international activities has been recognised since an important seminar held in Nantes, 2—4 July, organised by IFREMER. In that context, it appeared interesting to organise a symposium between French and Japanese specialists, in order to make them meeting for the first time on that topic, and in order to exchange their ideas about biological recruitment in the sea.

It is specifically the role of Maison Franco-Japonaise (Nichi-Futsu Kaikan) first of all to promote such exchanges between French and Japanese scientists in that specialized field of research.

We have invited several French scientists working in Recruitment, in order to make them exchanging their experiences, and their knowledges, with their Japanese colleagues.

We are confident that this first France-Japan meeting in that field will be followed by several ones, very presumably with the same scientists in France, in Japan, or in other countries. The exchanges of scientific informations will be very much facilitated as these scientists have already a mutual acquaintance.

The final aim will be to make these scientists working together in common France-Japan programs of research, in the future.

This is the role of the two Sociétés franco-japonaises d'Océanographie: the French one, settled in Institut océanographique in Paris, and the Japanese one, settled in Maison Franco-Japonaise in Tokyo. We would like to thank respectively their Presidents, Professor Roland BILLARD and Professor Yushio ARUGA, at this opportunity.

The main mission of Maison Franco-Japonaise since long years, remain the same, since more than 67 years and it represent, the better mean to communicate and to understand not only another country, but also another civilisation. Today, both sides need such a deep understanding. We are very glad to thank specially Professor ARUGA and the editorial board of "La Mer" to publish the content of this France-Japan Symposium.

It is a concrete proof of our scientific cooperation.

(Maison Franco-Japonaise, 3, Kanda Surugadai
2-chome, Tokyo, 101 Japan)

La mer 28: 165, 1990
Société franco-japonaise d'océanographie, Tokyo

Welcome address

Yusho ARUGA

On behalf of La Société franco-japonaise d'Oceanographie, Tokyo, I have a greatest honor and pleasure to express my heartfelt welcome to all the participants of the French-Japanese Symposium on Determinism of Biological Recruitment in the Sea. I would like to express my deepest gratitude especially to those who have come from France for this symposium.

As it is recognized by marine biologists, biological oceanographers, fishery managers and aquaculture specialists, a better knowledge on the survival of eggs, larvae and juveniles of marine animals is very important for understanding a variety of marine life. Several scientist groups are involved in this research area both in France and Japan. I believe that the French scientists are interested in research by Japanese scientists, and the Japanese scientists are also interested in research developed by French scientists. Therefore, this symposium is a very good opportunity to have intimate contact with each other for the exchange of information especially in the fields of biology, ecology and distribution of larvae of marine animals.

In this symposium there are two main themes chosen to be developed by French and Japanese scientists: one is "Ecology in natural environment" and the other is "Experimental biology and recruitment". I am expecting excellent presentation and fruitful discussions for mutual understanding and future development of scientific cooperations between France and Japan both in basic and applied biological sciences. I do hope a great success of the symposium. Finally, I would like to express my respectful thanks especially to Professor CECCALDI for his enthusiasm and excellent arrangement of the symposium.

Thank you very much for your participation.

(President de la Société franco-japonaise d'Océanographie)

La mer 28 : 167-168, 1990
Société franco-japonaise d'océanographie, Tokyo

Main concepts dealing with biological recruitment in the sea

Hubert J. CECCALDI*

Recruitment is a term differently used by several specialists. In the army, it defines the number of soldiers arriving every year for their military service. For a director of a company, it represent the number of workers who are beginning to work every year in its company. For a specialist in fisheries, it represents the number of animals, mainly fishes, who are caught by the nets of a fishing vessel.

But if one consider the different marine ecosystems, the significance of recruitment varies from a species to another one, and for instance, if the considered species belongs to necton, benthos or plankton.

In fact, we need to know the biological cycle characters of each step of aquatic species between the genitor to the following juvenile who ocuupy the same place in the water mass or in the marine environment.

That period of biological cycle of each species is constituted by gametes generally emitted in the sea water, by eggs, by different larval and post-larval forms, sometimes followed by metamorphosis and then by the juveniles. If, for several species, descriptive studies have been already done, the quantification of the growth and the evolution of each stage in open sea have very seldom be realized.

Gametes are transported by sea waters always in movements, and the risk of not to encounter the other gamete of the same species in a moving medium is very high.

After fecundation, the eggs are very often eaten by some predators or some filter-feeder; the eclosion occurs after the consumption of vitellic reserve, and represent also an important critical phase.

Then, each larval stage constitutes another critical step of the biological life with several difficulties concerning the food, the adaptation to a variable environment, the predators, and, for sessile species, the settlement.

The quantification of these factors, and on their effects on the survival and on the success of the individuals born in the same time is not known for almost all aquatic species, especially those producing large number of eggs.

But the study of cycles is not sufficient; all biological cycles occur in a constantly moving medium, who perturbates these cycles.

Marine ecosystems are dynamic; it is necessary to know the basic mechanisms and the laws dealing with the success of recruitment in cyclic variations of these ecosystems.

These dynamic variations are usually natural, and, sometimes, produced or induced by man activities or human industries.

One of the final aims of these studies is to reconstitute natural stocks or exploitable stocks, and to adjust them to the economic development of concerned countries.

For instance, it is absolutely necessary to quantify the natural variability of the stocks in order to predict the economical and social consequences of the catches variations, as well as the predictable losses of the industries linked to fisheries; the future of fisheries management necessitate a better knowledge of this variability.

From biological point of view, recruitment may be considered differently if on consider bivalves for instance, where recruitment is linked to metamorphosis, or if one consider fishes, where recruitment is linked to the period where they constitute a cohort, or if one consider the similar behaviour of larval in artificial propagation of marine species in extensive aquaculture for instance. Anyhow, a common effort of standardization of such

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concepts, species by species, and from one country to another, is necessary, as well as the typical detailed biological cycles of these species. We need also more fundamental knowledge of the specific effects of environmental factors on survival, growth and physiology of different steps of larval and juvenile stages of marine species, and these informations will be adcquired by experimental works in hatcheries, as well as in field observations. To cover our knowledge, we have also a profound need of the effect of environmental factors on the fecundity of genitors. Then, the theoretical critical phases of the growth have to be identified, especially where the mortality is high; we have to know also the variability of this mortality on these critical phases in order to begin to establish models of evolution of natural populations in oceans.

Finally, we have to understand the mechanism of dispersion of plankton's forms, turbulence, vertical currents, advection, who constitute the origin of the distribution of larvae in marine water masses.

The physical factors constitutes a very important aspect of the pluridisciplirary research of that field, and the use of satellite observation, as well as buoys who record currents, salinity, temperature, oxygen, salts and other physical and chemical parameters will give us the general framework where the living organisms, at different steps of their life spend their biological cycles, passing from one ecosystem to another one.

The most difficult problem to resolve is the scale of the observations and of the studies; macro-scale, meso-scale, micro-scale; we need a deep analysis of the phenomenons to plan these future studies at the appropriate levels, i. e. large scale physical processes, small scale physical processes, edimentology, chemicals processes, population studies, individual studies, physiology, biochemistry, etc. The main effort to develop is the integration of the researches and of the results of the research. These different approaches necessitates also the constitution of pluridisciplinary research group, and long term studies, at least to make the scientists understanding each other, which is not so easy that it seems.

Until now, the fisheries management have not taken great care on the recruitment problem. Actually, with the increase of the efficiency of fishing technology, and with the stocks reduction, exploitation of marine resources need a better prediction of catches, the productivity of fishing boats have to be better managed than in the past. But the transformation of coastal management will necessitate a better knowledge of natural populations, as well as the evolution of natural ecosystems when men wish, for instance to implant artificial reefs, or to use intensively different types of aquaculture, or to increase the artificial propagation of economical species. Great successes have been obtained in sea ranching of salmon, and for scallops extensive aquaculture and it will be of prime interest to know if we may control the development of other species in natural environment. We are reaching actually a new era of the use of the sea. Our seas-not yet oceans, nor ocean itself-are at the beginning of a true management, and what we are observing in some parts of coastal zones, as to take some French examples, in Vendee, in Normandy, in some parts of Mediterranean coast, or, in Japan, Kumamoto, Nagasaki, Yamaguchi Prefectures for instance, where aquaculture attains large developments, prefigures what we shall observe in the future: a true management of marine fields.

The competition for the use of coastal areas between fisheries, aquaculture, tourism, marine sports, industries, towns, airports, artificial islands, etc, will increase the pressure on the natural populations. There is no doubt that it become more and more important to evaluate with precision the specific impacts of these different uses on natural population, and especially in their younger forms.

Marine biological recruitment remains ascientific thema of a great actuality.

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Société franco-japonaise d'océanographie, Tokyo

Larval settlement of a bivalve *Theora lubrica*[*]

Hiromichi IMABAYASHI[**]

1. Introduction

A small semelid bivalve *Theora lubrica*, selective deposit-feeder, predominates on the extreme surface of soft muddy sediment in eutrophic waters of Japan, and has largely increased in recent years (KIKUCHI and TANAKA, 1976; IMABAYASHI and ENDO, 1985). The benthic juveniles die out gradually as an ambient dissolved oxygen reduces, but a small number of adults barely survives even in late summer when oxygen-deficient water develops markedly at bottom layer(TANAKA and KIKUCHI, 1979; IMABAYASHI, 1989). On the other hand,the bivalve is capable of spawning all the year round except for some populations (KIKUCHI and TANAKA, 1976), and therefore the planktonic larvae can settle continuously on a favorable area.

Other characteristics of the bivalve are as follows;

1) The benthic juveniles are eaten by large benthos, e.g., penaeid shrimp buried in sediment.
2) The yearly production is estimated 21 g dry weight/m² in the Seto Inland Sea (unpubl.).
3) The species takes an opportunistic life in macrobenthic community (KIKUCHI and TANAKA, 1976).

The study deals with a mechanism of its larval settlement. Investigation was mainly conducted in Hiuchi-Nada, the Seto Inland Sea, which has been greatly eutrophicated and polluted because of industrial development (OCHI and TAKEOKA, 1986; KAGAWA, 1986). Seasonal fluctuations and distributions of the planktonic larvae and benthic juveniles are examined in relation to oxygen deficiency and tidal current. The survival rate and growth are also estimated.

2. Distribution and tolerance to oxygen level in benthic life

The bivalve, together with polychaetes, was abundant in the muddy sediment of eastern Hiuchi-Nada. In late summer when thermal stratification was formed (OCHI and TAKEOKA, 1986), dissolved oxygen concentration was generally diminished in near-bottom layer while the planktonic bivalve were found at ovarall bottom layer. During summer, although the bottom water located 0.5 m above sediment frequently decreased to 1 ml/l (oxygen saturation: 15%), the bivalve was last survived among macrobenthic community. The density was remarkably low at stations under 3 ml/l (45%). These oxygen-deficiency produced hydrogen sulfide from muddy sediment including much organic substances.

Respiration was measured in a laboratory. The oxygen uptake kept a given level to almost anoxic condition at a temperature of 10 and 15℃, while decreased at higher oxygen saturation (about 20%) at 20℃. It means that the bivalve has a strong tolerance to low oxygen, especially at low temperature.

It is, therefore, deduced that the death in late summer is directly caused by hydrogen sulfide.

In 1972, most of the macrobenthos died out because the anoxic water mass developed on a large scale. Before long the bivalve firstly increased, and thereafter several kinds of polycheates recovered the densities in eastern Hiuchi-Nada. In recent years the bivalve has been gradually dispersed to the western region (IMABAYASHI and ENDO, 1985). From its opportunistic life, western Hiuchi-Nada is considered to be steadily affected by oxygen-deficient water.

3. Distribution and density of planktonic larvae

Larval settlement was examined in a favorable

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nursery area for benthic juveniles (IMABAYASHI, 1984; IMABAYASHI and IWATANI, 1988, 1990), a collection of which was made with a core-typed bottom sampler. The settlement occurred at metamorphosing stage, which widely ranged from 132 to 196 μm in shell length. Planktonic larvae collected with plankton net were represented by umboned stage, larger than 125 μm, because this size is the smallest size for identification (TANAKA, 1981).

Seasonal change in the density of planktonic larvae was different from that of benthic juveniles, which died out in late summer. Planktonic larvae hardly decreased during summer, although fluctuated from 10^2 to 10^4 shell/m^3 in a year.

Vertical and horizontal distributions indicated that the density was high at bottom layer and near coast. On the other hand, planktonic larvae were always migrating along the bottom, according to a large tidal oscillation with a spring range of 2.9 m. Hence it is due mainly to these larval migration that a large settlement occurs at a favorable area and period for benthic life.

Survival rate at the settlement was estimated from the wild and reared populations. Umboned larvae (132–164 μm) and metamorphosing larvae were simultaneously collected at the peak of settlement (May-July) and at the recovery of settlement (September-December). Survival rate of the umboned larvae was approximately 20%, whose value was the same rate as that during metamorphosing stage. On the other hand little mortality was observed after the settlement by rearing the metamorphosing larvae obtained in a field, and thereafter benthic juveniles hardly died within 2 weeks. Before umboned stage a high and constant mortality was expected from various rearing conditions.

It is, therefore, suggested from a schematic survival process that the survival rate changes remarkably after the settlement (Fig. 1).

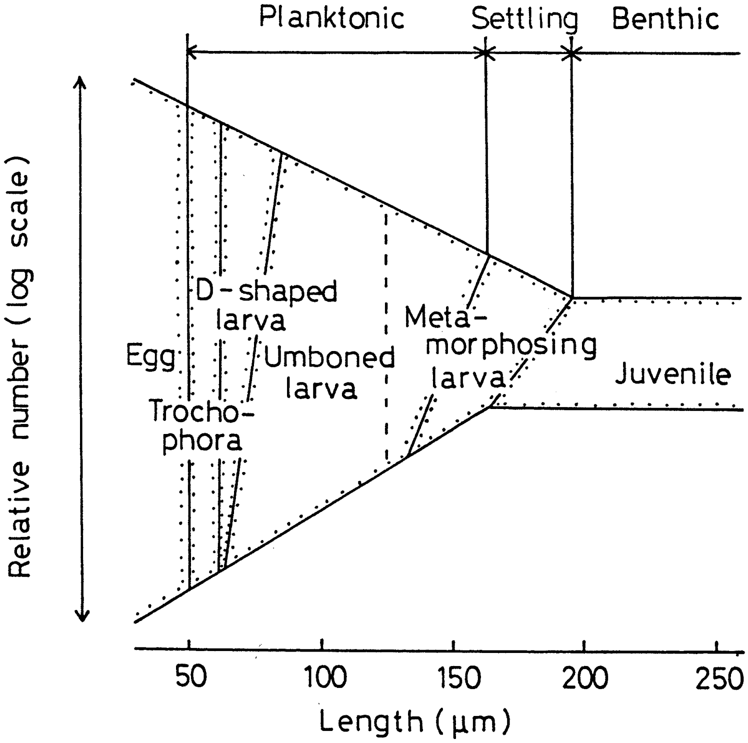

Fig.1. Schematic survival process at the settlement of *Theora lubrica*.

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Spatial distribution and recruitment of pelagic larvae of sand bubbler crab, *Scopimera globosa*[*]

Hiroshi SUZUKI[**] and Taiji KIKUCHI[***]

Abstract: *Scopimera globosa* burrows its nest into the sand beach of upper littoral zone. The larval migratory process seems to be influenced by both hydrographical conditions and spatial distribution pattern of larvae. The surveys were carried out at fixed time intervals (daily to biweekly) in Tomioka Bay in the summer of both 1980 and 1981. Samples were collected by a Kitahara-type plankton net with NGG 54 cloth and hand-made sledge net with the same cloth.

Pelagic larvae of all stages tended to be distributed in a particular area near the adult habitat. Their vertical distribution patterns also tended to be concentrated at the bottom layer. The larvae after stage III zoea strongly showed a concentration in their spatial distribution patterns. Their spatial distribution seems to be induced by not only the physical oceanographic conditions but also the compound effect of a larval responsive behavior to environmental conditions and water movement.

The zoeae and megalopae migrate between the sublittoral zone and the littoral zone (adult habitat) by riding on every tidal current. This migratory process has not yet been reported and is smaller in scale than the assumed migratory models. This process seems to be a peculiar characteristic of *Scopimera globosa* larvae.

1. Intruduction

The persistency of benthic population depends strongly on the process of larval recruitment. This process is influenced by both environmental condition and spatial distribution pattern of pelagic larvae. In brachyuran species, the larval distribution have been studied in three large bays of Japan (*Pinnixa rathbuni* in Ise and Sendai bays: SEKIGUCHI, 1979, 1981, 1983, 1988; SEKIGUCHI and ODATE, 1983; some brachyuran species in Tosa bay: YATSUZUKA and IWASAKI, 1980), in the pacific coastal region of North America (*Cancer magister*: LOUGH, 1976), and in Chesapeake Bay on the Atlantic coast (some brachyuran species: SANDIFER, 1973, 1975; DITTEL and EPIFANIO, 1982; EPIFANIO, 1987; EPIFANIO and DITTEL, 1982). They have revealed that there is specific difference in large scale horizontal distribution patterns of larvae.

MCCONAUGHA (1988) mentioned that the pelagic larvae of crustaceans belong to any of the following three patterns of distribution: 1) larvae retained within the estuary; 2) larvae advected to the adjacent continental shelf (20-30km offshore); and 3) larvae expelled and widely distributed across the shelf. EPIFANIO (1988) also reviewed the spatial distribution patterns and the responsive behavior of estuarine larvae and assumed four models of recruitment mechanism in the estuary and the shelf. As the surveys in their study were always conducted in a large bay or in an extensive coastal area, the models are assumed in a large scale and applied in the recruitment mechanism of the crustacean species with an extensive habitat. It will be, however, difficult to apply the same models to the sand bubbler crab, *Scopimera globosa*, inhabiting locally and in a very limited habitat. In this species, the larvae collected by a large scale sampling are not regarded as a concern in recruitment, but in dispersion and/or death migration. An attentive survey, therefore, has to be conducted

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Contributions from the Amakusa Marine Biological Laboratory, Kyushu University, No. 359.
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in an area of small scale so as to elucidate the temporal and spatial distribution patterns of the larvae contributing to the recruitment.

In the present study, the spatial distribution pattern of *S. globosa* larvae is revealed by intensive survey. This study also discusses the larval migration and recruitment process in relation to tidal cycle.

2. Materials and Methods

The investigations were carried out in Tomioka Bay in the summer of both 1980 and 1981. The bay is a small semi-open sea region which is located on the northwest coast of Amakusa Shimoshima Island, western Kyushu. The *S. globosa* population inhabits only limited area of the upper beach (Fig. 1). The area is located in the innermost part of the sand flat called the Higashi Hama, and opens to the sea in the northern direction. The distance from Mean Low Water of Spring tides (MLWS) to the lower margin of *S. globosa* habitat is about 500m.

Plankton samplings in the crabs' habitat (Stn. A in Fig. 1) were nocturnally carried out at high water from June 24 to July 6, 1980. The samples were collected by a Kitahara-type plankton net with NGG 54 cloth towed horizontally for ten minutes. To elucidate the relationship between the occurrence of pelagic larvae and tidal rhythm, the plankton samplings were conducted at station B on August 29 and 30, 1980. The samplings were made at intervals of one hour at the surface, middle and bottom layers. The sampling for the spatial distribution of larvae were carried out weekly or biweekly from May to August, 1981 at stations 1 to 16 in Tomioka Bay. The samples were collected at the surface and bottom layers. On the sampling at the bottom layer of stations 1 to 16 and B, a hand-made sledge net based on Kitahara-type plankton net with NGG 54 cloth was used. A Kitahara-type plankton net was horizontally towed at the surface and middle layers. All nets were towed for 100m at all sampling stations.

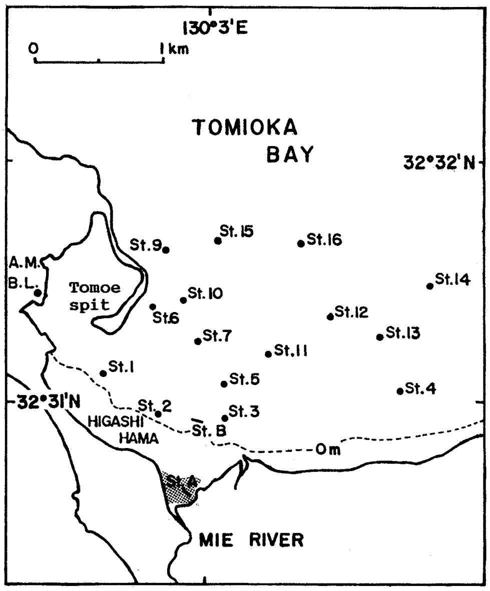

Fig. 1. The vicinity of study area, sampling stations and habitat of *Scopimera globosa* (shadow area) in Tomioka, western Kyushu.

All samples were preserved in 10% formalin-sea water for later sorting and counting. Samples were taken to the laboratory, scanned under a binocular microscope, and the larvae were removed. Developmental stages were determined by the number of natatory hairs. Staged individuals were counted and preserved in 70% alcohol.

The samples in 1980 were condensed into 100ml and their aliquot subsamples of 1ml were made with a pipette. The larvae contained in each subsample were counted three times and the total captured numbers were estimated. Individual larvae in all samples obtained in 1981 were counted.

3. Results

It was expected that the migratory patterns of pelagic larvae and their spatial distributions in the coastal region correlate each other. At first, the horizontal and vertical distribution patterns of each larval stage in the coastal region will be elucidated. Then the larval migration and recruitment will be examined on the basis of the distribution patterns.

Fig. 2 shows the changes of horizontal distribution patterns of *S. globosa* zoeae in Tomioka Bay from May 26 to August 4, 1981. Zoea larvae of stages I to III appeared in low densities from May to June (early

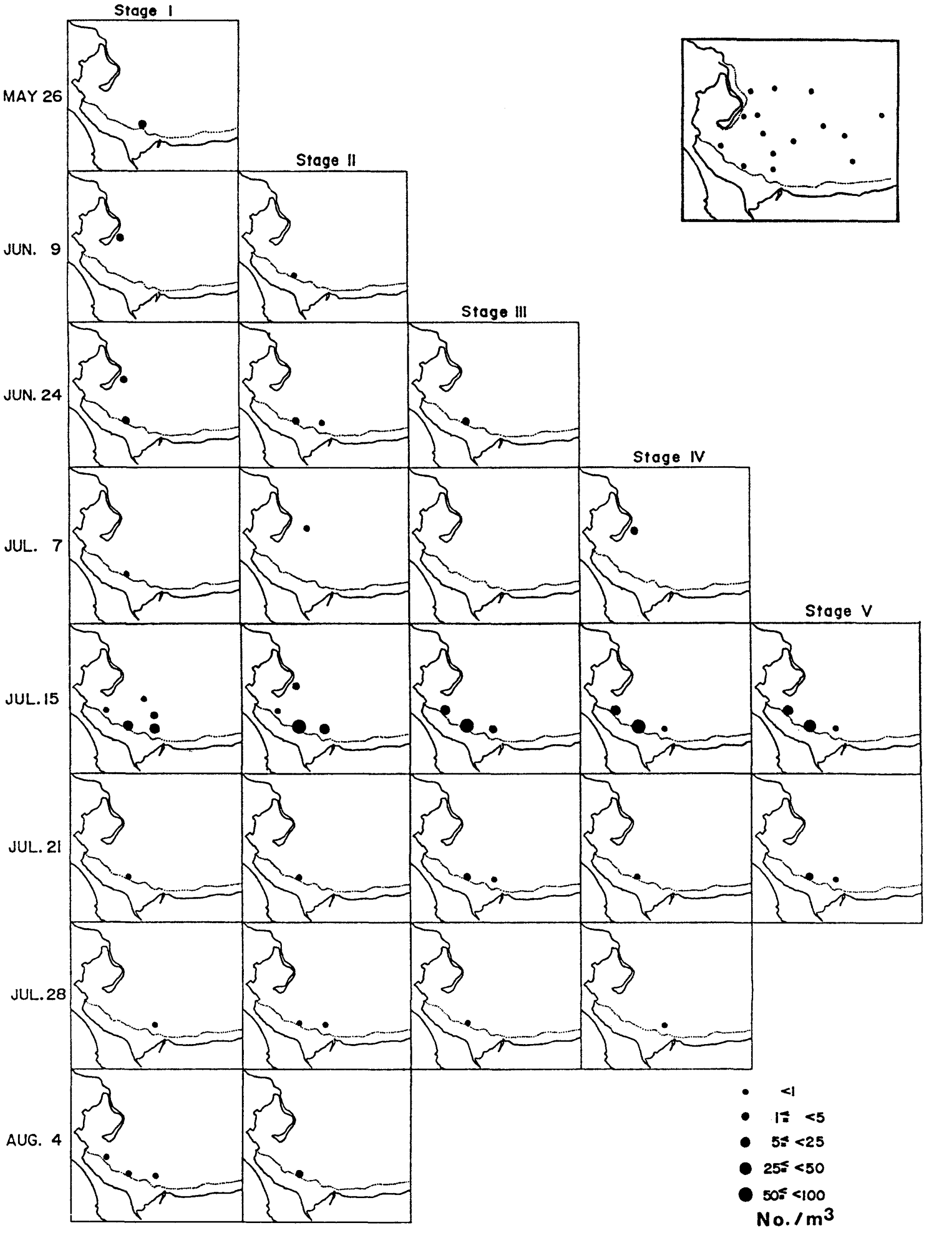

Fig. 2. Horizontal distributions of each zoeal stage of *Scopimera globosa*. The figure at upper right hand corner shows the sampling points.

reproductive season); and zoeae of all stages appeared abundantly in the middle of July.

The stage I zoeae were distributed at station 3 (nearest to the adult habitat) and at station 6 off Tomoe spit on the west of the bay from May 26 to June 24 during the early reproductive season. In the middle of July, though a few zoeae of stage I were distributed at stations 5 and 7 about 600m offshore, most of them were distributed at stations 1 to 3 located along MLWS line. The distribution patterns of zoeae after stage II showed similar tendency as that of stage I zoeae. Zoeae of stages II to IV were mainly distributed at stations 2 and 3 adjacent to the adult habitat; while the last stage(V)

Table 1. Appearance ratio of *Scopimera globosa* zoeal stages at each station.

Stations	1	2	3	4	5	6	7	9	10	11	12	13	14	15	16
Stage 1	2.8	64.1	20.3		2.7	8.9	1.2								
2	0.6	83.6	13.7			1.2			0.9						
3	5.4	90.0	4.6												
4	6.7	91.1	1.0			1.2									
5	14.1	84.5	1.4												

zoeae were distributed only at stations 1 to 3 during the survey period.

According to the variations in appearance ratio of all stages at the stations (Table 1), the zoeae of stages I and II were distributed more extensively than those of the other stages. Stages I zoeae appeared at six stations (1, 2, 3, 5, 6, and 7) and the stage II at five stations (1, 2, 3, 6, and 10). The appearance ratio of stage I zoeae at stations 5, 6, and 7 were 2.7%, 8.9%, and 1.2%, respectively. These stations were located away from the adult habitat. The appearance ratio of stage II zoeae were also very low at two offshore stations (1.2% at station 6 and 0.9% at station 10). On the contrary, at stations 2 and 3, which were located along MLWS line, the appearance ratio of stages I and II zoeae were in the high range from 84.4% to 97.3%. The ratio of stage I zoeae were 64.1% at station 2 and 20.3% at station 3; and those of stage II were 83.6% at station 2 and 13.7% at station 3.

Most zoeae after stage III were distributed at stations 1, 2, and 3 along MLWS line. The especially high appearance ratio at station 2 of stages III, IV, and Vwere 90.0%, 91.1%, and 84.5%, respectively. The pelagic larvae of *S. globosa* were thus distributed intensively in the region neighboring the sand beach, although the distribution range of the early stage zoea was relatively extensive. The main distribution region of larvae did not shift horizontally with the development of larvae.

The vertical distribution patterns of each zoeal stage were expressed as the appearance ratio at each layer (Table 2). The stage I zoeae were distributed at the surface layer with the appearance ratio of 11.8% and at the bottom layer with 88.2%. More than 96.0%of the zoeae after stage II, however, appeared at the bottom layer, and the ratio was higher as the stage of larva developed. As this result was obtained in the day time, there was still a problem on the diurnal changes in the vertical distributions for each larval stage.

Table 2. Appearance ratio of *Scopimera globosa* zoeal stages at each layer.

Stages	1	2	3	4	5
Surface Layer	11.8	3.6	3.1	0.7	0.8
Bottom Layer	88.2	96.4	96.9	99.3	99.2

The hourly changes of appearance of each larval stage were, therefore, examined at station B (Fig. 3). Station B was located between stations 2 and 3 where the zoeae of all stages appeared abundantly. Stage I zoeae were collected plentifully at the bottom layer from low tide to flood tide (from 18:00 to 19:00 in August 29; from 5:00 to 9:00 in August 30). While, from high tide to ebb tide (from 23:00 in August 29 to 4:00 in August 30; from 10:00 to 14:00 in August 30), stage I zoeae appeared at all layers in almost equal number.

The zoeae after stage II appeared more abundantly at the middle and bottom layers. Compared with stage I zoea, they were more abundant at bottom layer in both flood and ebb tides. The zoeae appeared more frequently at the bottom layer as the larva developed to more advanced stage. The *S. globosa* larvae of all stages were

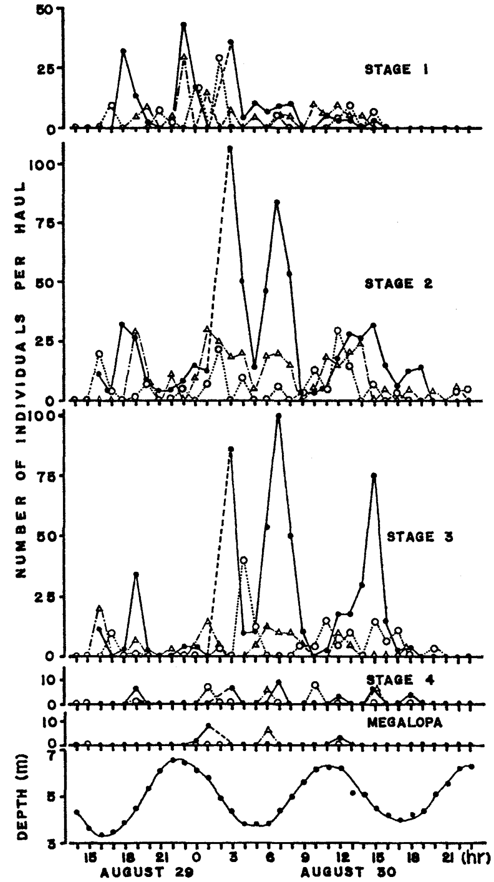

Fig. 3. Hourly changes of individual appearance of *Scopimera globosa* larvae at station B from August 29 to 30 in 1980. The open circles, open triangles and closed circles show the surface, middle and bottom layers, respectively.

distributed in large number at the bottom layer, not only in the day time but also in the night time.

According to the daily samplings carried out at nocturnal high tide from June 24 to July 6 in 1980, the density of stage I zoeae reached the first maximum at quarter moon, three or four days before the spring tide (Fig. 4). The density then were gradually reduced and increased again at neap tide. This continuous sampling also revealed that all larvae after stage II zoea appeared occasionally and became abundant on both June 30 and July 6.

These results indicate that appearances of these larvae are irregular without the apparent influence of semi-lunar cycle. This also demonstrates that the pelagic larvae of *S. globosa* as they develop always migrate in relation to tidal current between the sublittoral and the littoral zones, where the adult crabs inhabit.

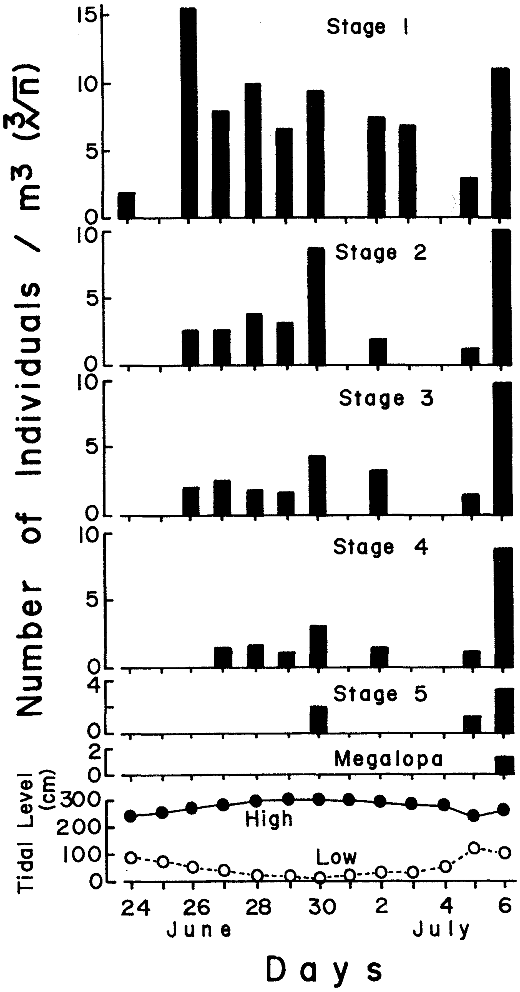

Fig. 4. Diurnal changes of individual appearance of *Scopimera globosa* larvae at station A from June 24 to July 6 in 1980.

4. Discussion

The distribution pattern of pelagic larvae is known to play an important role in the recruitment of larvae and in the persistence of adult population (BURTON and FELDMAN, 1982; CRONIN, 1982; EPIFANIO and DITTEL, 1982; EPIFANIO, 1988; FORBES and HAY, 1988).

SANDIFER (1973, 1975) had surveyed Chesapeake Bay and emphasized that the distribution pattern of larvae was nearly related to the adult habitat; larvae of the species which were heavily dependent on estuarine habitats tended to be abundantly retained within the estuary; and those of the species which were not restricted to estuarine habitats tended to be dispersed to the open sea. In Ise and Mikawa Bays the *Pinnixa rathbuni* larvae released in the adult habitat were rapidly transported in a counterclockwise circulation toward the opposite side of the habitat where they formed a belt-shaped distribution (SEKIGUCHI, 1979, 1981, 1983, 1988). After at least one month the larvae moved and were recruited to the adult population. He also suggested that the distribution pattern and recruitment process of larvae were influenced by residual flow and seasonal winds.

The present study demonstrated that pelagic larvae of *S. globosa* were abundant in the region horizontally along MLWS line; and those of all stages were mainly distributed in the bottom layer. On the bottom current system of Tomioka Bay, there is a current curtain on the north of the bay and the waters of the bottom layer constantly flow landward in the region along MLWS line (SUZUKI et al., 1982). These oceanographical conditions indicate the possibility of larvae being passively accumulated by the current curtain and the landward flows. The similar pattern of spatial distribution is, however, not always observed in the larvae of all decapod species appearing in Tomioka Bay (unpublished). The larvae of *S. globosa*, therefore, seem to remain actively within the region near MLWS line. The spatial distribution pattern of *S. globosa* larvae seems to be determined by not only the physical oceanographic factors, such as waves and water current, but also the combination of the scale and location of adult habitat and larval behavior. The spatial distribution is also considered as a species-specific characteristic.

The region, where *S. globosa* larvae remained, is located at only 500m from the habitat of adult crabs, and probably in the lower part of surf zone. It has been reported that the surf zone is an important area for fish larvae; and abundant fish larvae exist in this zone and its adjacent waters (SENTA and KINOSHITA, 1985; BENNETT, 1989). The region near MLWS line also seems to play a role as nursery area and to supply sufficient amount of food (phytoplankton, zooplankton, and detritus) for *S. globosa* larvae, although the existence of abundant fish larvae may give a risk of predation.

Most models of the previous studies (EPIFANIO, 1988; MCCONAUGHA, 1988) assume that the larvae migrate to the adult habitat first during late pelagic or post-larval stage. In *S. globosa*, zoeal and megalopal larvae always migrate between the littoral zone and the sublittoral zone by riding on the tidal current. This migratory process is first reported by the present study, and is smaller in scale than the previous models. The retention and migration of all larval stages seem to be necessary for *S. globosa* inhabiting littoral zone in order to recruit benthic population.

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コメツキガニ *Scopimera globosa* 浮遊幼生の分布と回帰

鈴木廣志・菊池泰二

要旨: 砂質干潟に穴居するコメツキガニの浮遊幼生の分布と回帰過程を明らかにする目的で、1980年および1981年の夏季に西九州天草下島の富岡湾において調査を行った。

コメツキガニの浮遊幼生は、水平分布では全令期にわたり成体生息地に近い大潮平均低潮線（MLWS）付近に最も多く分布した。垂直分布では、第1令および第2令ゾエア幼生では、底層への分布の偏りは若干弱いが、第3令ゾエア期以降になるとほとんどの個体が底層に分布する傾向を示した。これら水平、垂直分布様式は幼生の発育に伴って大きく変化することはなかった。富岡湾に出現した全ての幼生が、必ずしもコメツキガニ幼生と同じ分布様式を示さなかったことから、本種幼生のMLWS付近における集中化は、物理的にのみ起きているのではなく、塩分や光量等に対する幼生の反応習性の違いと水塊移動の複合結果として考えられる。また、コメツキガニ各令期のゾエア幼生は、毎日の潮汐流に乗り沿岸域と成体生息地の潮間帯域を、行き来していることが明らかになった。このような移動は、従来の幼生研究で想定されていた規模よりはるかに小さく、また未だ報告されていない特徴と考えられる。

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Vertical variations of larval release and settlement of the intertidal barnacle, *Chthamalus challengeri* Hoek*

Keisuke MORI**

Abstract: The intertidal barnacle, *Chthamalus challengeri* Hoek, is common in the high tide zone of rocky shores in Japan. The total number of settlers and total reproductive output of the species were estimated different tidal levels at Amakusa, Kyushu, Japan. The larvae of this species settled throughout the intertidal zone. However, most of the settlement was occurred near the *Chthamalus* zone, which is actual high tide zone. In the lower half of the *Chthamalus* zone (high density zone), larval settlement and total reproductive output were high because of high density. In contrast, in the upper half of the *Chthamalus* zone (upper zone), larval settlement was only moderate but total reproductive output was high because of existing largest barnacles. In the middle and lower intertidal zones (*Tetraclita* zone and limpet zone), most barnacles died before reproduction.

Contribution to the next generation (total reproductive output per unit area) from the upper zone was as much as that from the high density zone, even though the adult density and coverage at the reproductive season were lower. The ratio of total number of settlement to total number of the reproductive output was estimated as 0.107% of the total population of entire intertidal zone which differed greatly for various tide levels (0.02−64%). The ratio at the upper zone was 0.02%, which was the lowest value, and that of the high density zone was 0.079%. The highest value of this ratio was observed at upper *Tetraclita* zone.

1. Introduction

Many marine invertebrates have a planktonic larval stage (THORSON, 1950; CHIA, 1974). When studying the life history or population dynamics of benthic species with a pelagic larval stage, usually only the life cycle after settlement has been investigated, because planktonic stages make larval survivorship impossible to measurve. Also, mortality after settlement is more important than mass mortality in the planktonic stage in determining the total level of the population (THORSON, 1966). Ecological distribution of a benthic species is generally limited or determined by the settlement patterns with time and space. Therefore, detailed investigation of settlement pattern (spatial distribution and temporal variation in the amount of settlement) is needed to understand the population dynamics of a species.

ROUGHGARDEN and his colleagues proposed a demographic theory, which is basically constructed by two components (adults population and larval pool), for an open marine population with space-limited recruitment (ROUGHGARDEN *et al*., 1984, 1985; ROUGHGARDEN, 1986). However, they did not consider the vertical variation of population characteristics and life history traits, that varies greatly with tidal level (CONNELL, 1961a, 1961b; LEWIS and BOWMAN, 1975, and many others).

The acorn barnacle, *Chthamalus challengeri* Hoek, is common in the high tide zone on both exposed and sheltered rocky shores in Japan, and juveniles settle throughout the intertidal zone (MORI *et al*., 1985a, 1985b; MORI and TANAKA, 1989). An exposed natural rocky shore covering the whole intertidal zone was selected for the study. In this paper, vertical variation of total number of settlers and total reproductive output of *C. challengeri* subpopulation at several tidal levels are reported. Then, the population system model for an open population is proposed, and mechanisms for the persistence

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of this population are discussed.

2. Study sites, materials and methods

The main study station, E13, is located in the west coast of Tsuji-shima Island, Amakusa, Kyushu, Japan. Topography and the community structure at Tsuji-shima Island has been reported in previous papers (MORI *et al*., 1985a, 1985b; MORI and TANAKA, 1989; TANAKA *et al.*, 1985). Full details of environmental conditions and community structures of E13 station were given in MORI and TANAKA (1989).

The lower part of Fig. 1 shows the profile of the E13 station and the arrangement of the sampling quadrats. A belt transect method was adopted for sampling, and 22 quadrats (50 cm × 50 cm) were set up from the 290 cm tide level to the 0 cm tide level. Field population dynamics were investigated by photo-sampling the permanent quadrats. Permanent quadrats were set up on the shore with no conspicuous marks to eliminate artificial disturbances. However, I could find the position of every quadrat at every sampling time by using the photographs in which the crevices, bumps and small grooves of the rock surfaces have been taken. From April 1981 to August 1987, routine photo-sampling was carried out biweekly (every ebb tide of spring tide) in the warm seasons and monthly in the cole seasons. At a sampling time (one spring tide), about seven days continuous photo-sampling was carried out.

The field population of the barnacle *C. challengeri*, at various stations were estimated by photo-sampling. As described before, 50 cm × 50 cm permanent quadrats were set up at Stn. E13 and each quadrat was divided into twenty-five 10 cm × 10 cm sub-quadrats. Five to fifteen sub-quadrats were randomly selected, and monochrome photographs were taken from an overlooking position. In order to investigate the juveniles just after settlement, a close-up photograph at the center of each sub-quadrat was taken with a 35 mm camera using a 50 mm macrolens with a focal framer. By this method, half of the real size picture was documented on film, and clear printed copies could be obtained after high magnification enlargement. We could recognize cyprid larvae just after settlement in those photographs.

Reproductive output of the subpopulations at different tide levels was estimated as the number of eggs produced during the reproductive season from April to August in 1982. This gave a precise assessment of their respective contributions to the next generation. Possible number of eggs per unit area (10 cm^2) was estimated using the data of the population characteristics and reproductive characteristics of the barnacle. Reproductive characteristics of the barnacle, such as size-egg number relation, size-maturity relation, brooding percentage and number of broods were investigated in two tide levels, E13-2 and E13-4. Reproductive characteristics at E13-2 were applied to E13-1 and E13-3, while those at E13-4 were applied to the rest of the quadrats. Thus, the total reproductive output for E13 station was estimated from the data of reproductive output of each quadrat.

3. Results

Vertical distribution

The vertical distribution of coverage and density of *C. challengeri* in July 2, 1982 is shown in the middle part of the Fig. 1. High values of percentage cover (more than 50%) were recorded in the upper intertidal zone and this zone was recognized as the *Chthamalus* zone. No barnacle was found in zones higher than E13-1. Below E13-20, there was a calcareous algae zone with about 100% calcareous algae cover. *C. challengeri* has never been seen in this zone. The highest coverage (80%) was recorded in the quadrat E13-3, and henceforth decreased continuously to 10% at E13-7. The coverage never exceeded 10% in the middle and lower intertidal zones. The highest value of density was recorded at E13-5. Even though the peak of density was observed at a lower tide level than that of the coverage, the pattern of distribution remained same. In quadrats E13-19 and 20, variance was larger than the other quadrats because the barnacles showed patchy distribution within the quadrat (50 cm × 50 cm). Almost

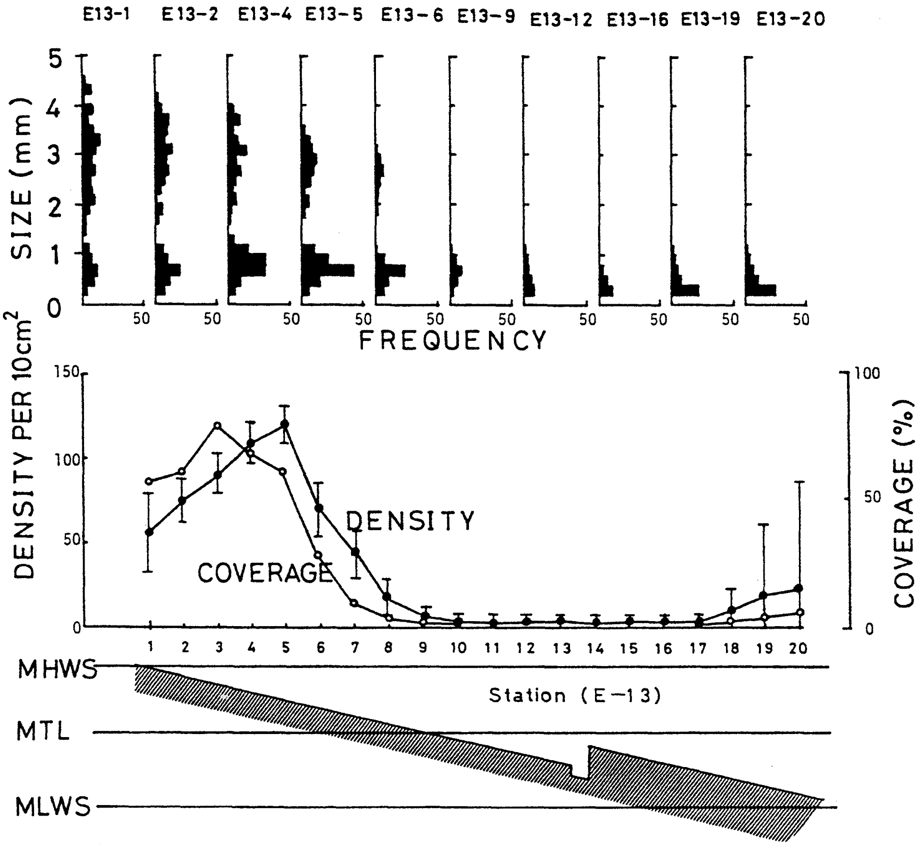

Fig. 1. Vertical variations of size composition, coverage and density of the barnacle at E13 station, in July, 1982, and profile of the E13 station. The size of barnacle is represented by length of the opercular portion. Vertical bar of density shows standard deviation.

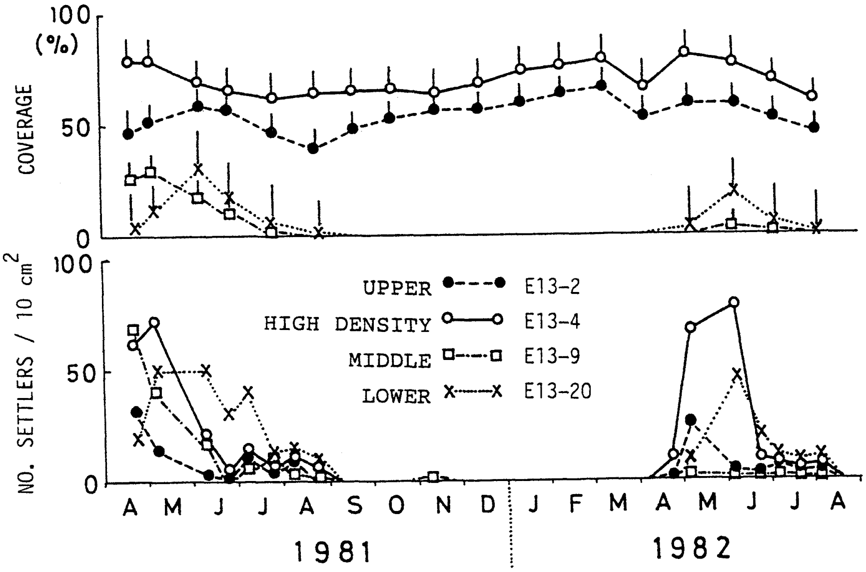

Fig. 2. Seasonal fluctuations of percentage coverage and settlement of *C. challengeri* at four tidal levels of E13 station, Tsuji-shima in 1981 and 1982. Each value for coverage shows the mean ±standard deviation.

the same density as the upper tide zone was recorded in some small quadrats (25 cm², 10 cm²) but no barnacles were recorded in other small quadrats.

The size frequency distribution of the barnacle at each quadrat is shown in the upper part of Fig. 1. Individuals with an opercular length greater than 1.4 mm (indicating the 1 +and older year classes were collected from E13-6 and upward. Larger individuals (based on the mean and maximum size) appeared at the higher tide levels. Small barnacles with an opercular length less than 1.2 mm (indicating the 0+ year class) occurred in all zones. In the upper zone, the larger size (0.6-0.8 mm) barnacles were the dominant size within the 0+ year class. Individuals of 0.2 mm to 0.4 mm occurred densely in the lower quadrats. The size range suggested that they settled within two weeks and the absence of large size classes suggest quick elimination of barnacles after settlement.

Seasonal changes of settlement and percent coverage

Fig.2 shows the seasonal changes of settle ment and percentage cover of *C. challengeri* at four tide levels, E13-2, 4, 9 and 20. Few barnacles settled even in mid-winter, and more than 99% of the barnacles settled from April to August. Generally, the settlement season is from April to August, and most settlement occurs between April and May. The beginning and peak of settlement at E13-20 were later than the rest of the tidal levels. Furthermore, the spatial distribution of settling at E13-20 was patchy.

At middle and lower tidal zones, almost all the barnacles died off by September, although in April 30% coverage was observed in the lower zone (E13-20). At E13-9, settlement was dense in 1981, but sparse in 1982. At the upper two tidal zones, coverage was observed to be high in all the years. Available space for settlement was 40% to 60% at E13-2 and 20% to 35% at E13-4. Number of recruits per available space at E13-4 was five to ten times more than that of E13-2 and E13-20.

Vertical variation of total number of settlements

Table 1. Total number of settlements at each subpopulation and that of E13 station during the settling season in 1982.

Sub-population	Total number of settle. /10 cm²	%
E13-1	22.4	2.5
E13-2	51.4	5.8
E13-3	93.3	10.5
E13-4	178.7	20.2
E13-5	196.5	22.2
E13-6	113.2	12.8
E13-7	79.3	8.9
E13-8	18.1	2.0
E13-9	9.3	1.1
E13-10	5.1	0.6
E13-11,14	2.2	0.2
E13-12,15	4.1	0.5
E13-13,16	2.7	0.3
E13-17	4.4	0.5
E13-18	27.1	3.1
E13-19	30.1	3.4
E13-20	47.3	5.3
Total	885.2	99.9
Mean settlements /10 cm²		52
Total settlements in St. E13 (0.5m × 8.5m =4.25 m²)		221,300

Total number of settlements of each sub population (E13-1 to E13-20) and that of Stn. E13 based on the data from 1982 are shown in Table 1. High values of total number of settlements were recorded in upper zone, and the highest settlings occurred at E13-4 and E13-5, which was located at the lower part of *Chthamalus* zone and below. No barnacles settled in higher tide levels than E13-1.

Reproductive output of each subpopulation

Table 2 shows the estimated reproductive output as the number of eggs per unit area during the reproductive seasons, based on the data from 1982. Details of reproductive traits and population characteristics of each subpopulation are under preparation. The total reproductive output of the subpopulation at 5 quadrats in the high tide zone (E13-1 to E13-5) reached 96% of that of whole population of Stn. E13. It is clear that the low and mid intertidal zone subpopulations hardly contribute to the next generation of

Table 2. Possible reproductive output per unit area during the reproductive season in 1982 and total reproductive output of E13 station.

Sub-population	No. of eggs per 10 ㎠	%
E13-1	99,742.0	12.1
E13-2	176,252.8	21.4
E13-3	188,756.9	23.0
E13-4	225,937.0	27.5
E13-5	96.741.5	11.8
E13-6	30,381.0	3.7
E13-7	123.6	0.02
E13-8	103.8	0.01
E13-9	201.5	0.02
E13-10	210.0	0.02
E13-11,14	317.2	0.04
E13-12,15	105.6	0.01
E13-13,16	97.7	0.01
E13-17	321.0	0.04
E13-18	274.1	0.03
E13-19	1,006.0	0.12
E13-20	1,247.3	0.15
Total	821,819.0	99.97
Mean output per 10 ㎠ in St. E13		48,342
Total output in St. E13 (0.5m x 8.5m =4.25㎡)		205,454,775

the population. In the *Chthamalus* zone, subpopulations in the upper quadrats (E13-1 to 3) characterized by low density, moderate coverage and large size of the barnacles by low density, moderate coverage and large size of the barnacles played an important role in the reproductive output compared to the lower quadrats (E13-4, 5) characterized by high density and high coverage.

Maximum total reproductive output (number of released nauplii) in 1982 of a subpopulation (10 ㎠) was estimated at about 200,000 and that in E13 station (4.25 ㎡) reached 220,000,000. Total number of settlements in 1982 at Stn. E13 (4.25 ㎡) was reached about 220,000 and maximum number of settlement of a subpopulation (10 ㎠) was estimated to about 200 (Table 1). At Stn. E13, about 0.1% of the total nauplii released were estimated to settle back. Regarding each subpopulation, 0.02% to 64% of nauplii did come back. Upper subpopulations from E13-1 to E13-3 show a low recruitment rate but high reproductive output. While middle and lower subpopulations below E13-5 show high recruitment rate but low reproductive output.

4. Discussion

Estimation of reproductive output with respect to tidal level is important to understand persistence of a population. A few studies have estimated the reproductive output of integrated barnacle population (Connell, 1970; Hines, 1979), but, unfortunately, none of them considered the significance of tide level difference.

In the present study, the contribution of subpopulations from upper to lower tide levels were represented by means of reproductive output of each subpopulations (Table 2). The contribution of subpopulations in the upper zone is disproportionately high. This is the result of the occasional and sparse settlement and low rate survival of barnacles in the middle and lower intertidal zones. In regard to the difference of total reproductive output per year within the *Chthamalus* zone, the subpopulation in the upper part of the *Chthamalus* zone had a larger reproductive output. At the upper *Chthamalus* zone (E13-1 to E13-3), subpopulations included a considerable number of large sized overwinter generations resulting from higher survival rates. These larger individuals produce more eggs and hence the total reproductive output per unit area was high. Based on the distribution of adults, *C. challengeri* can be regarded as an organism of the high intertidal zone. In the present study, population processes of the barnacle from the settlement of larvae, reproduction and mortality at different tide levels were investigated. Large variation of those population characteristics was observed among the subpopulations at different tide levels. Then, the predominance of the subpopulation in the *Chthamalus* zone was established by estimating its contribution to the total reproductive output.

The existence of a planktonic larval stages is an important feature in the benthic marine invertebrate life history, and it forms an open system (Roughgarden *et al.*, 1985, Roughgarden, 1986). The open system means

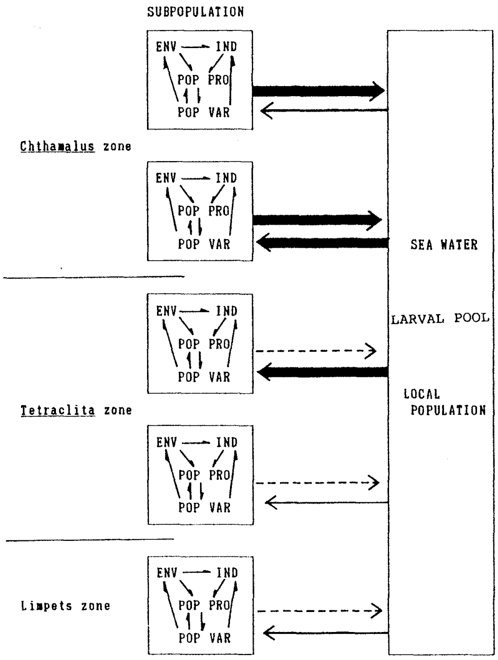

Fig. 3. The population system of *C. challengeri*. Arrows from the subpopulation to the larval pool indicate the relative amount of reproductive output (larval release), and reverse arrows indicate the relative amount of recruitment (settlement).ENV: Environmental properties, IND: Individual properties, POP PRO: Population processes, POP VAR: Population state variables Terminology was used following BERRYMAN (1981).

that planktonic larvae disperse widely (near and away) from the system where they were released. This can also enter into an another system of similar kind. The settlement rate on a particular substrate reflects the number of larvae in the water column and the time of exposure of the substrate to the water column (de WOLF, 1973; HAWKINS and HARTNOLL, 1982; GERACI and ROMAIRONE, 1982). A demographic theory for an open marine population with space-limited recruitment was proposed by ROUGHGARDEN and his colleagues, and is composed basically of two components, one, the subpopulation of adults, and two, their larval pool in water column (ROUGHGARDEN *et al*., 1984, 1985; ROUGHGARDEN, 1986). The main premise of the model, however, is that the total settlement rate into the system is proportional to the amount of unoccupied space (free space) in it. Although this assumption can not apply directly to the *C. challengeri* population because of wide variation of population characteristics according to tidal levels. However, the subpopulation-larval pool system for open populations is useful for population system of *C. challengeri* as a basic concept.

The structure and persistence mechanism of an open population (in the meaning of ROUGHGARDEN, 1986), is discussed using a new system model (Fig. 3). According to BERRYMAN (1981), the open population system is organized as a system of subpopulation systems. From this model, importance of the upper half of *Chthamalus* zone of this study area was demonstrated. Larval release is necessary for the persistence of a population. Release from the upper half of the *Chthamlus* zone was as high as from the lower half of the *Chthamalus* zone (high density zone). In the upper half of the *Chthamalus* zone, larval settlement was only moderate and initial mortality was high, but subsequent survivorship was very high and individuals showed high longevity. Since the growth was continuous, some barnacles reached large size, and they could produce a large number of eggs. This system model analysis indicated that although the abundance of the upper half of the *Chthamalus* zone was only moderate this zone was important in maintaining the population.

As shown in Fig. 3, The values of population parameters varied greatly with tide level, and therefore, the population parameters from only one point (main habitat, or distribution center) may differ from the whole population system. Moreover, since the population traits are functioned by biotic and abiotic environmental factors, it is suggested that the local population should be divided into representative subpopulation. And also, structure of subpopulation has to be measured quantitatively at each tide level that based on population characteristics and environmental conditions.

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イワフジツボの幼生放出と定着の垂直変異

森　　敬介

潮間帯性小型橈脚類イワフジツボ（*Chthamalus challengeri* Hoek）は高潮帯を代表する種であるが、幼生は潮間帯全域に定着している。九州西岸、天草（潮位差3.5m）の緩傾斜の岩を17の潮位に細かく分割し、イワフジツボの個体群動態を調査した。潮位ごとの総定着量と総繁殖量を推定し、個体群維持における生息潮位の重要性を論議した。本調査地においては繁殖期は３月から８月であった。幼生定着の垂直分布中心はイワフジツボ成体の高密度域およびその下部であった。一方、総繁殖量の垂直分布中心は、イワフジツボの高密度域およびその上部（最上部）であった。最上部は成体密度は低いが大型個体が出現した。中・低潮部では定着が少なく、空間的ばらつきや年変動が大きかった。また翌年の繁殖まで生存できる個体は稀であった。潮間帯全域での幼生放出に対する定着の割合は0.1％であったが、各潮位ごとでは0.02-64％と非常にばらつきが大きかった。次世代への貢献に関しては、多数の定着と多数の幼生放出がみられた高密度域とならんで、少数の定着ながら多数の幼生放出がみられた最上部が重要な役割を果たしていた。

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Société franco-japonaise d'océanographie, Tokyo

Early life history and oceanic migration of the eel, *Anguilla japonica* *

Katsumi TSUKAMOTO** and Akima UMEZAWA**†

Abstract: The first attempt to outline the whole aspects of early life history and migration mechanisms of the eel *Anguilla japonica* was made by synthesizing the recent information on the otolith microstructure of 1045 fish and the offshore collection data of 110 leptocephali and 9 glass eels. Waters east of Philippine, 10°–20°N, 140°–150°E, were one of the most possible spawning areas of *A. japonica*. Age determinations of leptocephali and glass eels showed that *A. japonica* spawned in April-November with a peak in August. Larvae grew linearly at 0.56mm/d until 45mm in TL and 74d in mean age. Analysis of otolith increment width showed that metamorphosis occurred at 85 d and 61.3mm corresponding to a zone of wider increments (2–4 μm) in the sagitta. Metamorphosis lasted for 12 days with body shrinkage at − 0.22mm/d. A negative linear relationship between age at metamorphosis and otolith growth rate suggested that leptocephali with a larger growth rate began to metamorphose at a younger age. Leptocephali were slowly transported northwestward in complicated eddies from spawning area to the origin of the Kuroshio Current for 2–3 months. Larvae were entrained by the strong Kuroshio Current and transported northward for 2–27 days to exit from it after completion of metamorphosis. Fish metamorphosing at a younger age were transported a shorter distance and exit from it at lower latitude. More glass eels recruited at a full and new moon than at other lunar phases. Age at metamorphosis was positively correlated with age at recruitment. Age at recruitment to the estuary or the time required for oceanic migration was 4–7 months and gradually increased with the sampling date or the recruitment timing, whereas body size of the glass eel was roughly constant, about 55–60mm TL. Birth date and recruitment timing positively correlated. Thus, the earlier-born fish or fish with the larger growth rate metamorphosed and recruited earlier at lower latitude, at a younger age and with more advanced pigmentation, but with a constant body size.

1. Introduction

Migration study is one of prerequisites to determine the recruitment mechanism of a fish. In spite of its commercial importance in Eastern Asia, the recruitment mechanism of a catadromous eel, *Anguilla japonica* Temminck et Schlegel, is poorly known, since knowledge of the early life history and larval migration of this species is still lacking, *e.g.* its spawning place and season, larval growth and metamorphosis, larval transportation and inshore migration.

The objective of this study is to outline the whole aspects of early life history and migration mechanisms of *A. japonica* from its spawning ground offshore to coastal waters by synthesizing the recent information based mainly on the otolith microstructure and the offshore collection data of larvae.

2. Materials and Methods

For 9 years from 1982 to 1990, a total of 1012 glass eels*** and elvers*** were collected at 13 stations in Taiwan, Korea and Japan (TSUKAMOTO, 1990; UMEZAWA, 1991). Thirty three leptocephali*** obtained in eastern waters off the Philippines and Taiwan in 1986 and 1990 were also analyzed (KAJIHARA,

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*** "Leptocephalus" means larva before and during metamorphosis, while "glass eel" is a juvenile after metamorphosis without pigmentation except the spots at skull, rostral and caudal regions (stage IV−V after BERTIN, 1956). "Elver" has more developed pigmentation (stage VI).

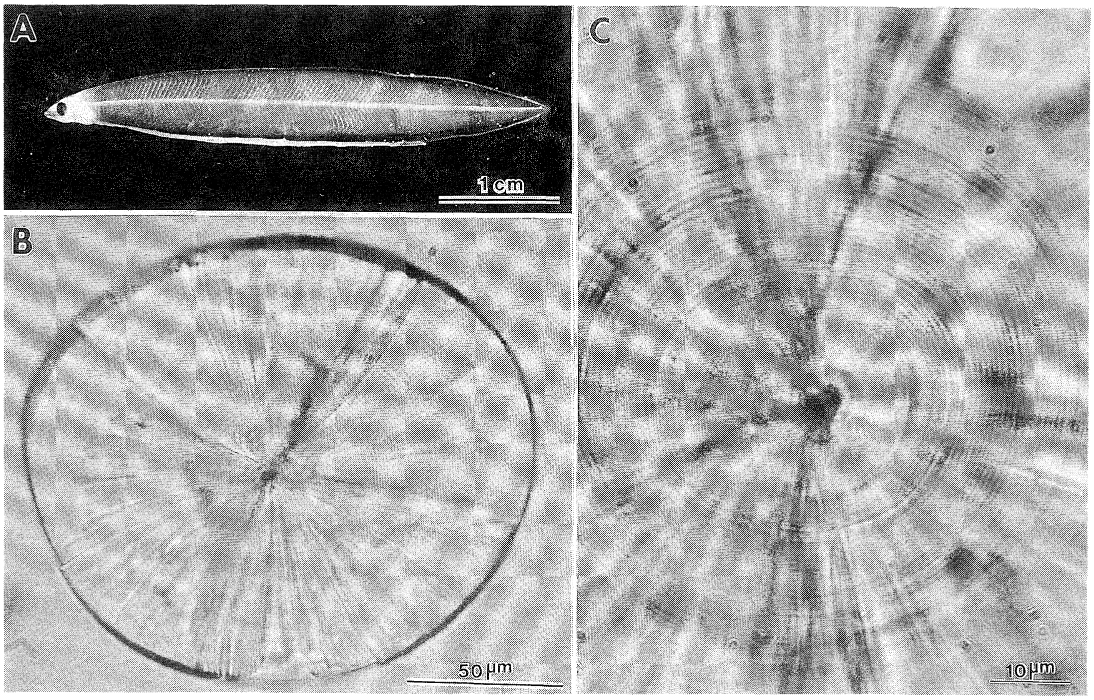

Fig. 1. A: *Anguilla japonica* leptocephalus of 41.0 mm in TL (Specimen No. 10) collected at 18°59.1′N, 129°13.5′E, 23 September 1986. B: Sagitta of *A. japonica* leptocephalus of 45.9 mm in TL, 78 d old (Specimen No. 17). C: Central region of sagitta of *A. japonica* leptocephalus. Otolith daily increments are shown around the core of 5–10 μm diameter (dark region in the center).

1988; OZAWA *et al.*, 1991, TSUKAMOTO *et al.*, 1992).

Sagittal otoliths were extracted and mounted distal side up on a glass microscope slide with a drop of epoxy resin. They were ground with emery paper #1200–#12000 to just before the sagittal plane with the otolith core, and etched in 1 % HCl solution for 1–3s. A bipartite structure of a narrow opaque band (discontinuous zone) and adjacent wider translucent band (incremental zone) was regarded as one otolith increment or ring (Fig. 1). Increments were traced at ×900–1500 under a light microscope with a camera lucida (TSUKAMOTO, 1989). Fish were aged by counting daily increments outside the hatch ring of 8.3 μm diameter (UMEZAWA *et al.*, 1989). The birth date of each specimen was backcalculated from the estimated age and the date of sampling. Changes in increment width from the otolith core to the edge were also examined based on the increment trace of some 300 glass eels and elvers and of 33 leptocephali by measuring the radius of each increment along the 'longest radius' of an otolith (UMEZAWA, 1991, see Fig. 1).

3. Results and Discussion

Breeding place

Spawning areas of the Atlantic eel were outlined in the early part of this century by SCHMIT (1922, 1925), whereas that of the Japanese eel in the Pacific Ocean has not yet been determined. Relatively little is known of *A. japonica* leptocephali compared to Atlantic eels; *i. e.* the number of *A. japonica* leptocephali collected is only 110 individuals (MATSUI *et al.*, 1968; TABETA and TAKAI, 1975a, b; TANAKA, 1975; TAKAI and TABETA, 1976; TABETA and KONISHI, 1986; KAJIHARA, 1988; OZAWA *et al.*, 1989; OZAWA *et al.*, 1991; TSUKAMOTO *et al.*, 1992) and its smallest recorded

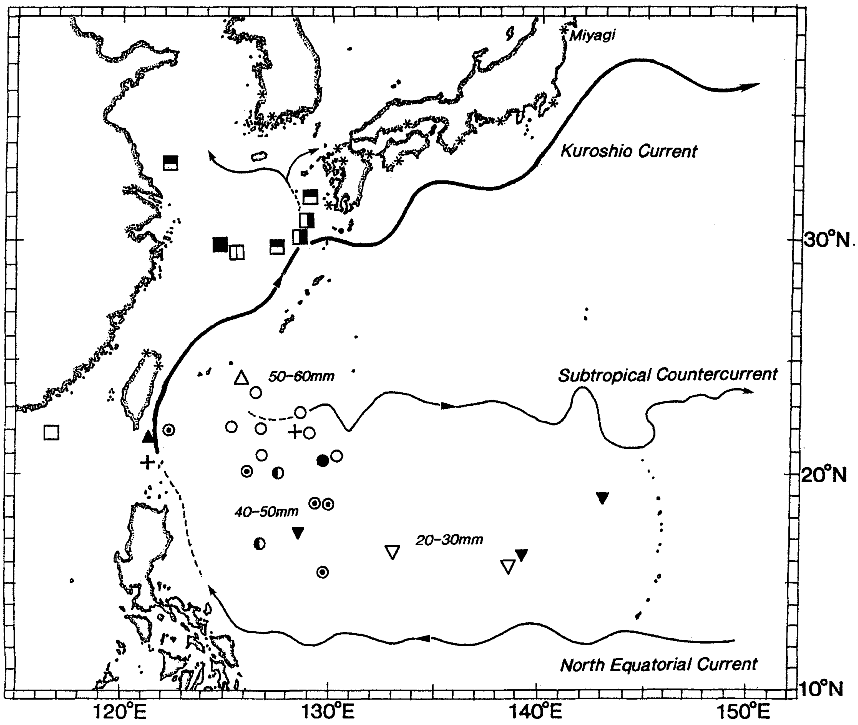

Fig. 2. Larval migration and recruitment of *A. japonica* to coastal waters. Squares indicate offshore collections of glass eels (solid square, SHOJIMA, 1966; square with vertical bar. SHOJIMA, 1967; solid half upside, TSUKAHARA, 1971 cited in TABETA, 1981; open square, TABETA and TAKAI, 1973; solid half rightside, SHOJIMA, 1990). Crosses are metamorphosing larvae (TABETA and TAKAI, 1975a; TANAKA, 1975 cited in TABETA and TAKAI, 1975b). Other symbols indicate leptocephali (solid triangle, MATSUI *et al*., 1968; open circle, TANAKA, 1975; semi solid circle, TAKAI and TABETA, 1976; open triangle, TABETA and KONISHI, 1986; double circle, KAJIHARA, 1988; inverted triangle, OZAWA *et al*., 1989; inverted solid triangle, OZAWA *et al*., 1991; solid circle, TSUKAMOTO *et al*., 1991). Numerals indicate TL, Asterisks show the sampling locations of glass eels recruited to the coastal waters.

size at capture was 19.5 mm TL (OZAWA *et al*., 1991), while more than twenty thousand Atlantic eels have been obtained (BÖETIUS and HARDING, 1985; KLECKNER and MCCLEAVE, 1985) and its minimum size was as small as 3.9 mm TL, corresponding to 4 days after hatching (WIPPELHAUSER *et al*., 1985).

Developing leptocephali of *A. japonica* of about 50–60mm in TL were collected in eastern waters of Taiwan, 20°14′–23°40′N, 125°01′–130°00′E in November-December (TANAKA, 1975; Fig. 2). In the more southern waters, east of Luzon, 15°56′–22°02′N, 122°25′–129°37′E, smaller larvae of ca. 30–50mm with an age of 67–78 days after hatching were collected in September (KAJIHARA, 1988; TSUKAMOTO *et al*., 1989). Based on these results and the water flow in this area, the breeding of *A. japonica* was predicted to occur in June or July farther east than has been surveyed to date (KAJIHARA, 1988; TSUKAMOTO *et al*., 1989). In fact, smaller larvae of ca. 20–30mm were collected in a more eastern area, 15°46′–16°22′N, 132°59′–138°43′E in June-July (OZAWA *et al*., 1989). More recently, 21 small leptocephali of ca. 20mm were obtained in only one haul at 16°17′N, 139°12′E (OZAWA

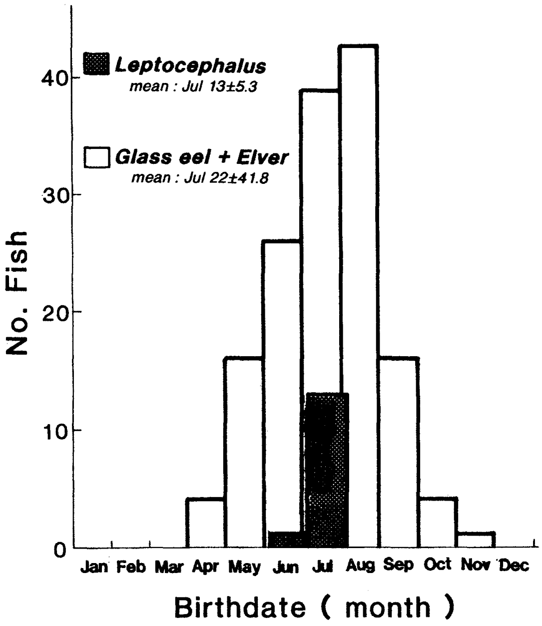

Fig. 3 Birth dates of the glass eels and elvers collected at the estuaries of the Japanese coast (TSUKAMOTO, 1990). Heavily shaded area shows the birth date distribution of leptocephali collected in the Western North Pacific (TSUKAMOTO *et al.*, 1989).

et al., 1991: Fig. 2). A wider area, especially to the east (10°–20°N, 140°–150°E) should be investigated in May-July to determine the spawning area of *A. japonica*.

Spawning season

The age of the glass eel upon arrival at the Japanese coast was roughly constant, 218±29 d (mean±SD) for 149 individuals (TSUKAMOTO, 1990). Glass eels arrived at Taiwan at an age of 100–140 d (40 fish; UMEZAWA and TSUKAMOTO, 1990) and 95–175 d (61 fish; TZENG, 1990). The birth date estimated for each individual ranged from April to November and the mean was 22 July (Fig. 3; TSUKAMOTO, 1990). Later examination of 1012 glass eels including samples from Taiwan, Japan and Korea showed that the age at recruitment (age upon arrival at the coast) was 117±12.7 d (about 4 months) and the birth date ranged from June to November with the peak in August (UMEZAWA, 1991). Although the estimated ages at recruitment were different among investigators, the peak of the hatch date (August) coincided with one another (Fig. 3). Age determination of *A. japonica* leptocephali collected in the Western North Pacific in September 1986 showed that their birth dates ranged from 28 June to 18 July 1986 with a peak in mid July (TSUKAMOTO *et al.*, 1989). The estimated birth date was consistent with that of the glass eel (Fig. 3). The birth date can be regarded about the same as the spawning time since the duration of the egg stage of this species was less than 2 days (YAMAMOTO *et al.*, 1974; SATO, 1979). Therefore, it can be summarized from these results that *A. japonica* spawns in summer and the offspring takes ca. 4–7 months to migrate from the spawning area to the estuaries of East Asia. This is in striking contrast to the common belief *Anguilla japonica* spawns in winter and that the larvae take 1 year to recruit to the Japanese coast (MATSUI, 1952; TABETA, 1981).

The long estimated duration of the spawning season (*e.g.* April-November; 7 months in TSUKAMOTO, 1990) should not be caused by the counting error in age determination since the latter did not exceed 10 % (about 20 days at most for glass eel). Multiple subpopulations of adult eel might prolong the duration of estimated spawning season.

The reported peak spawning of Atlantic eels was February and April for *A. rostrata* and *A. anguilla*, respectively (HARDEN JONES, 1968; BÖETIUS and HARDING, 1985; WIPPELHAUSER *et al*, 1985), which is earlier than that of *A. japonica* estimated here. Assuming that otolith increments were formed daily, the birth dates of the leptocephali collected in the southwestern Sargasso Sea in August 1984 were estimated to be May-June 1984 for both *A. rostrata* (mean TL, 34mm) and *A. anguilla* (32mm) larvae (CASTONGUAY, 1987). *A. rostrata* (mean TL, 36.8mm) and *A. anguilla* (53.6mm) collected in the Atlantic Ocean and the Mediterranean Sea in December 1989 and January 1990 hatched in September –October 1989 (TSUKAMOTO *et al.*, 1991). Further age determinations, coupled with experimental validation of the frequency of otolith increment formation, will be needed to explain this disparity.

Silver eels of both *A. japonica* and *A. anguilla* begin their downstream migration in autumn. Based on their estimated spawning dates, the migration of silver eels from freshwater to the breeding place takes ca. 10 months for *A. japonica*, whereas *A. anguilla* requires only ca. 6 months to the Sargasso Sea, if it is assumed that the peak spawning is in April.

Growth

Age and body length of artificially hatched preleptocephali (2–6mm. 0–6d) and field collected developing leptocephali (ca. 20–50 mm, 25–78d) were linearly related, suggesting that early growth of eel larvae was linear with a growth rate of 0.56mm/d (Fig. 4, TSUKAMOTO *et al.*, 1989; UMEZAWA and TSUKAMOTO, 1992a). After metamorphosis, the body lengths of glass eels and elvers became relatively constant, ca. 60mm (UMEZAWA and TSUKAMOTO, 1992a). When examined in detail however, glass eels shrank 0.22mm/d (UMEZAWA and TSUKAMOTO, 1992b; see below) and body lengths of elvers increased 0.09mm/d till ca. 150 d (UMEZAWA and TSUKAMOTO, 1992a).

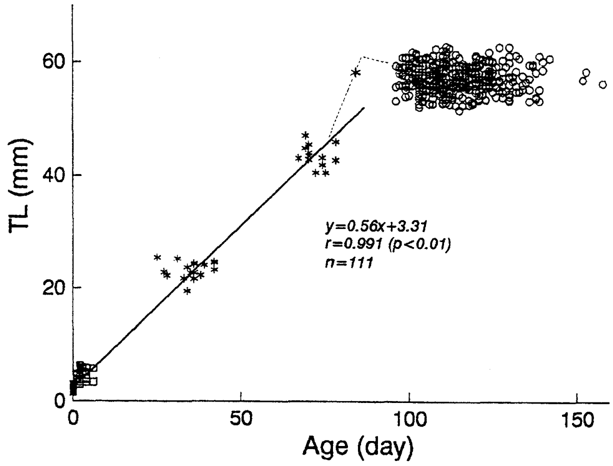

Fig. 4 Early growth of *A. japonica*. Asterisks indicate leptocephali collected offshore, and circles, glass eels and elvers at recruitment. Squares are preleptocephali artificially hatched. Solid line was fitted to data of preleptocephali and leptocephali. Dashed lines were drawn by hand between leptocephalus and glass eel stages.

The growth rate of glass eels recruited to Taiwan was estimated with otolith increments as being 0.35–0.60mm/d (TZENG, 1990), a value which would have included the shrinkage period during metamorphosis.

The growth rate of Atlantic eel leptocephali (both of *A. rostrata* and *A. anguilla*) was estimated via otolith microstructure as being 0.38mm/d (CASTONGUAY, 1987), a value which is smaller than that of *A. japonica*. However, a more recent otolith examination showed that growth rates of *A. rostrata* (0.46 mm/d) and *A. anguilla* (0.62mm/d) were similar to that of *A. japonica* (TSUKAMOTO *et al.*, 1991a). BÖETIUS and HARDING (1985) concluded that there was no differential growth rate in 0-group leptocephali of *A. rostrata* and *A. anguilla*. However, estimates of growth rates based on regressions of TL on date of capture are indirect and have tendency to underestimate (CASTONGUAY, 1987). In fact, the larval growth of the Atlantic eels previously reported (0.17–0.24mm/d; BOETIUS and HARDING, 1985; KLECKNER and MCCLEAVE, 1985; WIPPELHAUSER *et al*, 1985) was mauch lower than that estimated from otolith examination (0.38–0.62mm/d: CASTONGUAY, 1987; TSUKAMOTO *et al.*, 1989; TSUKAMOTO *et at.*, 1991; UMEZAWA and TSUKAMOTO, 1992a;). Future research should include intensive age determination of a wide range of lengths of specimens collected from various area in the north Atlantic and the Mediterranean Sea at different times of the year.

Metamorphosis

The change in otolith increment width from the center to the edge showed a similar pattern in both *A. japonica* glass eels and elvers examined (TABETA *et al.*, 1987; UMEZAWA and TSUKAMOTO, 1992b): the width was roughly constant, ca. 1 μm, from 0 d until 74 d increasing rapidly to a peak of ca. 4 μm at 85 d, and then decreasing to be constant again from 97 d until the otolith edge (Fig. 5). Every glass eel and elver examined, even the youngest glass eel (95d, 58.8 mm), had such a "Wide Increment Zone (WIZ)", whereas there was no such WIZ in every leptocephalus at developing stage. This suggests that the WIZ is formed during metamorphosis from the leptocephalus to the glass eel (Fig. 5). The largest leptocephalus examined (58.2 mm, 84 d) had several wide increments at the peripheral part of the otolith, suggesting that this specimen was just starting to form a part of the WIZ. In Fig. 4, this fish had a positive residual on the growth regression line for leptocephali, which suggests that leptocephali might grow rapidly at the end of the developing stage until the beginning of metamorphosis, although this assumption was based on only 1 specimen. Otolith radius (Y: μm) and total length (X: mm) were linearly related in the leptocephali ($Y=1.89X-1.60$, $r=0.988$, $N=110$; UMEZAWA and TSUKAMOTO, 1992a). Glass eels and elvers also presented a linear relationship but with a different regression coefficient ($Y=2.89X+7.99$, $r=0.875$, $n=1349$; UMEZAWA and TSUKAMOTO, 1992a). These considerations lead to the conclusion that leptocephali begin to metamorphose at the mid point of WIZ of the largest increment width, at a mean age of 85d, and that body size shrinks afterwards (Fig. 5). Assuming that the latter half of the WIZ represents metamorphosis, it lasts for 12 d. Duration of metamorphosis estimated in the study does not differ from that of beach conger *Conger japonicus*, 11–14d (OCHIAI *et al.*, 1978). The total length of glass eel (Y: mm) and the days (X) after the mid point of WIZ or the beginning of metamorphosis showed a negative linear relationship ($Y=-0.22X+61.3$, $r=0.519$, $n=40$; UMEZAWA and TSUKAMOTO, 1992b). The equation suggests that the size of the leptocephalus at the maximum developing stage would be 61.3mm in TL and the eel shrank at 0.22mm/d in length after the beginning of metamorphosis until the elver stage (Fig. 5). This estimation is consistent with the collection data: the largest size of leptocephalus ever collected was 59.2mm in TL (TABETA and KONISH, 1986), the 4 metamorphosing larvae ranged from 52.0 to 60.2mm, 9 glass eels collected at

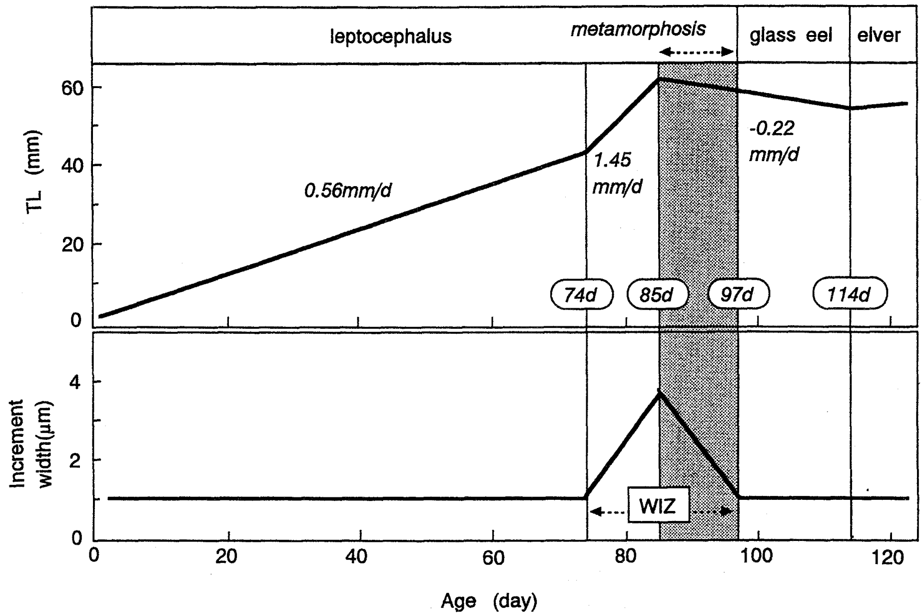

Fig. 5 Correspondence between early growth pattern of *A. japonica* and change in otolith increment width against age, or increment number from the inside to the edge. A zone of wide increments (WIZ) occurred between 74 and 97 d in a series of otolith increment width from the core to the edge. Metamorphosis started at 85 d or the mid point of WIZ showing the largest value of increment width.

open sea, 53.0–61.2mm (SHOJIMA, 1966, 1967; TSUKAHARA, 1971; TABETA and TAKAI, 1973; TABETA, 1981; SHOJIMA, 1991), and 260 glass eels obtained at surf zone of Kanagawa, Japan, 52.1–62.4mm (UMEZAWA, 1990). There was a negative linear relationship between age at metamorphosis (the mid point of the WIZ) and otolith growth rate (UMEZAWA and TSUKAMOTO, 1992b). This shows that leptocephali with a larger growth rate begin to metamorphose at a younger age, since otolith growth is positively related to body growth (see above).

The leptocephalus phase of *A. rostrata* is believed to last for 10–12 months (SCHMIDT, 1922), or 8–12 months (KLECKNER and MCCLEAVE, 1985). *A. anguilla* is supposed to metamorphose into the glass eel stage 2.5–3 years after hatching (SCHMIDT, 1922, 1925), 3–4 years (UTRECHT and HOLLEBOOM, 1985), or 12–15 months (BÖETIUS and HARDING, 1985). LIEW (1974) suggested that *A. rostrata* spent 2 years in the sea, and *A. anguilla*, 3 years. A metamorphosing leptocephalus of *A. anguilla* (63.0mm TL) collected in the Mediterranean Sea in January 1990 had only 102 increments (presumed daily) in the otolith (TSUKAMOTO *et al.*, 1991), suggesting a much shorter duration (3–4 months) of leptocephalus stage than has been previously reported (TSUKAMOTO *et al*, 1991). The duration of the leptocephalus phase and the time required for oceanic migration vary greatly among *A. japonica* and both Atlantic species. Such disparity could well be the subject of future research.

Oceanic migration

The process and mechanism of oceanic migration by eels is poorly known (OZAWA *et al.*, However, it can be assumed at least from the present collection data on *A. japonica* leptocephali that spawning may occur in the waters east of the Philippines (see above, Fig. 2). Accordingly, oceanic migration of the eel from the spawning area to an estuary can be roughly divided into three periods: (1) long drift from the spawning area to the origin of the Kuroshio current, (2) rapid northward transport in the Kuroshio, and (3) inshore migration toward the estuary after the exit from the Kuroshio.

Long Drift: Ocean circulation is complex in waters east of Taiwan and the Phillipines, lat. 15°–25°N and long. 125°–135°E (NITANI, 1972; HASUNUMA and YOSHIDA, 1978), where the eel spends its leptocephalus stage. Based on the dynamic topography of the sea surface relative to the 1000 db surface (HASUNUMA and YOSHIDA, 1978), small leptocephali (20–30mm TL) were caught in the southern slope of the north equatorial ridge of the geopotential anomaly, or near the northern boundary of the North Equatorial Current (see Fig. 2). Old leptocephali just before metamorphosis (*e. g.* 77–87d, 50–60mm) and metamorphosing larvae were recorded just east of the origin of the Kuroshio (Fig. 2). The eel larvae might be slowly transported northwestward in complicated eddies from the spawning area to the origin of the Kuroshio (OZAWA *et al.*, 1992). Duration of the drift in this area is supposed to be 2–3 months before metamorphosis (UMEZAWA and TSUKAMOTO, 1992b). If it is assumed that the spawning area is located 10°–20°N, 140°–150°E, larvae would drift through 2000–3000 km in distance at ca. 40 km/d.

Kuroshio Transport: All of the leptocephali which have been collected were found east of the Kuroshio, whereas glass eels collected offshore were recorded west of the Kuroshio (Fig. 2; SHOJIMA, 1966 1967; TSUKAHARA, 1971; TABETA and TAKAI, 1973; SHOJIMA, 1990). Although no eel larvae have ever been collected in the Kuroshio, it is probable that larvae which arrived at waters just southeast of Taiwan, the beginning of the Kuroshio (NITANI, 1972), would be entrained by the strong Kuroshio and transported northward. Timing and developmental stage at the time of entrainment to the current would vary in each individual because the transport in eddies during long drift would be entirely passive and indefinite. However, the exit from the Kuroshio may occur at the same stage in all individuals, *i. e.* during or just after metamorphosis. Buoyancy would be lost during metamorphosis because of decreases in the area of the body surface and water content (Callamand, 1943) and increases in specific gravity (Sinha and Jones, 1975; Hickman, 1981). *Conger japonicus* began active swimming when metamorphosis started (Ochiai *et al*, 1978). The records of offshore catches of glass eels and metamorphosing leptocephali (Fig. 2) suggest that the eel, in general, begins metamorphosis in or just east of the Kuroshio, and completes it in the current (Umezawa and Tsukamoto, 1992b) or in the marginal waters of the continental shelf (Tabeta and Takai, 1973).

Kuroshio Transport Distance, the distance an eel might be transported by the Kuroshio from its origin (0 km) to a point of exit, varies from 250 km to 3000 km for fish recruited to Taiwan and Miyagi in Japan (the northernmost sampling station in Fig. 2), respectively. Since the velocity of the Kuroshio is ca. 2–3 kt (Nitani, 1972), the duration of Kuroshio transport is estimated to be 2–27 days. The Kuroshio Transport Distance and age at metamorphosis of fish collected at each coastal station showed a positive linear relationship except for samples from Korea and Miyagi whose stations do not face the Kuroshio directly. This suggests that fish metamorphosing earlier would be transported a shorter distance and exit from the current at a lower latitude.

Inshore Migration: How the eel migrates inshore after exit from the Kuroshio is unclear. Since a total of 9 glass eels has ever been collected offshore (Fig. 2), there is insufficient information to explain the process of inshore migration of a billion glass eels recruiting to coastal waters of East Asia. Although glass eels collected offshore were recorded at comparatively shallow depths near the surface (Shojima, 1990), there remains the possibility that settlement to the bottom occurred after metamorphosis, followed by movement inshore along the sea bed. However, the glass eel at recruitment had no characteristic microstructure in the otoligh, *e. g.* check, corresponding to the settlement to the sea bed accompanied by a drastic decrease in environmental temperature of about 20℃.

Otolith examination suggests that mean duration between metamorphosis and recruitment to a coast is 20–32 days (Umezawa and Tsukamoto, 1992b). Assuming that the cruising speed of glass eels (60 mm TL) is 120mm/s (2 TL/s), and that active swimming occurs only 16 h at night since the eel is nocturnal (Umezawa, 1991), it was calculated that a glass eel might migrate 138–221 km distance by itself after exit from the Kuroshio following metamorphosis. This estimation might explain a distance of 56–206 km from the Kuroshio flow axis to each sampling station along the coast. However, the situation may not be so simple because the eel would not swim directly to a coast, and countercurrents of the Kuroshio and complicated coastal currents might affect the inshore migration.

The utilization of tidal current in the entry to estuaries was reported in *A. rostrata* (McCleave and Kleckner, 1982; McCcleave and Wippelhauser, 1987) and *A. anguilla* (Creutzberg, 1958). Similarly, the recruitment of *A. japonica* to the estuary might be controlled by a tidal rhythm. Birth dates of the glass eels on arrival to the coast increased in stepwise following the sampling date, and the duration of each step was about 14 d which coincided with the half of lunar phase (Umezawa, 1991). Age at recruitment and tidal range were negatively correlated. Furthermore, CPUE and tidal range showed a positive linear relationship. These results suggested that the glass eels recruited to the coast at the full or new moon, and

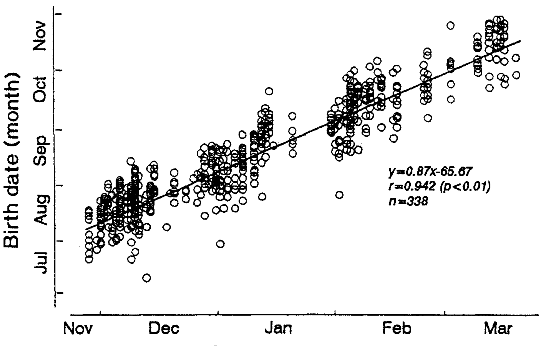

Fig. 6 Relationship between sampling date and birth date of glass eels collected on the Japanese coast.

stayed there until the next spring tide (Umezawa, 1991).

Migration mechanism

Clear correspondence was observed between birth date and the time of arrival at the coast (Fig. 6; Tsukamoto, 1990; Umezawa, 1991). A similar relationship was confirmed in fish recruited to Taiwan (Tzeng, 1990). The age at metamorphosis was positively correlated with the age at recruitment to the coastal waters of Taiwan and Japan (Fig. 7; Umezawa and Tsukamoto, 1992b). The age of glass eels or the time required for oceanic migration increased gradually with the date of recruitment (Tsukamoto, 1990). However, the body size at recruitment was roughly constant, about 55–60 mm TL (Tzeng, 1990; Umezawa, 1991). The growth rate of glass eels recruited to Taiwan was inversely correlated with age at recruitment, suggesting that fast-growing larvae took a shorter time for oceanic migration than slow-growing larvae (Tzeng, 1990). Pigmentation developed at a lower latitude (Tsukamoto, 1990). Thus, the migration mechanism of the eel *A. japonica* can be summarized as follows: The earlier-born fish or fish with a faster growth rate metamorphose and recruit earlier, at a younger age to the lower latitude with the more advanced pigmentation, but with a constant body size (Fig. 8; Tsukamoto, 1990; Umezawa, 1991).

Fig. 7. Relationship between the age at metamorphosis (the mid point of WIZ) estimated by otolith microstructure and the age at recruitment in the glass eels collected in the coastal waters of Taiwan and Japan.

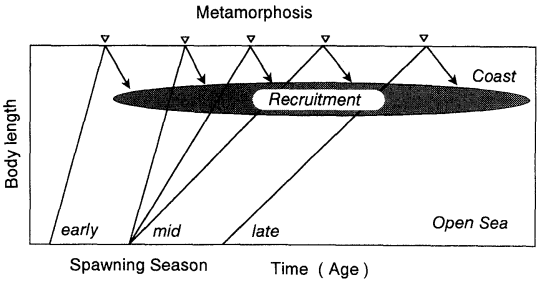

Fig. 8. Migration mechanism of *Anguilla japonica*, with special reference to the correspondence among birth date, growth rate and timing of recruitment. Solid lines with arrows each represent a diagrammatic growth curve of an individual for each timing of birth.

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Recruitment of soft-sediment infaunal invertebrates : the importance of juvenile benthic stages*

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Abstract: Spatial and temporal variability of marine benthic communities depends, to a great extent, on the success or failure of recruitment, which is influenced itself by all the events that occur during the course of ontogenetic development. In species with a benthoplanktonic life cycle, several critical stages may be identified: (1) maturation of sexual products, (2) spawning, (3) planktonic larval phase, (4) larval settlement and metamorphosis, and (5) postlarval or juvenile stages. Invertebrates with a holobenthic life cycle do not undergo a larval phase nor metamorphosis, and the first free-living stages are benthic juveniles.

Settlement is often a transient phenomenon and settling organisms are usually found in the meiofaunal size range. Hence, the quantitative assessment of young bottom stages requires both small sieving mesh sizes and short sampling intervals, which explains, to a large extent, our lack of knowledge of settlement patterns of benthic invertebrates in the field. High mortality rates have been recorded during early benthic life of molluscs and polychaetes: 70–99% of the settled individuals disappear within about three months. This juvenile mortality is likely to be of the same order of magnitude as larval mortality in the plankton.

The growth rates of juveniles may be low, especially when settlement coincides with adverse thermal and/or nutritive conditions; in such a case, juveniles may stay within the meiofaunal-size class for several weeks or months. Estimates of production and annual P/$\bar{B}$ ratios in populations including the juvenile stages show that the productivity of benthic macrofauna is considerably underestimated by using only 1 mm-sieves.

1. Introduction

The dynamics of natural marine benthic communities primarily results from two antagonistic processes: (1) the supply of larvae, and (2) the mortality which occurs during the whole benthic life of settled organisms. As it is generally agreed that marine invertebrates experience extremely high mortality during the early stages of their life history (THORSON, 1950), the maintenance as well as the balance of composition of benthic assemblages depend, to a great extent, upon the survival/mortality ratio of larvae and juveniles (PÉRÈS, 1971; MILEIKOVSKY, 1974a). Hence, most of the temporal variability of benthic communities may be ascribed to the success or the failure of recruitment.

Recruitment is not, however, a true life-history stage, but is observer-defined (KEOUGH and DOWNES, 1982; BUTMAN, 1987); it is rarely measured at the time of larval settlement, but instead when settled organisms have survived and brown to a size collected by some sampler (HADFIELD, 1986). Therefore, the number of recruits present at a given time reflects all past events since the elaboration of gametes in the parental organisms. In his pioneering work on larval ecology of marine bottom invertebrates, THORSON (1950) stated that the heavy waste found in most marine invertebrates takes place during the free-swimming, pelagic larval life. He later (THORSON, 1966) acknowledged that survival rates after settlement might be extremely low. This implies that the causes of recruitment variability must be researched, not only during the larval period, but also during the early post-settlement period. Recent studies conducted within the framework of the French National Program on the Determinism of Recruitment

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have provided quantitative data on juvenile populations of infaunal molluscs and polychaetes. The present paper summarizes some of these data, which emphasize the importance of the early benthic stages as a comprehensive tool for recruitment studies.

2. Critical phases in the life histories of marine benthic invertebrates

The life history of every animal species includes several successive stages (gametes, embryos, larvae, juveniles, adults) which are more or less well protected against external factors. Since our purpose is to identify some critical phases in the ontogenetic development of marine invertebrates, it may be useful, before going further, to specify some definitions. TURNER *et al.* (1986) draw attention to some problems of terminology dealing with embryos and larvae, because these stages may be defined morphologically or ecologically. In a morphological sense, an embryo is an early developmental stage which precedes the first distinctly recognizable, immature form-the larva. Ecological definitions were given by GIESE and PEARSE (1974), focusing on the location of the developmental stages: embryos are stages which develop

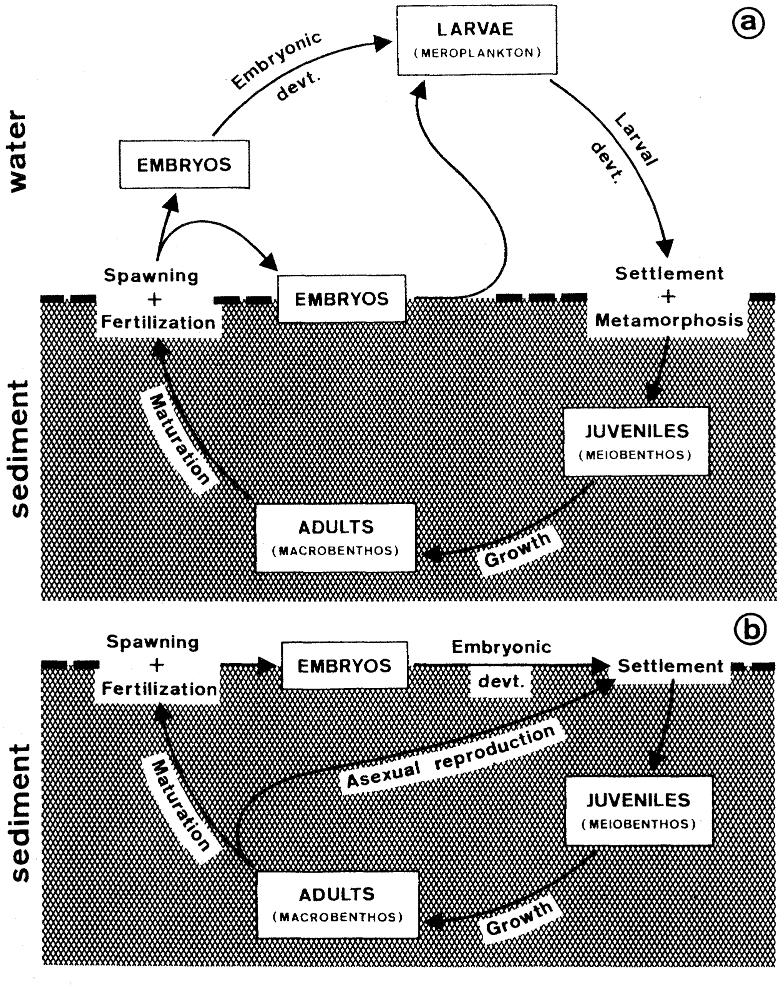

Fig. 1. Diagrammatic representation of the ontogenetic development of marine infaunal macroinvertebrates with (a) benthoplanktonic or (b) holobenthic life cycle.

Fig. 1. Schéma du développment ontogénique des invertévrés de l'endofaune marine à cycle de vie venthoplanctonique (a) ou holobenthique (b).

within the parent, egg mass, or egg membranes, whereas larvae are free-swimming stages, which pass through a metamorphosis to form the juveniles. HERMANS (1979) also underlined the difficulty in distinguishing between larvae and embryos in polychaetes. For example, in species whose gametes are freely liberated in seawater, HERMANS (1979) thought that there was not a true embryonic stage, but instead a lecithotrophic larval stage which may or may not, be followed by a planktotrophic larval stage before metamorphosis.

The ability to move freely is a creterion, both morphological and ecological, which facilitates clearer distinction between larvae and embryos (CAZAUX, 1981). This property will be used in our definitions. An *embryo* is an immature, prelarval form possessing two main characters: (1) lack of motility, and (2) inability to survive spontaneously after separation from the protective structure in which it normally develops. Hence, the term "embryos" may be applied to: (1) the stages which develop within the parent or some other protective structure (shell, egg capsule, etc...) until hatching, and (2) the early cleavage stages, when fertilization occurs in seawater, until the appearance of the first larval swimming devices. In the former case, embryonic development occurs at the expense of the female parent or through yolk reserves, and may last a relatively long time; in the latter, the embryonic period is relatively short. A *larva* is an immature, free-living stage, which is morphologically and biologically different from a juvenile or an adult and ends with metamorphosis; it is able to live outside any protective structure, and feeds on yolk reserves (lécithotrophy) or plankton (planktotrophy). *Juveniles*, or *postlarvae*, are recently settled organisms, possessing adult organs and behavior; their maximum size is usually limited by the smallest screen of the observer.

Attempts to categorize the types of larval development in marine benthic invertebrates have been proposed by various authors (THORSON, 1950; MILEIKOVSKY, 1971, 1974b,; CHIA, 1974). These classifications may be redressed in accordance with the appearance of larval stages (as defined above) and the type of developmental environment. Two main types of life history are now distinguishable: (1) species with a benthoplanktonic developmental cycle, and (2) species with a holobenthic developmental cycle (Fig. 1).

Species with a benthoplanktonic life cycle develop through pelagic larval stages of varying durations (Fig. 1a). In some species, development is entirely pelagic: fertilization of gametes, embryonic and larval development occur in the water mass. Other species undergo a partially pelagic development, with embryos protected within egg masses or brooded by the parents, before hatching of larvae. This type of life cycle is analogous to the 'pelagic development' described by MILEIKOVSKY (1971, 1974b). According to CAZAUX (1981), the 'demersal development' proposed by MILEIKOVSKY will be considered here as a particular case of pelagic development, because demersal larvae possess some swimming ability which may have an effect on their dispersal by water currents. The larval planktonic phase ends with a period of competence during which larvae are capable of settling if the appropriate environmental cues are encountered (CAMERON, 1986). SCHELTEMA (1974) defined settlement as the termination of the pelagic existence and the assumption of a sedentary life; it is a behavior, presumed to be under nervous control. The loss of swimming ability is more or less concomitant with metamorphosis, which refers to morphological and physiological changes (destruction of larval organs, differenciation of adult structures), through which a larva is transformed into a juvenile (SCHELTEMA, 1974; CHIA, 1989). As noted by BURKE (1983), settlement is a repeatable process, whereas metamorphosis is an irreversible phenomenon that happens only once in the life of an individual.

Species with a holobenthic life cycle have no free-living developmental stages (Figure 1b). The embryo gradually differentiates to the adult form without distinct stages, and hatches directly into a completely formed juvenile that begins its independent existence in the same benthic habitat as the adult.

Unlike the benthoplanktonic species, there is no metamorphosis in holobenthic species; they retain only the behavioral phase of settlement. Several developmental patterns of marine invertebrates are involved in this type of life history (MILEIKOVSKY, 1971, 1974b): (1) direct development, where embryos develop up to juvenile bottom stages inside protective egg capsules released by the parents into the bottom environment; (2) ovoviviparity (*sensu* TURNER *et al.*, 1986), where complete development up to juvenile occurs within the parental organism, without any tissue connection; (3) germiphory, or external gestation, which is known for example in syllid worms (*Exogoninae*); (4) asexual reproduction.

The distinction between these two types of life history is important as far as methodology is concerned: benthic samples will allow the collection of all the developmental stages of holobenthic species, whereas sampling of the complete cycle of benthoplanktonic species requires both plankton and benthos samples. Moreover, environmental and biological constrains are not the same for developmental stages that remain on the bottom and for larvae that undergo a change in habitat.

During the course of species development, several stages are decisive for the maintenance of benthic populations. In macrofaunal organisms with benthoplanktonic life-cycle, there are at least five such crucial stages: (1) maturation of sexual products, (2) spawning, (3) planktonic larval life, (4) larval settlement, and (5) postlarval growth, as observed from the time of settlement to a size large enough to be retained by sieves used for macrobenthos studies. The intensity of settlement is dependent upon the availability of larvae. This supply of larvae is directly influenced by mortality during the pelagic stages and by larval transport, but also by the fertilization success, and, ultimately, by the reproductive effort of adults. Unlike species with a benthoplanktonic developmental cycle, direct development and ovoviviparity are generally considered as processes ensuring good protection from predators and unfavourable environmental conditions (THORSON, 1946, 1950), and limiting dispersion of young stages. However, PECHENIK (1979) found several examples where egg capsules were ineffective against predation.

3. Sampling the juvenile stages

In soft sediments, two conditions must be fulfilled in order to quantitatively sample the juveniles (WILLIAMS, 1980): (1) using sieve sizes small enough to retain the smallest settled individuals, and (2) sampling at short time intervals.

The inadequacy between settling sizes of marine infaunal invertebrates and sieving sizes used in most macrobenthic studies was stressed by THORSON (1966) who noted that about 2/3 of macrofaunal species settle on the substrate as temporary members of the meiofauna. However, THORSON used a sieve with 2 mm mesh opening to separate macro- and meiofauna, which is larger than the 0.5 or 1 mm meshes currently used in modern studies. Size at the time of settlement was reassessed from literature data for a number of infaunal bivalves and polychaetes (Fig. 2). These data show that nearly all bivalve species settle with a shell length <0.5mm; most of them are even smaller. In polychaetes, size spectrum at settlement is rather wide (up to 3 mm) when size is measured as body length. Nevertheless, worm morphology is such that body length greatly exceeds body width in most species; a size spectrum drawn with body width shows that settling polychaetes cannot be retained by meshes >0.5 mm if they fall vertically over the sieve. Therefore, sieve screen sizes >0.5 mm are too large to retain newly settled individuals of most invertebrate species. BACHELET (1990) suggested that sieves with 0.1–0.2 mm mesh openings should be used in studies involving population dynamics of macrofauna, to provide an adequate estimate of juvenile abundances.

Another important bias source in recruitment studies is the frequency of sampling (LUCKENBACH, 1984): the time between settlement and sampling must be as small as possible, due to the transience and unpredictability of settlement patterns. LIVINGSTON (1987) provided direct evidence that sampling at monthly or quarterly intervals might obscure the weekly variations of environmental and biological

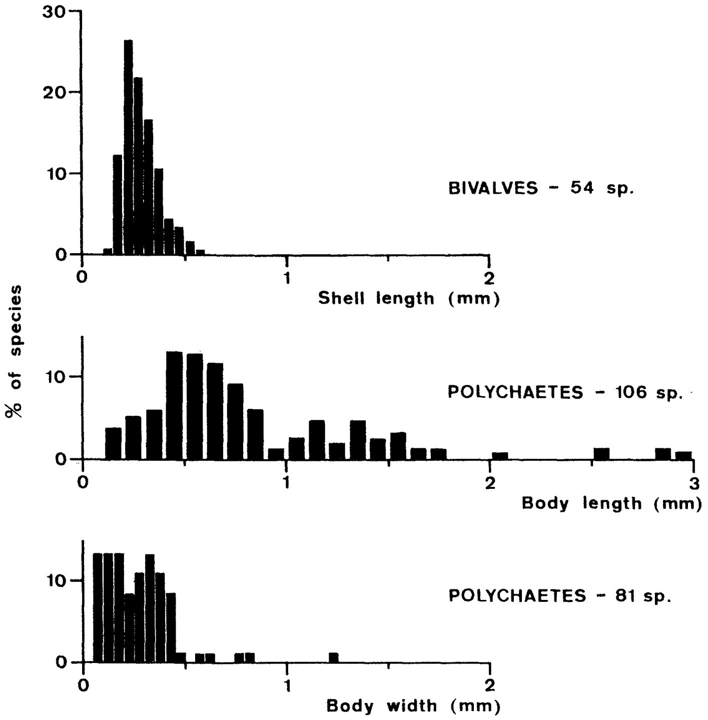

Fig. 2. Size spectrum of marine infaunal bivalves and polychaetes at settlement. In bivalves, shell length was measured along the anterio-posterior axis. In polychaetes, size spectrum is shown both for body length, measured from the anterior end of prostomium to the posterior end of pygidium (palps and urites excluded), and for body width, measured at the widest segment (setae excluded); larval stages which stay on the bottom most of the time (nectochaetes, erpochaetes, etc.) are here regarded as the first benthic stages. Histograms drawn from literature data (references are available upon request to the author).

Fig. 2. Spectre de taille des bivalves et polychètes de l'endofaune lors de la sédentarisation sur la substrat. Chez les bivalves, la dimension retenue est la longueur de la coquille, mesurée selon l'axe antéro-postérieur. Chez les polychètes, le spectre de taille est représenté en considérant soit la longueur du corps, mesurée entre l'extrémité antérieure du prostomium et l'extémité postérieure du pygidium (appendices non compris), soit la largeur du corps, mesurée au niveau du segment le plus large (à l'exclusion des soies); dans ce dernier phylum, les stades larvaires passant une grande partie de leur temps sur le fond (tels que nectochètes, erpochètes, etc.) ont étéicl considérés comme les premiers stades bentniques. Les histogrammes ont été tracés à partir de données de la littérature (références disponibles auprès de l'auteur).

(including recruitment) data in estuarine habitat.

4. The extent of juvenile mortality vs. larval mortality

To a large extent, our lack of knowledge of settlement patterns of benthic invertebrates in the field is likely to result from sampling biased towards small sizes. It is clear that densities of juveniles can be assessed only through specific benthic sampling schemes, focusing on the "temporary meiobenthos". Such a study was conducted in an intertidal mudflat located in the polyhaline zone of the Gironde Estuary, SW France. In order to obtain quantitative, reliable data on early post-settlement survival of infaunal macroinvertebrates, sampling was performed at fortnight intervals using a 100 μm sieving mesh size (see BACHELET, 1987, for further details on sampling methodology). In this low-diversity estuarine community, nine species showed clear recruitment patterns from which juvenile mortality rates could be determined; they included five polychaetes (*Nephtys hombergii* Aud & M. Edw., *Nereis diversicolor* O.F.Müller, *Polydora ligni* Webster, *Pygospio elegans* Claparède, *Streblospio shrubsolii* (Buchanan)), three bivalves (*Abra tenuis* (Montagu), *Cerastoderma edule* (L.), *Macoma balthica* (L.)), and a gastropod (*Hydrobia ulvae* (Pennant)). As reproduction (and settlement) period extended over several weeks in most of these species, juvenile

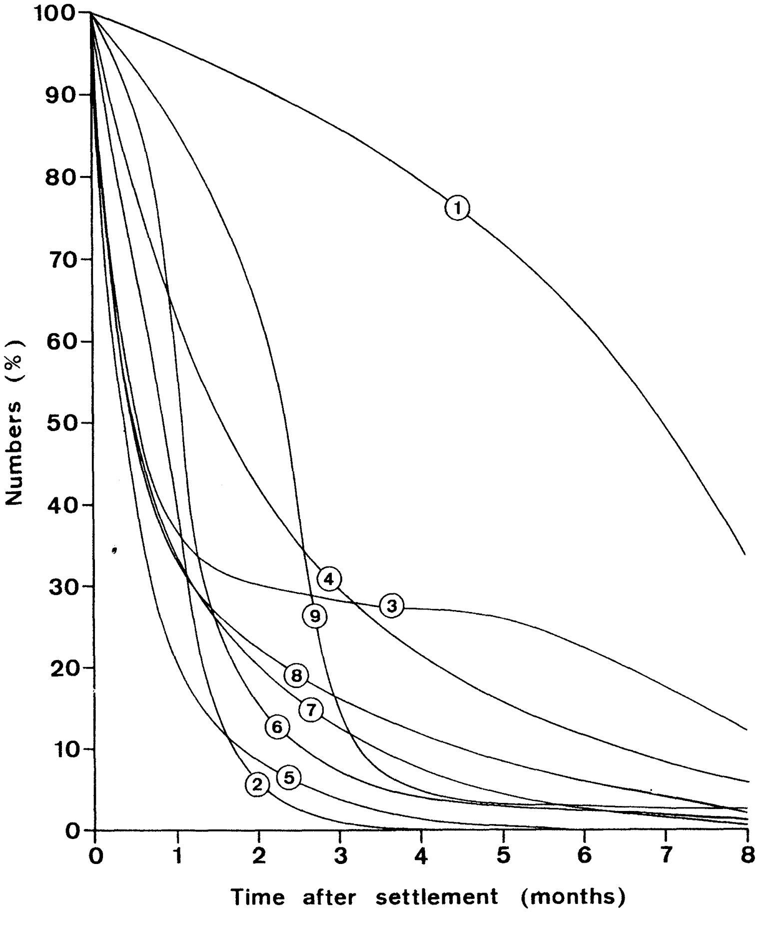

Fig. 3. Survival curves of some infaunal species from an intertidal mudflat of the Gironde Estuary. Seven species have a benthoplanktonic life cycle: development is entirely pelagic in *Nephtys hombergii* (1), *Cerastoderma edule* (2), and *Macoma balthica* (3), and partially pelagic in *Nereis diversicolor* (4), *Polydora ligni* (5), *Pygospio elegans* (6), and *Hydrobia ulbae* (7). Direct development (i.e., holobenthic life cycle) occurs in *Streblospio shrubsolii* (8) and *Abra tenuis* (9).

Fig. 3. Courbes de survie des principales espèces endogées d'une vasière intertidale de l'estuaire de la Gironde, établies à partir de l'installation des juvéniles sur le sédiment. Sept espèces présentent un cycle benthoplanctonique, avec un développement soit entièrement pélagique (1: *Nephtys hombergii*; 2: *Cerastoderma edule*; 3: *Macoma balthica*), soit partiellement pélagique (4: *Nereis diversicolor*; 5: *Polydora ligni*; 6: *Pygospio elegans*; 7: *Hydrobia ulvae*). Un développement direct (c'est-à-dire un cycle holobenthique) se rencontre chez *Streblospio shrubsolii* (8) et *Abra tenuis* (9).

mortality was only assessed for the most easily distinguishable cohorts. Figure 3 shows the decrease in population densities from the time of maximum settlement as a function of (benthic) age. For eight species, 70–99% of the settled individuals disappeared within three months, and only 1–13% of them survived the first eight months of benthic life (*C. edule* totally collapsed after 4 months in this site). In some species, the largest loss occurred during the first month after settling when the density decreased by 42% in *P. elegans*, 57% in *C. edule*, 65% in *M. balthica*, *H. ulvae*, and *S. shrubsolii*, and 80% in *P. ligni*.

The survival curve of *Nephtys hombergii* notably diverged from the pattern found in other species (Fig. 3). Actually, biometrical data suggested that *Nephtys* larvae settled subtidally, then migrated to the intertidal (BACHELET, 1987); therefore, the survival curve in Figure 3 might represent the survival of juveniles some weeks old, after a secondary recruitment.

Although different cohorts may have a different survival rate depending on whether they stem from early or late spawnings, our data show two important features:

1/With the exception of *Nephtys hombergii*, the mortality rates recorded during the early benthic period are high and the bulk of the population of settled juveniles is decimated within 2–4 months. These data are consistent with previously published estimates (Table 1). In a *Venus*-community in the Øresund, Denmark, THORSON (1966) also estimated that approximately 98.6% or even more of the young, settling on the bottom, died during the post-larval period; in a study of eleven species of bivalves in the same area, MUUS (1973) found post-larval mortality rates of 67–100% for all species.

2/Juvenile mortality is of the same order of magnitude, whatever the type of development (see Fig. 3). Assuming a low mortality rate during embryonic development in species

Table 1. Summary of literature data on post-settlement mortality rates of marine infaunal invertebrates. Only studies involving sampling with sieving mesh sizes small enough to retain early juveniles are included.

Species	Mortality rate %	Period after settlement (months)	References
Polychaetes			
Nephtys hombergii	90	4	SMIDT (1951)
Nereis diversicolor	99	3	〃
Lagis koreni	96	2	KIRKEGAARD (1978)
Myriochele oculata	96	8	〃
Nephtys hombergii	97	12	〃
Scoloplos armiger	99	9	〃
Nereis diversicolor	99	3	MÖLLER (1985)
Polydora ligni	90	2	LAMBECK and VALENTIJN (1987)
Bivalves			
Macoma balthica	95.4	5	ANKAR (1980)
Tapes japonica	57	2	WILLIAMS (1980)
〃	90	6	〃
〃	98.8	9	〃
Cerastoderma edule	91	6	MÖLLER and ROSENBERG (1983)
Mya arenaria	98	6	〃
Echinoderms			
Dendraster excentricus	88	12	CAMERON and RUMRILL (1982)
Amphiura filiformis	90	8	DUINEVELD and VAN NOORT (1986)
〃	97	9	〃

with a holobenthic life cycle implies that fecundity and/or fertilization success must be higher in species with benthoplanktonic life history to compensate for embryonic and larval mortalities during the pelagic phase.

Although mortality of the larval stages is supposed to be enormous (THORSON, 1950), very little is known whether mortality is greater during planktonic larval development or during the post-settlement period. Actual estimates of larval mortality are rather rare in the literature because of the obvious technical problems of following a cohort of larvae in the plankton (HINES, 1986). Moreover, some of these estimates are conflicting. For example, high mortality rates during larval life have been found in bivalves with high fecundity: 98–99% in *Ostrea edulis* (KORRINGA, 1941), about 98% in *Crassostraea gigas* (QUAYLE, 1964), 97.4% from the straight-hinged to the setting stage of *Mercenaria mercenaria* (CARRIKER, 1961), 98.5% in *Mytilus edulis* (JØENSEN, 1981). On the other hand, BHAUD (1979) calculated high survival rates during the planktonic phase of three Mediterranean polychaetes: 50–60% in *Lanice conchilega*, about 50% in *Poecilochaetus serpens*, and 44–53% in *Mesochaetopterus minutus*; he also noted that these figures were probably underestimated because of larval emigration and displacement of water masses, and hypothesized that larval mortality rates might actually be only 30% for these species.

In addition to methodogical problems, several reasons make reasonable estimates of larval mortality rates difficult to obtain; (1) the rate of mortality is unlikely to remain constant throughout larval life (SCHELTEMA, 1986), (2) the longer the larval life the higher the mortality by predation and/or starvation (THORSON, 1950; CHIA, 1974), and (3) disappearance of larvae may be due to mortality as well as passive transport out of the area of investigation. Nevertheless, the existing data do not support THOSON's (1950) view on the prevalence of pelagic events over post-settlement processes in the mortality of early life history stages. Mortality rates of benthic juveniles are likely to be within the same range of values as mortality rates of pelagic larvae.

5. Growth rate and production of juvenile benthic stages.

Although these points are not directly related to the determinism of recruitment, it is interesting to point out some recent results about the individual growth rate during the juvenile phase and the contribution to production estimates of young bottom stages.

In her study of growth of young bivalves in the Øresund, MUSS (1973) found very low growth rates during the first year after settlement which disagreed with previous data on the same species. Such a depressed growth was also found in some intertidal and shallow subtidal molluscs by BACHELET (1986, 1987, 1989), BACHELET and YACINE-KASSAB (1987), and MADANI (1989). These observations could be made only because the small size of the sieving mesh which was used allowed the collection of the juveniles as soon as they settled. The size frequency distributions gained with a coarse sieving mesh are biased by a methodological truncation against the smaller sizes, and the juveniles may remain hidden from the macrobenthologist during several weeks or months. For example, BACHELET (1989) showed that the very slow growth rate of *Abratenuis* during its initial benthic life caused the bulk of newly settled animals to remain within the meiofaunal size range for almost 1 year; in this special case, the numbers recruited into the macrobenthos (i.e., the numbers established by census with standard sieve sizes of 0.5–1.0 mm) were thus a consequence of events extending over a considerable period.

Other reasons may be set forth to explain low growth rates during the juvenile phase. In bivalve populations from northern areas, low seawater temperatures may depress growth (MUUS, 1973). In more southerly situations, it has been shown (BACHELET, 1986, 1987) that some cohorts of juveniles might experience a slow growth rate during settlement in adverse thermal and nutritive conditions: in the Bay of Arcachon, autumnal cohorts of *Abra alba* showed low growth rates, similar to those found by MUUS (1973) in Danish waters, whereas the growth was faster for cohorts which settled in spring and summer, when phytoplankton concentration was high (MADANI, 1989).

In marine macrofaunal studies, the computation of secondary production is usually restricted to the macrobenthic phase of organisms. Estimates of the "true" production of a macrofaunal population over its whole lifespan should, however, include production of both larvae and juveniles (WARWICK, 1980). Because larvae usually settle in very high numbers and survival rates and biomass are often low in juveniles, high production and production/biomass ratio may be expected in early benthic life. Comparison of figures calculated according to size-selective sampling methods (sieving mesh$\geqq$0.5mm) or with techniques allowing the capture of juveniles (sieving mesh<0.5mm), showed that the former results in an underestimate of the annual P/$\bar{B}$ ratio (Table 2). Using a mesh size too large to retain small benthic stages was previously suspected to overwhelmingly bias production estimates in macrobenthos (ROBERTSON, 1979; WATERS, 1979). Table 2 shows, in any case, that estimates of production based on literature values must be treated with caution and that annual population P/$\bar{B}$ are probably higher than it is usually accepted in macrobenthic species.

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Table 2. Estimates of annual P/$\bar{B}$ ratios in some populations of benthic marine molluscs. Values are compared between populations sampled with 0.5–1 mm mesh and populations with juveniles included.

Species	Sieving mesh size (mm)	P/$\bar{B}$ ratios (yr^{-1})	References
Abra alba (Wood)	0.5–1.0	1.3–3.4	Review of literature data by DAUVIN (1986)
	0.2	7.5–17.0	MADANI(1989)
Abra ovata(Philippi)	1.0	1.2–2.5	GUÉLORGET and MAZOYER-MAYÈRE(1982)
	0.2	0.9–4.2	MADANI(1989)
Cerastoderma edule(L.)	10.0	1.1–2.6	HIBBERT(1976)
	0.2	2.2–21.0	MÖLLER and ROSENBERG(1983)
Mya arenaria L.	0.7	2.5	BURKE and MANN(1974)
	0.2	2.0–13.5	MÖLLER and ROSENBERG(1983)
Hydrobia ulvae(Pennant)	0.5–1.0	1.1–1.8	Review of literature data by BACHELET and YACINE-KASSAB (1987)
	1.0	0.9–4.8	BACHELET and YACINE-KASSAB (1987)
	0.1	5.1–6.1	

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Résumé: La vriabilité spatio-temporelle des peuplements benthiques marins est, en grande partie, conditionnée par la réussite ou l'échec du recrutement, qui est, lui-même, la résultante de l'ensemble des évenements intervenant à tous les stades du développement ontogénique des organismes, depuis la phase de reproduction. Chez les esp èces à cycle de vie benthoplanctonique, plusieurs étapes critiques peuvent être identifiées: (1) la maturation des produits sexuels, (2) la ponte, (3) la phase larvaire planctonique, (4) l'installation des larves sur le substrat et leur métamorphose, (5) la phase postlarvaire ou juvénile. Dans le cas des espèces à cycle de vie holobenthique, il n'existe pas de phase larvaire au sens strict, donc pas de métamorphose, et les premiers stades libres sont des jubéniles benthiques.

La sédentarisation des larves s'effectue dans la phase dimensionnelle du méiobenthos, et il s'agit d'un phénomène souvent fugace: l'évaluation quantitative des jeunes stades benthiques nécessite donc une méthodologie contraignante (finesse des mailles de tamisage pour l'extraction du sédiment, fréquence rapprochée des échantillonnages) qui explique, dans une large mesure, notre méconnaissance de la phase postlarvaire. L'application de cette méthodologie a permis de mettre en évidence l'importance du taux de mortalité des juvéniles, qui atteint rapidement des valeurs élevées : 70–99% des individus disparaissent ainsi dans un délai voisin de 3 mois après leur installation sur le sédiment. Cette mortalité juvénile est probablement du meme ordre de grandeur que la mortalité larvaire dans le plancton, alors que cette derniere a longtemps été considérée comme déterminante pour les fluctuations du recrutement.

Les taux de croissance des juvéniles sont, par ailleurs, parfois très faibles, en particulier lorsque l' installation des cohortes coencide avec de mauvaises conditions thermiques et/ou trophiques; dans ce cas, la population de juvéniles peut rester durant plusierus semaines ou meme plusieurs mois au sein de la phase méiobenthique. Inversement, les taux de renouvellement de la biomasse (rapports P/$\bar{B}$) des populations sont très élevés si l'on incorpore les stades juvéniles dans les estimations de production.

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Role of instantaneous and long-term water movements on the recruitment and life of benthic fauna in the English Channel*

Jean Claude SALOMON**

Abstract : In some cases, the state of the art in hydrodynamical coastal studies now makes possible a good estimation of water movements at time scales ranging from a few minutes to a few months or years. The Channel which is tidally dominated, is in this favourable situation.

Taking the example of the benthic fauna, a discussion is presented on the possible responsibility of hydraulic factors on the life conditions of marine animals :

–eggs and larvae dispersion by instantaneous currents.

–passive transport of those elements during a few weeks by residual currents.

–stress exerted on the bottom and on adult animals by maximum velocities.

Some theoretical hypothesis are proposed and a numerical simulation is done to explain how animals may manage in their energetic environment to maintain and increase their populations.

1. Introduction

The life of marine organisms, their abundance, morphology and their reproductive conditions are probably dependent on a number of external factors, some of which may have an hydrodynamic origin. Marine currents may carry animals, eggs, larvae and nutrients. They may also model bed morphology and determine superficial sediment composition. They are thus, directly or indirectly, a fundamental component of the many factors responsible for the existence of benthic communities.

Investigations in that direction requires, at least, a detailed knowledge of currentologic characteristics at time scales ranging from a few seconds to several weeks, which is very difficult to obtain. However in some circumstances, mathematical models now give this information and make possible to progress. This is attempted here for the case of the English Channel, which is quite shallow (depths generally lower than one hundred meters) and where marine currents are essentially induced by the tide, which is an easy situation from the modelling point of vue.

2. Some hydrodynamic peculiarities of the channel

The main characteristic of the Channel is the intense tidal currents. Two knots is an average value for a medium tide (Fig.1 and 2). As the waters are generally shallow and bathymetry often irregular, tidal currents create long term velocities which are called tidal residuals (CHENG *et al.*, 1986; ORBL and SALOMON, 1988; SALOMON *et al.*, 1988). Their average amplitude is about 5cm/s but can be much higher (Fig. 3).

The wind is another driving mechanism for water movements. It cannot be compared, in strength, to the instantaneous tidal movements, but may be greater than tidal residuals. The main difference is that wind being always changing in speed and direction, part of its effect vanishes on long time scales. In contrast although modulated on different periods (14 days, 28 days...) tide is permanent and continuously reinforces its action.

Density gradients are due to temperature and salinity differences. Both are weak in the Channel due to the intense mixing action of the tide, a moderate insolation and the absence of high fresh water discharge, except locally near the Seine estuary (average flux of 400 m^3/s).

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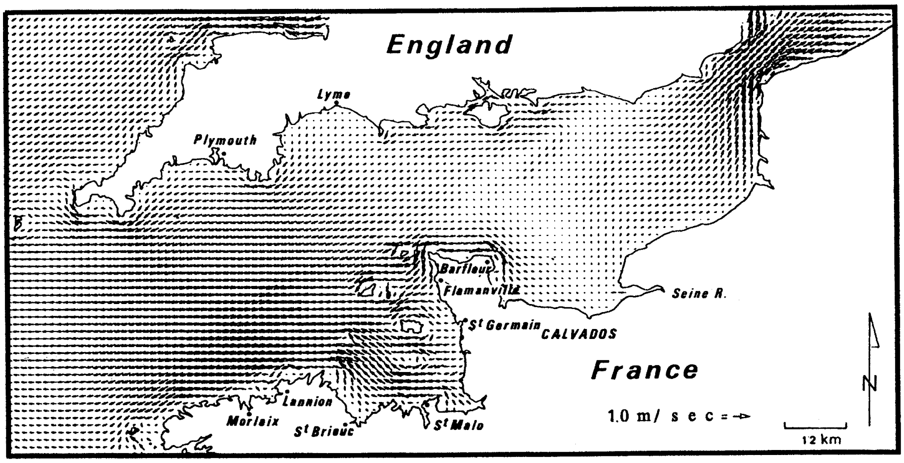

Fig. 1: Example of instantaneous velocity field.

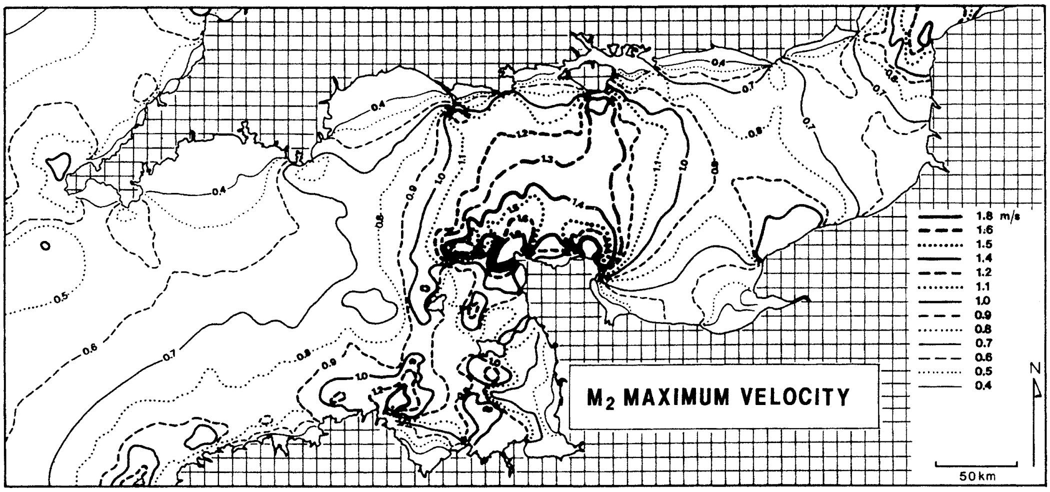

Fig. 2. Isolines of maximum instantaneous velocity during a tidal cycle.

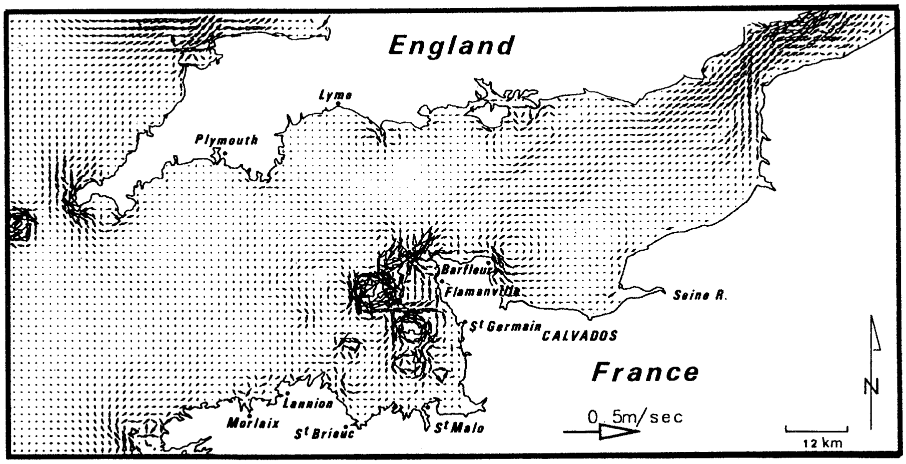

Fig. 3 · Residual velocities.

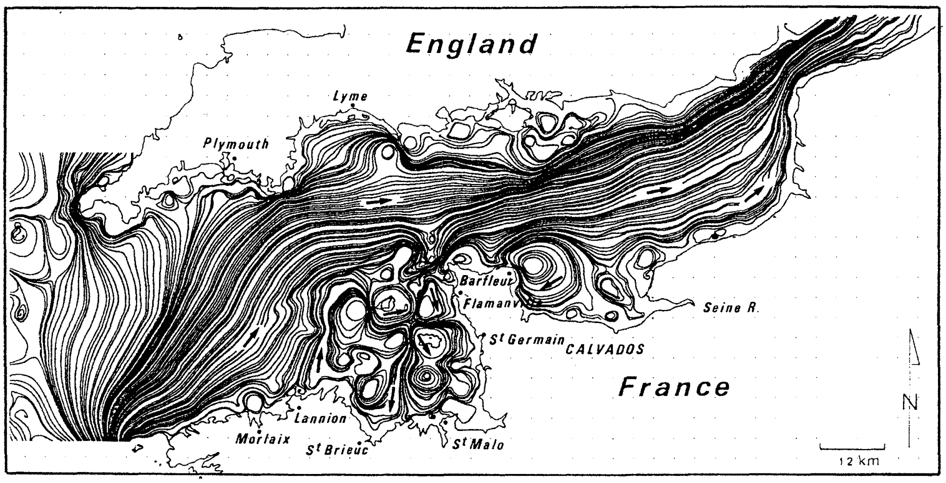

Fig. 4 : Long-term trajectories.

3. Materials and methods: The two-dimensional numerical model

All information presented herafter is derived from a two dimensional vertically averaged currentologic model of the Channel (SALOMON et BRETON, 1990a). It is a submodel inserted inside a more global one of the whole North European shelf (SALOMON et BRETON, 1990b).

The numerical technique involves finite differences and allows for an automatic treatment of the coast and shoaling banks. The mesh size is one square nautical mile. The model computes instantaneous and residual velocities and trajectories through the "barycentric technique" detailed in SALOMON *et al.* (1988). Fig. 1 shows an example of an instantaneous velocity field and Fig. 4 presents long term trajectories for a yearly averaged tide and wind situation.

To compute also the relative effect of mixing and transport the model is completed by a sequence of advectiondispersion calcula tion. This second part of the model uses the same grid to solve the advectiondiffusion equation in its usual form :

$$\frac{\partial C}{\partial t} + u\frac{\partial C}{\partial x} + v\frac{\partial c}{\partial y} - k\frac{\partial^2 C}{\partial x^2} - k\frac{\partial^2 C}{\partial y^2} = 0$$

c : concentration, or number of elements per unit volume.
u, v: velocity components.
k : dispersion coefficient.
x, y: horizontal coordinates.
t : time.

More computational details can be found in SALOMON *et al.* (1991).

4. Results and discussion

a) *Theoretical arguments*

Bottom stress

Marine currents exert a force which is roughly proportional to the square of speed, on the sea bed and the marine organisms to be found there. Thus it is not surprising that a very close similarity exists between superficial sediment composition and maximum tidal currents. It can also be imagined that this parameter plays a direct role by the force exerted on the animals which, unable to withstand it, are carried away, and indirectly by erosion/deposition of fine sedimentary particles. On the contrary, other species may appreciate such zones where fluxes of dissolved nutrients may be higher than elsewhere. As a consequence we may hypothesize Fig. 2 to be a rough indicator of the possibility for an adult population, having specific requirements about instantaneous velocities, to exist in any place.

-Residual movement and dispersion

Eggs and larvae, when released, are advected and dispersed by currents. The pelagic life time being usually longer than the tidal period, the resulting movement may be computed by the residual velocity, whereas dispersion may be evaluated by the following general considerations:

From a point source corresponding to an adult, a patch is created. Its width (B) increases with time, according to the OKUBO formula (1968):

$$B = at^m$$

where $a = 0.00208$

$m = 1.17$ m.k.s.

To compare this expansion with advection, a velocity (Ve) will be defined as the rate of increase of the patch dimension:

$$Ve = mat^{m-1}$$

This shows that the fringe spreads out with a velocity increasing with time. Ve is about 1 cm/s after an hour and 3 cm/s after a month. From which it is clear that the possibility for a patch to remain nearly at the same position as the adult colony depends on the relative magnitude of this expansion velocity and the residual velocity:

Where the residual velocity is weak (about 1 cm/s), it can hardly exceed the dispersion effects. A preferential direction of movement exists but dispersion makes it possible for larvae to proceed in all directions from the location of the adult colony and even back wards, against the current. This gives the larvae the possibility to remain at the same place in significant quantities (Fig. 5a) but inversely restrains the possible dissemination of the colony.

If the velocity is strong enough (order of 3 cm/s) larvae have no more possibility to resist and will be carried away from the original colony. For it to maintain at the same place it is then necessary that the trajectory be either closed (gyre) and travelled through in a time duration similar to the eggs and larvae lifetime, or connected to other colonies, each feeding the other (Fig. 5b).

Those criteria are supposed to apply more constraints to short lifetime species, for which every spawning has to be successful. In the opposite case one can imagine that occasional and favorable meteorological events may be enough to allow the colony to survive.

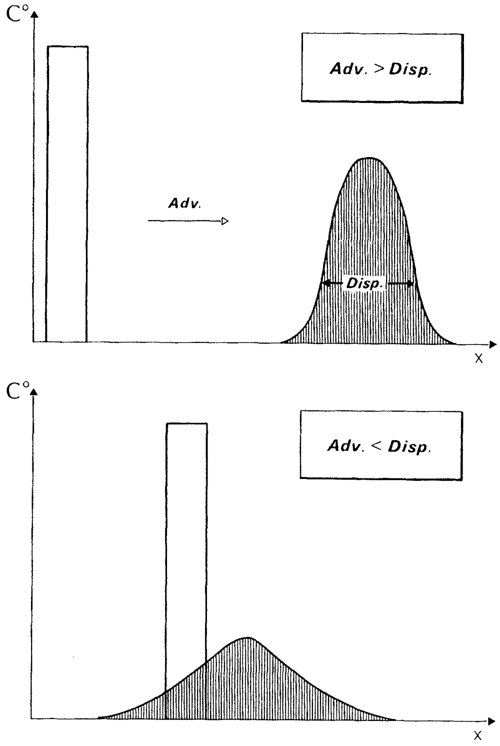

Fig. 5. Relative predominance of dispersion and advection.

In the case of medium residual velocity (here about 1–2 cm/s) which is the most frequent, the rate of maintenance of young animals around the spawning place will be rather low unless the settlement is of great geographical extent. Their trajectory will eventually remain highly dependant on meteorological and other fotuitous events. Those areas seem *a priori* favourable to uniformly distributed species, which means not very sensitive to other environmental parameters such as instantaneous velocities, sediment composition or depth.

b) Application to the Channel

Based on the preceeding arguments, one can try to exploit the knowledge of instantaneous and residual velocities to get a better understanding of how some species may use their physical environment to succeed in their recruitment task.

The first apparent feature of long term trajectories (Fig. 4) is the WestEast circulation in the axis of the Channel. It makes North-South connections difficult and may cause a separate development of colonies on both sides. This seems to be particularly true for the English coast from which no path exists for passive particles or animals to go southward. HOLME (1966) mentions more than twenty different species "present along the south coast of England but rare or absent from the French side", among which *Nucula turgida, Ensis ensis, Acrocnida brachiata, Nassarius reticulatus, Ophilura albida* and *ophiura texturata*... The same author gives fifteen examples of species present throughout the length of the Channel, but mainly on the French side in the eastern Channel: *Lithothamnion calcareum, Astarte triangularis*... Such observations give support to the present statement.

Some areas where residuals are weak and/or rotational seem suitable for the existence of important colonies. Such is the case, on the French coast, for the Bays of SaintBrieuc and the eastern part of the Bay of Seine, although this last one appears very sensitive to the wind and occasionally to fluvial discharge. On the English coast Lyme and Plymouth bays seem also favorable to permanent settlements.

The Channel islands region is of greatest interest. Intense gyres can be observed (the same for the Scilly surroundings), which are permanent and insensitive to meteorological conditions. Those vortices are places of high shear and probably of intense mixing. They may consequently produce a high dissemination of any passive material. An interesting point will be to investigate if the spatial distribution of other physical parameters to which the adult phase is linked (instantaneous velocities, depths...) is not too heterogeneous for a particular species to be widely distributed.

Generally speaking, a permanent point of convergence along the coastline may favour a discontinuity in coastal populations. Such is the case of the Barfleur headland and the vicinity of PerrosGuirec which seems to be the origin of a streamline which isolates the Channel island region. It is tempting here to make the hypothesis that the natural advective border is one of the reasons for the individualisation of "Sarnian" species (HOLME, 1966) such as *Venus verrucosa, Calyptraea chinensis*, etc.

On the contrary and divergence of coastal currents may favour an homogeneity of populations already existing off the coast (Bay of Seine, region of St Malo).

c) Quantitative results

In 9 arbitary and different locations, a source function has been assumed on the bottom, which introduces instantaneously in the water column a certain number of passive elements (eggs) which are then transported and dispersed according to the equation above for a duration of three weeks. Living particles are then supposed to fall down on the bottom. Fig. 6 is the result of this numerical simulation. It shows the ratio between the number of particles emitted per square meter at the source and the number which are collected on a similar bottom area after the hydrodynamic step. This indicator of the hydraulic efficiency during the pelagic phase is contoured for values of 1/100 and above.

Previous statements are then confirmed and detailed:

Colony n° 1 will recieve his own production in proportions of about 0.01, whereas the center of the patch is moved 25 kilometers to the east. Ratios there are about 0.1 of the initial value. The population appears to have more facility to be slowly translated eastward than to remain at the same place.

Colony n° 2 has both of these possibilities. It can either emigrate towards the northwest or stay at the same place in great proportions (>0.1). In reality the wealth of benthic populations which is observed in the Bay of Saint Brieuc, even for such heavily exploited populations as scallops, is probably related to these physical mechanisms.

Colony n° 3 suffers from a very high dispersion to the south and to the north-east. Compared to the previous example, Hydrodynamic parameters reduce the ability

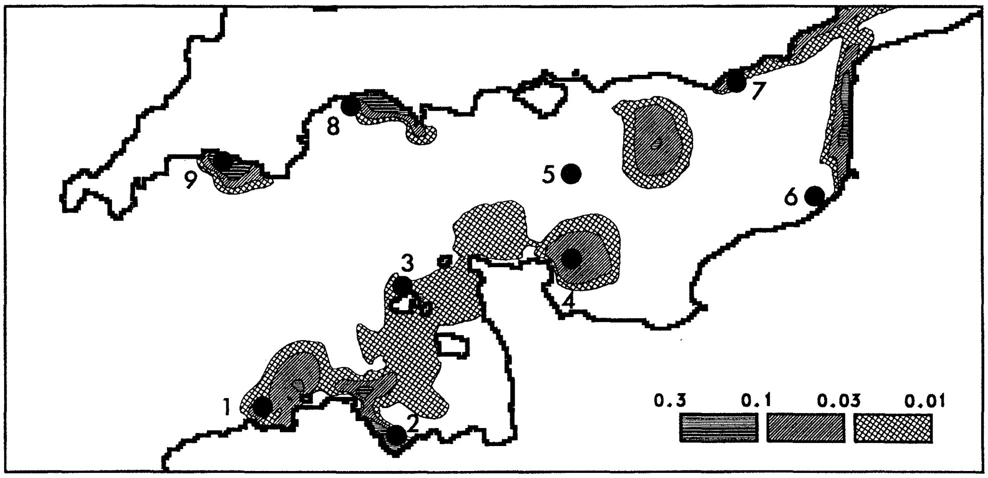

Fig. 6. Ratio collected/emitted larvae per unit bottom area after 3 weeks of movement and mixing. Discs indicate initial position of colonies.

of this colony to stay at the same place by a factor of 10. Inversely, if other interfering mechanisms were so favourable in this region that this ratio did not constitute a severe handicap, the population would have the ability to spread over hundreds of square kilometers in a single larval phase, which is not the usual case.

Juveniles from colony n° 4 are uniformly distributed and confined inside the gyre where they appeared. It seems to give a reasonable efficiency to its spawning without any spatial progression.

Colony n° 5 loses all its production. It cannot exist, except if other similar populations were existing upstream, i.e. west of it.

Colonies n° 6 and n° 7 are in similar situations. Most of their larvae remain along the coast with few perpendicular dispersion, but are translated some 40 km to the north or to the east. It reveals the continuous movement of the populations in direction of the North Sea, especially along the French coast. Such observations have already been done and reported by Lagadeuc and Brylinsky (1987) for *Polydora* ciliata larvae. These authors indicate a longshore drift of the animals at a speed ranging between 1.6 and 3.3 kilometers per day, perfectly coherent with what is found here. Nevertheless Colony 7 partially remains at the same place and keeps some chance to perpetuate even if being alone.

Colony n° 8 is essentially in a similar situation as the previous one. Its spawning is slowly carried to the east but part of it remains at the same place and may allow a settlement permanency.

Colony n° 9 is in the most favourable situation. No marked residual velocity and little dispersion make easy for the larvae to stay where they were spawned in amounts of the same order of magnitude as three weeks earlier.

The discussion above was restricted to advection and dispersion of eggs and larvae. It is clear that innumerable other factors exist which might be included and combined with the previous ones to go more deeply into the dynamic of the arbitrary species considered here. Even restraining our investigations to physical parameters it would be easy to combine factors related to the pelagic phase with those related to the benthic one: water depth, maximum and minimum velocity, bottom composition, temperature, etc. All parameters which are already known and will be incorporated to this work in the near future, for continuation.

5. Conclusion

In some circumstances, mathematical models now make possible to get a reasonable knowledge of water movements at time scales comparable with those concerning biology. In such cases it appeared fascinating to try, by theoretical computations, to imagine how animals manage to use their environment.

Instantaneous velocity fields give indications on the possibility for benthic animals to find adequate hydraulic and sedimentologic conditions to live ; residual circulation and dispersion reveal the possibility for the populations to spread, to be translated, or to remain confined during their pelagic lifetime. The numerical simulation quantifies the role of physical parameters and makes the basis for a discussion on the relative potentialities of different zones for recruitment of benthic populations, all other factors remaining unchanged.

The purpose of this paper was to make an attempt in that direction, based on the knowledge of long term movements. Although theoretical, the discussion seems to have raised some points confirmed by observations. It is thus considered promising and will be pursued by combining other physical param eters.

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Résumé: Dans certains cas, l'état de nos connaissances en hydrodynamique des zones côtières permet aujuord'hui de connaitre le mouvement des eaux à des échelles de temps allant de quelques minutes à quelques mois ou à quelques années. La Manche, dont la courantologie est dominée par la marée, se trouve dans cette situation favorable.

En prenant l'exemple de la faune benthique, on presente ici une discussion du rôle possible des facteurs hydrauliques sur les conditions de vie des animaux marins:
-la dispersion des oeufs et larves par les courants instantanés
-le transport passif de ces éléments durant plusierus semaines par les courants résiduels
-la force exercée sur le fond et les animaux adultes lors des instants de fort courant.

Quelques hypothèses théoriques et une simulation numérique sont présentées pour expliquer comment les animaux peuvent utiliser un environnement hydraulique fortement énergétique pour maintenir ou développer leurs populations.

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Possible food sources of eel leptocephali*

Tsuguo OTAKE**, Kinya NOGAMI*** and Keigo MARUYAKA***

Abstract: The gut contents and ultrastructure of midgut mucosal cells were examined in the leptocephali of *Anguilla japonica, Conger myriaster* and *Muraenosox cinereus*. Small detrital particles, less than 20 μm diameter, and fecal pellets, 100–250 μm long, were found in the gut of *C. myriaster* and *M. cinereus*. Detrital particles were found quite commonly and seemed to be a major food item. In *A. japonica* ciliates were found. The gut pigment content in *C. myriaster* leptocephali was low. And the Chlorophyll-*a*/Phaeopigment ratio was low. These facts indicated that leptocephali do not feed directly on phytoplankton. The ultrastructure of the midgut mucosal cells revealed that a lamellar membranous structure was well developed in the basal half of the cytoplasm, suggesting that water and ion were actively ingested by the cells. Dissolved organic matter may be part of the nutrition resource for leptocephali. The nitrogen isotopic composition of *C. myriaster* revealed that leptocephali were at the lowest trophic level in the food web. This also strongly supported the suggestion that leptocephali get their nutrition from detrital and dissolved organic matter.

1. Introduction

Larval mortality is a major factor determining recruitment of young fishes to a population. A major cause of larval mortality is starvation (THEILACKER and WATANABE, 1989). Information on the feeding of fish larvae, for example prey selection, feeding behavior, and digestion physiology, has been accumulated so as to examine the mechanism of larval mortality (see review in HUNTER, 1981; GOVONI *et al.*, 1986). However, little is known of the feeding of the eel leptocephalus during their long oceanic migration. In particular, nutrition is enigmatic since no food has been found in gut of any leptocephali (MOSER, 1981). In the present study gut contents, gut pigment content, and ultrastructure of gut mucosal epithelium were examined in the leptocephali of the anguilliformes, *Anguilla japonica, Conger myriaster* and *Muraenosox cinereus*. Isotopic distribution in animals was found recently to be closely related to dietary isotopic composition. The nitrogen heavy isotope (^{15}N) is regularly enriched by 3–4‰ per trophic level (MINAGAWA and WADA, 1984; FRY, 1988). We also examined nitrogen isotopic composition to estimate leptocephalus trophic level in food web and aid in discussion of possible food sources.

2. Materials and methods

Gut contents

Three leptocephali of *Anguilla japonica* (40.5–43.4 mm TL) collected in the western North Pacific during a 1986 research cruise of R/V Hakuho Maru (KH-86-4) of Ocean Research Institute, University of Tokyo (KAJIHARA, 1988), and 216 specimens of *Conger myriaster* and 77 of *Muraenosox cinereus* leptocephali collected in Harimanada, Seto Inland Sea (Japan) in 1989, were used for examination of gut contents. The specimens of *A. japonica* were collected by oblique hauls of an IKPT net (mesh aperture: 0.5mm) from 500m depth to the surface (KAJIHARA, 1988). *C. myriaster* and *M. cinereus* leptocephali were collected by bag net or bull trawl for sand eel fisheries. The specimens were preserved in 10% neutralized formalin or 2 % paraformaldehyde-2 % glutaraldehyde mixture in 0.1M cacodylate buffer (pH7.4). Measuremants

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and counting of myomeres followed the methods described by JESPERSON (1942) and CASTLE (1963). Identification followed MOCHIOKA (1988) and TABETA (1988).

After measurements and myomere counts, the specimens were examined for gut contents under a binocular dissecting microscope. Some identifiable gut contents were examined further with a scanning electronmicroscope.

For scanning eletronmicroscopy (SEM) the gut was removed and cut into several pieces. They were post-fixed in 2% OsO_4 for 2h, dyhydrated through a graded ethanol series, and dried in a Hitachi HCP-2 critical point dryer. The dried tissues were mounted on a brass disc, cut into halves using a needle and razor, and the inner surface exposed. They were subsequently spattercoated with gold in a Jeol JFC-1100 ion-spatter and observed under an Akashi-25α SEM.

Gut pigment contents

Five specimens of *C. myriaster* leptocephali were used for examination of gut pigment content. After total length measurement each gut was removed and dipped in dimethylformamid. Chlorophill-*a* and phaeopigment extracted by dimethylformamid were measured as gut content pigment with a Turner model 111 fluorescent photometer after STRICKLAND and PARSONS (1972).

Ultrastructure

For transmission electronmicroscopy (TEM) the midgut of some *A. japonica* and *C. myriaster* leptocephali were fixed in cold 2% paraform aldehyde-2% glutaraldehyde mixture in 0.1M cacodylate buffer (pH7.4) for several days and post-fixed in 2% OsO_4 for 2h. The tissues were dyhydrated through a graded ethanol and embedded in Epon 812 resin. Ultra-thin sections were cut by a LKB-ultro-tome (V), double stained with uranyl acetate and lead citrate, and examined by a Jeol JEM-100CX TEM. Some thicker sections were stained with toluidine blue and observed under a light microscope.

Stable nitrogen isotopic composition

Stable nitrogen isotopic compositions were measured for *C. myriaster* leptocephali and other animals, such as sand eel (*Ammodytes personatus*), squid (*Loligo* sp.), and jelly fish, collected at the same time in Harimanada in 1989. The isotopic composition of a mixed-species zooplankton sample and particulate organic matter were also measured. The latter was collected by filtering 15 liters of seawater (15m deep) using a precombusted (400 ℃, 5h) silica filter (pore size 0.22μm). Zooplankton was sampled by vertical haul of a handtowed plankton net (30 cm mouth diameter, 0.33mm mesh) from bottom (ca. 45m deep) to surface. All samples were dried at 60℃ and ground. The resulting powder was analyzed for $^{15}N/^{14}N$ with a Finnegan MAT-Delta E mass spectrometer after MINAGAWA and WADA (1984). Results are expressed as δ values, ‰ deviations from a standard (atmospheric nitrogen) by the following equation:

$$\delta^{15}N = (R\ sample/R\ standard-1) \times 1000$$

where $R = {}^{15}N / {}^{14}N$.

3. Results and discussion

Gut contents

Many spherical particles, possessing a large number of long, filamentous projections on the surface, were found in the gut of *A. japonica* (Fig.1). Each projection was found to contain microfilaments extending deep into the body, suggesting it to be a cilium (Fig.2). The particles were enveloped by a single membrane and included cell organelles such as a nucleus, vacuoles, and a myeline body. These suggested that the particles were unicellular organisms, possibly ciliates. In *C. myriaster* and *M. cinereus* two types of particles were identified from the gut. One was a small aggregation of fine particles and amorphous mucous material, and was less than 20μm diameter (Fig. 3, OTAKE, *et al.*,1992). TEM examination showed each fine particle to lack an obvious structure and suggested them to be detrital particles. This type of particle was found in considerable numbers in the gut of over 80% leptocephali examined (Table 1) and suggests that detrital

Table 1. Gut contents of *C. myriaster* and *M. cinereus* leptocephali collected in Harimanada.

Species	No. of specimen examined	Total length range (mm)	Number of specimens containing particulate matter (%)	
			Detrital particle	Fecal pellet
C. myriaster	216	89.0−127.0	172 (79.6)	16 (7.4)
M. cinereus	77	35.0− 90.2	74 (96.1)	32 (41.6)

Table 2. Chlorophill-*a* (Chl. *a*) and phaeopigment (Phaeo.) contents and their ratio in the gut of *C. myriaster* leptocephali collected in Harimanada.

No. of fish examined	Range of total length (mm)	Chl. *a* (ng/ind.)	Phaeo. (ng/ind.)	Chl. *a*/Phaeo.
5	103.0−118.0	0.27±0.11	1.35±0.56	0.21±0.07

particles are a major food item of leptocephali. Another type of particle, found in 16% gut examined (Table 1), had an oval shape some 100−250 μm long (Fig.4, Otake, *et al.*, 1992). Each was covered by a mucous membrane and included many fragments of cocoliths and diatoms (Fig.5,6, Otake, *et al.*, 1992), suggesting them to be fecal pellets of herbivourous zooplankton.

Gut pigment contents

The total gut pigment content of each *C. myriaster* leptocephalus was 1.62±0.13 (mean ±S. D.) ng ind^{-1} (Table 2). Following Strathman's equation (1967) wherein the Carbon/Chlorophill-*a* ratio is 50, this value corresponds to only about 45 unicellular flagellates (10 μm diameter) or 120 diatom cells (10 μm diameter). The latter figures are thought to be too low for phytoplankton to be considered a major food of leptocephali. Furthermore, the Chlorophyll-*a*/Phaeopigment ratio was also quite low (0.21±0.07) (Table 2), suggesting that the pigment stayed in the gut for a long time or that it originated from detrital matter such as fecal pellets. Leptocephali do not seem to feed directly on phytoplankton.

Ultrastructure of midgut epithelium

The midgut epithelial cells of *A. japonica* and *C. myriaster* leptocephali possessed a typical characteristic of absorptive cells such as a developed brush border, and were additionally characterized by two striking cytological features (Otake, et al., 1992). Numerous vacuoles were distributed in the upper half of the cytoplasm (Fig. 6), each including

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Fig. 1 SEM micrograph of spherical particles in the gut of *A. japonica* leptocephalus. Filamentous structures are seen on the surface of the particles.

Fig. 2 TEM micrograph of a spherical particle showing cytoplasmic projections. Microfilaments (arrow heads) extending into the cytoplasm are seen in the projections.

Fig. 3 SEM micrograph of a small particle in the gut of *C. myriaster* leptocephalus. It comprised fine particles and amorphous matter (Otake, *at al.*, 1992).

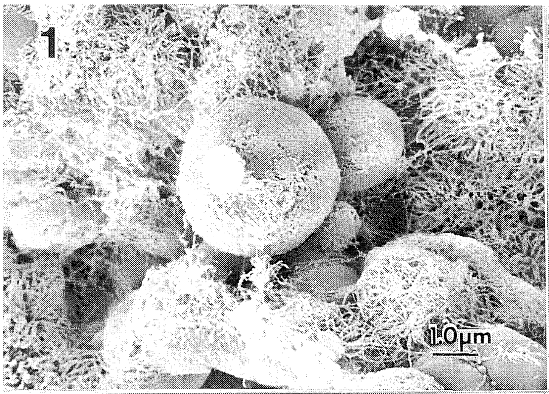
Fig. 4 Oval particles in the gut of *C. myriaster* leptocephalus (Otake, *at al.*, 1992).

Fig. 5 SEM micrograph of diatom fragment found in an oval particle (Otake, *et al.*, 1992).

Fig. 6 SEM micrograph of cocolith fragment found in an oval particle (Otake, *et al.*, 1992).

Fig. 7 TEM micrograph of the apical portion of the midgut epithelial cell of *C. myriaster* leptocephalus. Numerous vacuoles containing fine particles are present in the cytoplasm. Mv-microvillii.

Fig. 8 TEM micrograph of basal portion of the midgut epithelial cell of *C. myriaster* lepto cephalus. Membranous lamellar structure (Lm) associated with large mitochondria (M) are highly developed.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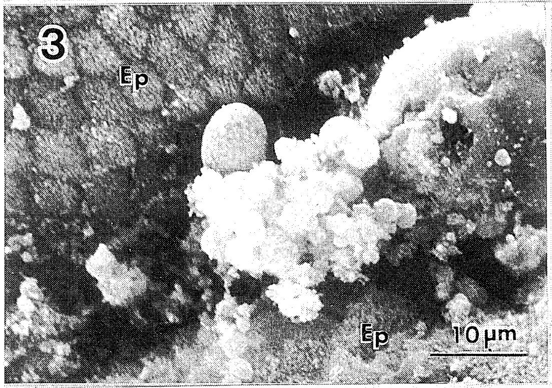
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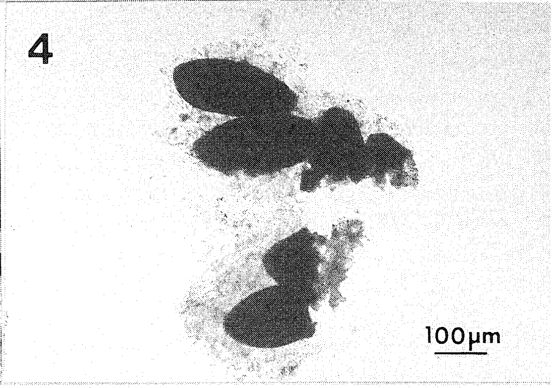
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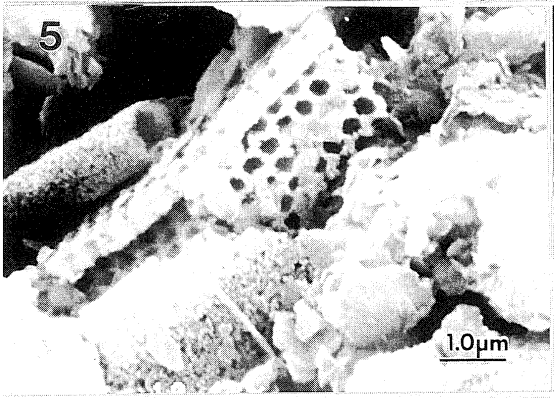
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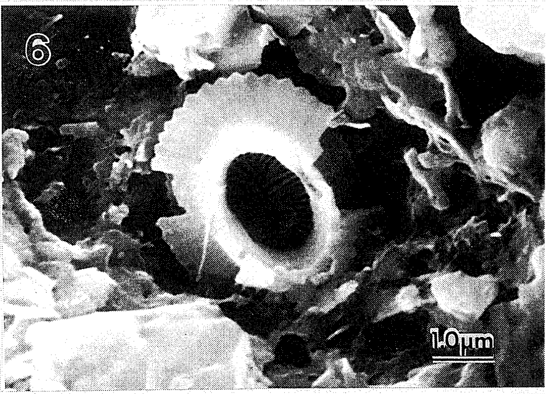
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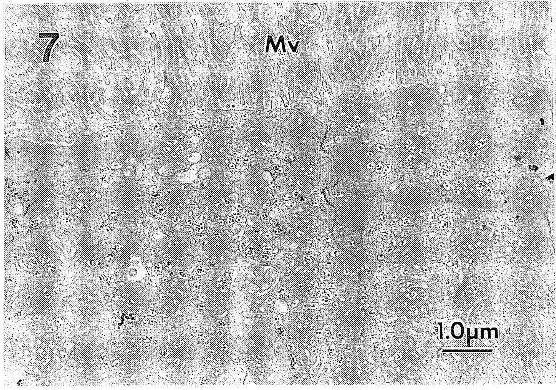
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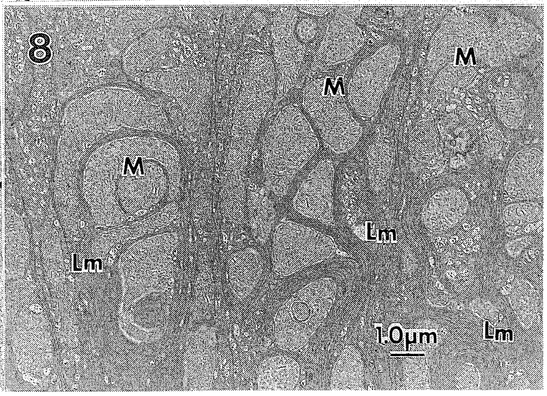
8
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Table 3. Nitrogen isotopic composition of biota from Harimanada.

Samples	No. of samples	$\delta^{15}N$ (mean±S. D.)
Particulate organic matter	1	11.6
Invertebrate:		
Zooplankton	1	11.9
Jellyfish	2	17.5±2.4
Squid (*Loligo sp.*)	1	17.6
Fish:		
Sand eel (*Ammodytes personatus*)	2	17.8±1.8
Leptocephalus (*Conger myriaster*)	3	11.1±0.9

fine particles with high electron density. The vacuoles were often found to be in contact with the surface plasmamembrane between microvilli, indicating active phagocytotic ingestion of intact macromolecules. Extremely highly developed membranous lamellar structure closely associated with large mitochondria was found in the basal half of the cytoplasm (Fig.7). A similar structure has been reported in the digestive system of various fishes (OZAKI, 1965; YAMAMOTO, 1966; IWAI, 1968; NOAILLIAC-DEPEYRE and GAS, 1976; STROBAND and DEBETS, 1978) and is thought to be involved in water and ion transport. Furthermore Na^+-K^+- ATP ase activity has been demonstrated on both the lamella membrane and the basal plasmamembrane of midgut epithelial cells in preleptocephali of *M. cinereus* (OTAKE, unpublished). This is direct evidence for the uptake of water and ions by the cells. The highly developed lamellar structure indicates that leptocephali absorb copious seawater in the midgut epithelium. It is known that leptocephali have a high water content and that their ionic composition is in equilibrium with that of seawater (HULET *et al.*, 1972; PFEILER, 1986). PFEILER (1986) reported that bonefish leptocephali contained high levels of essential amino acids which they were presumably unable to synthesize by themselves. Therefore, HULET (1978) and PFEILER (1986) suggested that dissolved organic matter was a plausible source of nutrition for leptocephali. Active seawater ingestion by the gut epithelium of *C. myriaster* leptcephali may support their suggestion.

Stable nitrogen isotopic composition

The nitrogen heavy isotopic composition in *C. myriaster* leptocephali was 11.1‰, which is much lower than that found in other herbivorous invertebrates and a planktivorous fish (Table 3, OTAKE, *et al.*, 1992). In addition, the isotopic composition of the leptocephali was rather lower than that of particulate organic matter, which comprised a mixture of phytoplankton, detritus, bacteria, microzooplankton, and small zooplankton. Leptocephali are obviously located at the lowest trophic level in the food web, and accordingly are unlikely to feed on zooplankton and other animals, which occupy higher trophic level. Particulate and dissolved organic materials are plausible nutrition resources for leptocephali.

4. Conclusion

Detrital particles, often collectively called "marine snow", are sites of dense community of phytoplanktons, bacteria, and protozoa, and are nutritionally enriched (SILVER *et al.*, 1978; SHANK and TRENT, 1979; CARON *et al.*, 1986). Accordingly, they are considered to be a potential food source for epipelagic and deep sea organisms (WANGERSKY, 1974; GERBER and MARSHALL, 1974; GOTTFRIED and ROMAN, 1984; SHANKS and TRENT, 1980; SILVER and ALLDREDGE, 1981). The results of this study showed that detrital particles are a possible major food item for eel leptocephali, and that dissolved organic matter could also be part of their nutritional resource.

The activity of digestive enzymes, such as trypsin and kitinase, have been shown to be quite low in the gut of *C. myriaster* leptocephali and *M. cinereus* pre-leptocephalus larvae (OTAKE, unpublished). This suggests that leptocephali cannot fully digest organic matter contained in detrital particles. Decomposition of such organic matter by associated microorganisms, such as bacteria and protozoa, would be important in increasing the nutritional value of detrital particles.

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Drifting seaweed and associated ichthyofauna: Floating nursery in the Tohoku waters*

Patrick SAFRAN**

Abstract: Drifting seaweed and associated ichthyofauna were sampled in the Tohoku Area, northwest Pacific, in spring of 1988, 1989 and 1990, to analyse the structure of these communities and ecological relationships of the dominant fish species. Results as a whole showed: 1) The abundance of drifting seaweed in the Tohoku Area peaked in May–June and decreased in July. The young and fresh algae were dominated by *Sargassum hornerii*, and seemed to drift mainly from the nearest coast: Sendai Bay and its northern part. While starting drifting, they were almost defaunated and they reached the Kuroshio Extension where they were mixed and entangled with other seaweed-some from the southern part. 2) *Seriola quinqueladiata* was the dominant species of the associated fish community, and its escort was composed of *Thamnaconus modestus*, *Sebastes inermis*, *Hyperoglyphe japonica* and *Enedrias nebulosus*. *E. nebulosus*, which fed essentially on Gammarid crustaceans, was collected mainly in Sendai Bay; the other species, found in offshore water, were plankton feeder and did not exhibit any strong competition, indicating close cohabitation. 3) Juvenile *S. quinqueradiata* seemed to use drifting seaweed (along with the warm Kuroshio current) as a means of transportation during their migration from the southern spawning ground to northern Tohoku Area; but the most likely hypothesis, taking into consideration the number of rings counted on otoliths, might be a passive drift of eggs and larvae with the Kuroshio during a maximum of 30 days (effective period of survival), then juveniles might have encountered the Tohoku drifting seaweed and be associated with them since a period of about 10 days. Drifting seaweed-associated fish community was made of juveniles, like if it was a result of a regular flow of individuals passing into it and replenishing the stocks with juveniles, like a floating nursery, and they might have an influence on species recruitment.

1. Introduction.

The aggregations of pelagic fishes near or beneath drifting or moored objects at sea forms the basis of a number of commercial fisheries. "Floating Fish Shelter" is a fish shelter to collect fish such as skipjack, tuna, dolphin, etc. in offshore waters, and shad, mackerel, etc. in the coastal waters, taking advantage of the habit of pelagic fish to gather under floating objects drifting in surface waves. The former aims at forming a fishing ground to attract stationary demersal fish and thereby to increase fisheries catch, and at establishing itself as a place to conserve and rear fish (KOBAYASHI, 1989). This fishing method is the most popular in the sea area of Asia and Southeast Asia (HARDENBERG, 1950; SOEMARTO, 1960; GALEA, 1961; HUNTER and MITCHELL, 1967). Japanese poleand-line fisheries and American purse seine and live-bait fisheries take advantage of the association of yellowfin tuna (*Thunnus albacores* Bonnaterre), and oceanic skipjack (*Katsuwonus pelamis* Linnaeus) with algae, logs, and other flotsam (UDA, 1933; Mc NEELY, 1961). Moored rafts of bamboo or palm fronds are used to attract dolphin-fish (*Coryphaena hippurus* Linnaeus), in Japanese seine fisheries (KOJIMA, 1956). In addition to these commercially important species, many others of lesser or no commercial value are also encountered (HIROSAKI, 1960; KOJIMA, 1960; SENTA, 1962; ANRAKU and AZETA, 1965; GOODING and MAGNUSON, 1967; IDA *et*

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al., 1967; HUNTER and MITCHELL, 1968; MITCHELL and HUNTER, 1970; DOOLEY, 1972; IKEHARA, 1977; NAKATA *et al*., 1988; SANO, 1989; TSUKIDATE, 1989; SAFRAN and OMORI, 1990; SAFRAN, 1990b).

These aggregations are dominated initially by small juvenile fishes. The factors influencing those migrations and temporary concentrations have yet to be determined. Fishery studies tend to concentrate upon commercial adult populations, and knowledge of factors that influence the juvenile populations is often poor (WEINSTEIN, 1982; ALDERDICE, 1985). Recruitment to adult stocks depends on the events occuring during the juvenile growth period. Drifting or moored objects at sea ensure the permanence of populations, but at the same time, owing to their specificity, their limited area and the possible competition between species, they constitute a limitation, and likely a regulation mechanism for stocks. It is therefore clear that spatio-temporal variations, abundance fluctuations, and cohort successions of sampled populations inside these aggregations cannot be analysed for one target-species without taking into consideration the fluctuations of the other species. This reflects the realization that single-species population dynamic models are insufficient for fisheries management purposes. Multi-species interactions must be considered as well as the impact on stocks caused by fishing, etc. (SAFRAN, 1987b, 1990a).

Moreover, among the various floating objects on the sea surface, drifting seaweed are the most usual :the major species found around Japan are of the genus *Sargassum* and allied genera (YOSHIDA, 1963; OHNO, 1984). Although the Pacific Ocean Sargassum Complex has been studied in southern waters off Japan(UCHIDA and SHOJIMA,1958; HIROSAKI, 1960, 1965; SENTA, 1962, 1966; IDA *et al*., 1967; NAKATA *et al*., 1988), few description of the fish fauna associated with drifting seaweed has been made in the Tohoku Area (Northwest Pacific). The study presented here describes in this area the drifting seaweed and associated ichthyofauna, providing information on the fish community structure, and on the ecological inter- and intra-relation of the dominant species which compose this association.

Special attention is also given to a well known drifting seaweed-associated yellowtail *Seriola quinqueradiata* Temminck et Schlegel (ANRAKU and AZETA, 1967), and its escorts, in order to clarify the drift-associated mechanism and to emphasize the role of the drifting seaweed on the fish behavior.

This work is a part of a survey performed in the Tohoku waters and published in SAFRAN (1990b).

2. Materials and methods

Study area

Drifting seaweed are mainly distributed in coastal waters, their abundance reaching a peak in May–June and decreasing after August (YOSHIDA, 1963; OHNO, 1984). Thus, series of sampling were performed in late spring of 1988 and 1989, and in spring of 1990. In 1988, a first cruise, in Sendai Bay on R. V. "Suiko" was from June 6 to June 10 in the vicinity of a station 141°E, 38°N, a second, in the Kuroshio Extension (along the 38°N), was from Sendai Bay to 160°E, on R. V. "Waka Chiba Maru" from May 22 to June 10; and a third was carried out, in the northern part of the Tohoku Area, by T. S. "Hokusei Maru" from June 20 to July 4. In 1989, a first cruise was from May 25 to May 30 on R. V. "Tansei Maru", along the line shown in Fig. 1a ; a second, in the Kuroshio Extension, was from Sendai Bay to 140°E, on R. V. "Shin Dai To Maru" from June 5 to June 8 (Fig. 1b), a third, in Sendai Bay, was on June 24 in the vicinity of a station 141°E, 38°N, on R. V. "Suiko", and a fourth, also in Sendai Bay, was from July 6 to July 7 on R. V. "Shin Dai To Maru" (Fig. 1c). In 1990, a cruise in the Perturbed Area, along the 36°N and the 38°N, was from Sendai Bay to 150°E, on R. V. "Waka Take Maru" from May 12 to May 24.

Sampling method

Daily samples were collected using a net ca 7 m long with 2 mm mesh opening,

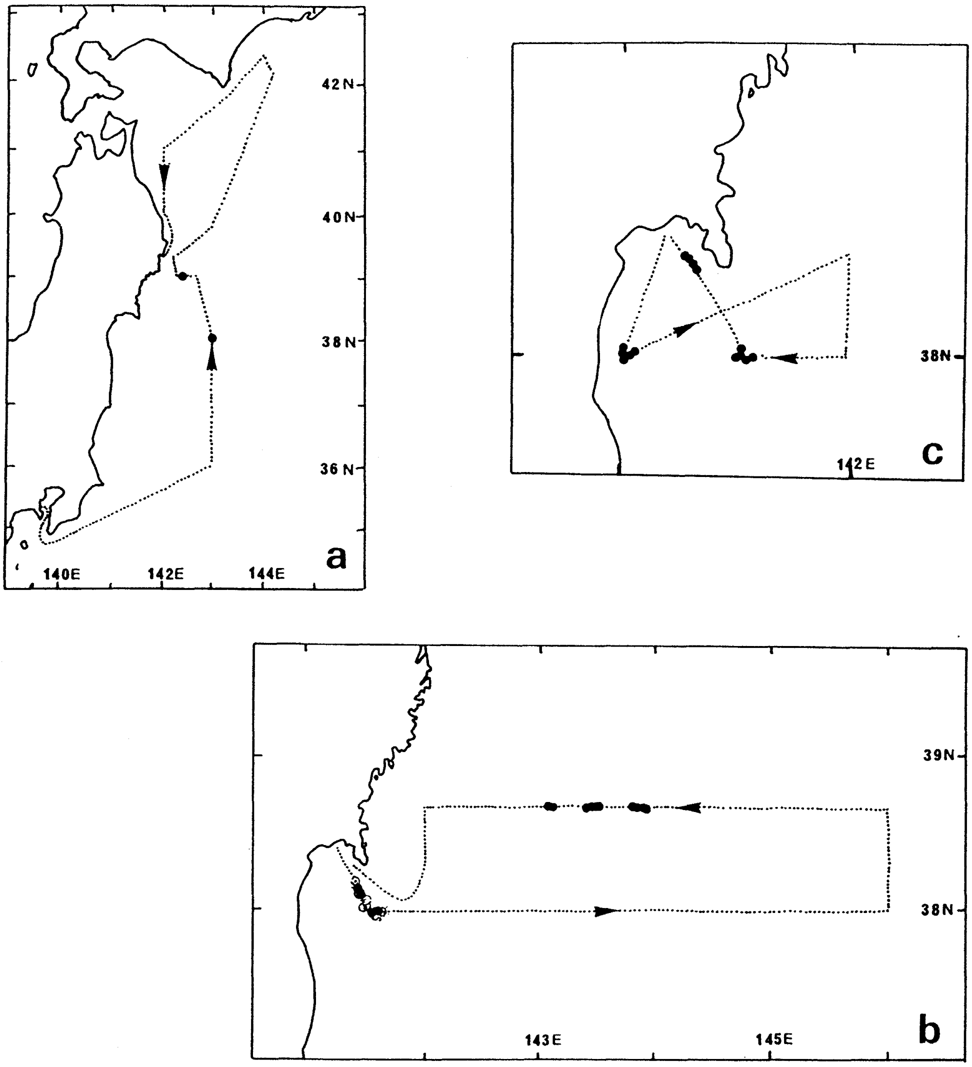

Fig. 1. Study area and sampling locations in 1989: overall location (a), the Perturbed Area along the Kuroshio Extension (b), and Sendai Bay (c). Dotted lines: the cruising routes; open circles: position of drifting seaweed; filled circles: sampling stations.

attached to a 2 m diameter mouth-ring. Two floats, fixed on the ring, allowed 2/3 of the mouth-ring to be immersed below the sea surface. A *Sargassum* patch that could be entirely caught was selected, when spotted on the sea surface, and sampled from the vessel's port side, at a speed of about 2 to 4 knots. Temperature and salinity were also recorded (in 1988). Though sampling errors were probably small, this method seemed to be unsuitable to collect the epiphytal fauna due to the turbulence of the water, the occurrence of eddies, and the inappropriate mesh size of the net. Algae samples were rinsed thoroughly in large tubs and the water strained through a sieve (<1 mm mesh opening). Organisms thus collected were preserved in 10% buffered formalin for later sorting and determination of stomach contents, in 1988. While in 1989, they were preserved in 10% alcoholic solution for later lecture of otoliths; and in 1990, they were frozen on board. The wet weight of seaweed was measured to the nearest 0.5 kg on a machete beam-balance, a portion of which was then preserved in buffered formalin for epibiotic analysis, and the remainder discarded. Fish standard lengths (SL) were measured to the nearest mm; the wet weight of each fish species was determined to the nearest g. Stomach contents analyses were conducted on preserved specimens of the dominant species to check a possible inter-and/or intra-specific competition phenomenon. The shortest distance to the shore from the location of each collection was measured to the nearest nautical mile to determine if the size, the growth or the number of fishes were related to the distance from the shore. Otoliths of *Seriola quinqueradiata* and some of *Tamnaconus* (*Navodon*) *modestus* (in 1989) were extracted to get a better idea of their age by observation of daily growth increments (CASSELMAN, 1983). Otoliths were washed and rinsed with a sodium hypochlorite solution, mounted on a glass microscope slide with a drop of nail varnish, and removed under a binocular microscope (Olympus, equipment from the Tohoku Regional Fisheries Research Laboratory), where growth rings were counted.

Data analysis

The haul composition was variable so the ecological diversity of the community was estimated by the Shannon Index (SHANNON and WEAVER, 1963), while Evenness was obtained by the Pielou Index (PIELOU, 1966). A good description of the specific diversity (H') of a sample is given by a representation of the distribution of individuals among species, which is the structure of a community as the arrangement in a definite pattern of organization and/or the aggregate of species of an entity in their relationships to each other (FRONTIER, 1985). Rank-Frequency Diagrams (RFDs) are used to model this distribution. The shape of the curve is generally irregular, smoothed curves are obtained by cumulating samples (following SAFRAN, 1987a and b). In this study, cumulative RFD were obtained by summing species by species; species are ranked after summing their abundances over the set of samples, due to the weakness of the sampling strategy (SAFRAN, 1990a). Qualitative similarity was estimated by the Ochiai Index (OCHIAI, 1957), based on the presence/absence of species.

Numerical data were arranged in ecological categories, obtained from stomach analyses of the dominant species in the drifting sea weed-associated community. Thus study of niche relationships and the ecological role of an organism in a community, especially in regard to food consumption could be performed. The niche breadth of a species can be estimated by measuring the uniformity of the distribution of individuals of that species among the resource states (COLWELL and FUTUYMA, 1971):the measure of species niche breadth is the Shannon-Wiener formula for information and uncertainty (SHANNON and WEAVER, 1963). Niche overlap, as the joint use by two or more species of a resource, or resources, regardless of resource abundance (ZARET and RAND, 1971), was estimated using the overlap measure of MORISITA (1959) as modified by HORN (1966). Diet similarity was estimated by the Ochiai Index (OCHIAI, 1957), based on the presence/absence of prey.

3. Results

Drifting seaweed

Drifting seaweed were mainly found in the Perturbed Area along the Kuroshio Extension, where waters were mixed showing a thermic front. In 1988, no obvious relation was evident between the distance from shore and the seaweed wight: r = −0.565 (Fig. 2a). Nevertheless, the bulk of drifting algae found in Sendai Bay (mean value 24.21±18.47 kg) were larger than those collected offshore along the Kuroshio Extension (mean value 9.42 ±7.41 kg). Similarly, the same kind of results were noticed in 1989 with a lower correlation: r = −0.133 (Fig. 2b), with a larger bulk of drifting seaweed in Sendai Bay (mean value 20.17±15.58 kg) than in the Kuroshio Extension (mean value 10.23 ±14.92 kg) . In 1990 (Fig. 2c), drifting seaweed caught near the coast (ca 21 nautical miles) were found in cold water (15.4℃), bigger (21.14 ± 8.21kg) and without fauna, while offshore samples, eollected in warm

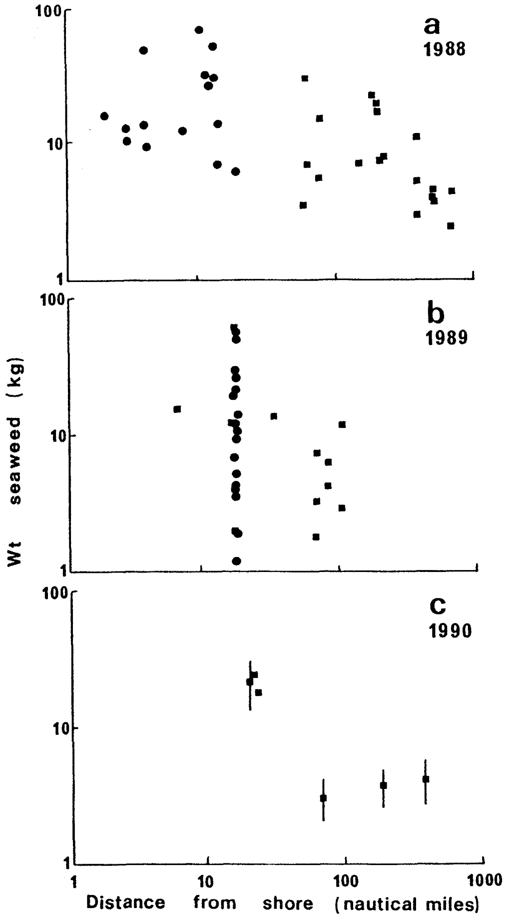

Fig. 2. Relationships between distance from shore and the weight of drifting seaweed in 1988 (a), 1989 (b), and 1990 (c). Filled circles: samples collected in Sendai Bay; filled squares: samples from the Kuroshio Extension.

water (17.26°±0.52℃), were smaller (3.59 ±0.34 kg) with fauna (epiphytal fauna and fishes). The difference in the size of the offshore samples were not highly significant (3.11±1.13 kg at 70 miles, 3.79 ±0.92 kg at 190 miles, and 3.88±1.71 kg at 390 miles).

In 1988, 7 species were found in Sendai Bay and were dominated by *Sargassum hornerii* (Turner) C. Agardh. In the Perturbed Area, 14 species were collected and the dominant species was *S. hornerii*, while only 3 species were caught near Hokkaido. The results obtained showed *S. hornerii* as the dominant species among 20 collected ($H' = 3.090$, $E = 0.715$). *Sargassum patens* was found only offshore along the Kuroshio Extension, while *Coilodesme japonica* was caught exclusively off Hokkaido and always associated with *Cystoseira hakodatensis*; and *Sargassum confusum* and *Eisenia bicyclis* were sampled in Sendai Bay. In 1989, 5 species were found in the Perturbed Area, While 4 species were sampled in Sendai Bay. *S. hornerii* was the dominant species among 7

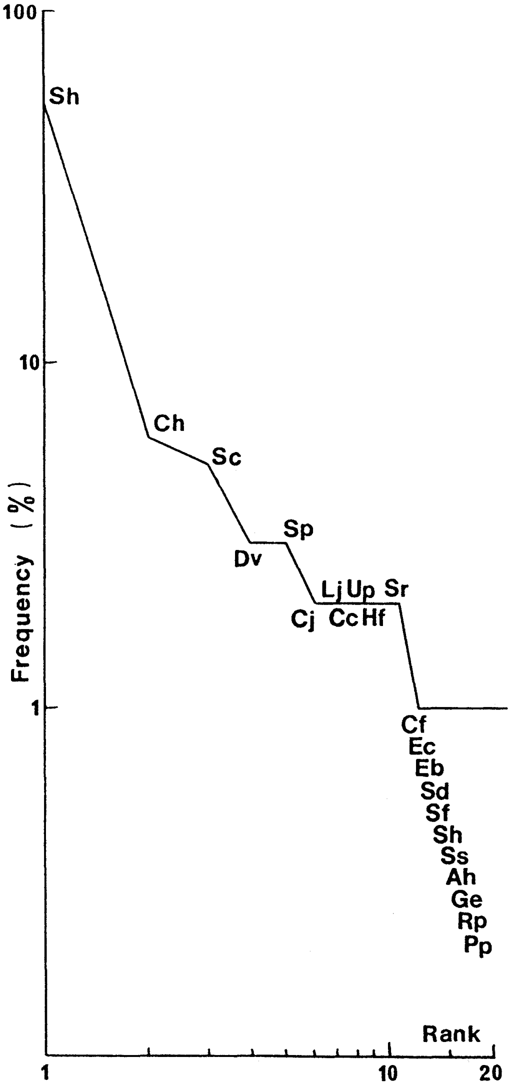

Fig. 3. Cumulative Rank-Frequency Diagram obtained for the drifting seaweed community in the Tohoku Area. Species abbreviations as in Appendix.

collected (H' = 1.634, E = 0.582). The 1990 samples were mainly *S. hornerii*. These results led to a cumulative RFD giving an overall picture of this drifting seaweed community in the Tohoku area (Fig. 3), which was made of 22 species (H' = 2.613, E = 0.586), and dominated by *S. hornerii*. The shape of the RFD showed a juvenile stage for the sampled aggregations of algae.

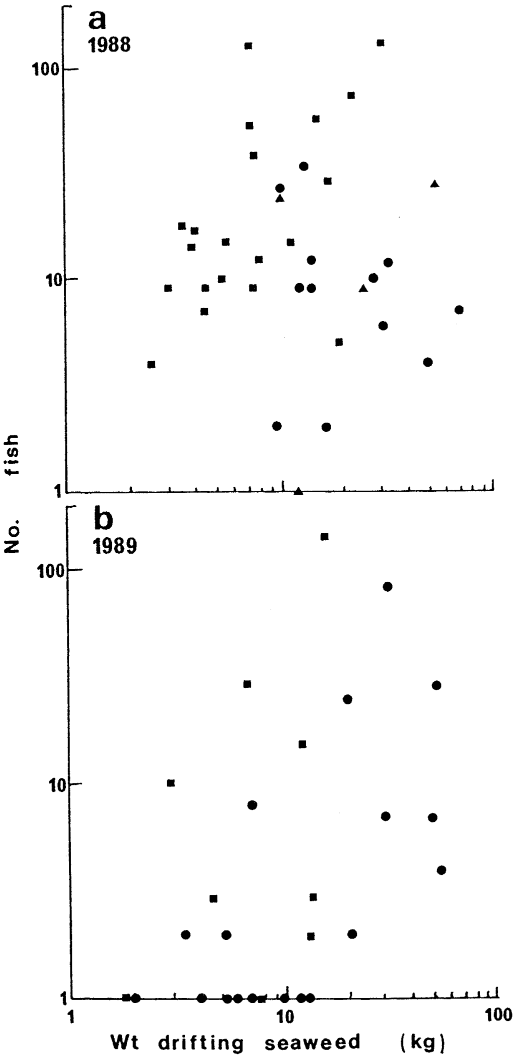

Fig. 4. Relationships between weight of drifting seaweed and number of fish gathering within in 1988 (a), and in 1989 (b). Filled circles: samples collected in Sendai Bay; filled squares: samples from the Kuroshio Extension; filled triangles: samples obtained at the outset of the cruise off Hokkaido.

Associated ichthyofauna

There was no obvious correlation between individual and species number of fishes, and/or seaweed weight, and hydrographic condition (but this last point is doubtful since most of the seaweed, where fish were found, were caught in similar hydrographic conditions and always in thermic fronts). Statistical analyses revealed a low correlation between the seaweed weight and number of fishes, the correlation coefficient was r = 0.557 with 30.8% due to the correlation and 69.2% residual, in 1988 (Fig. 4a). The correlation was lower in 1989: r = 0.248 (Fig. 4b); while there was no relation with the specific richness. Similarly, no obvious relation was evident between the distance from shore and the specific richness, while low correlations were found with the number of fishes with r = 0.443 in 1988, and r = −0.137 in 1989.

Considering the Tohoku Area as a geographical entity, as opposed to just the southern area, and grouping all samples, the cumulative RFD revealed a general condition for the drifting seaweed-associated fish community (Fig. 5a). The specific diversity was H' = 2.698 with an Evenness E = 0.596 for 1200 individuals of 23 species. *Seriola quinqueradiata* (42.56%) was dominant, and was accompanied by *Tahmnaconus modestus* (21.11%), *Sebastes inermis* (9.48%), *Hyperoglyphe japonica* (5.90%) and *Enedrias nebulosus* (5.74%). In 1989, nearly the same species were found. The results obtained led to a general cumulative RFD showing *Seriola quinqueradiata* (35.71%) in thi dominant position, and a good diversity H' = 2.536 with an Evenness E = 0.597 for 406 individuals of 19 species. *Thamnaconus modestus* (32.51%) and *Sebastes inermis* (6.40%) were the escort (Fig. 5b). In 1990, fishes sampled were mainly *Seriola quinqueradiata*.

In most of the sampled drifting seaweed, especially in the warm waters, eggs of Pacific Saury *Cololabis saira* were found. In 1989, a large quantity was noticed in the samples collected in Sendai Bay. Most of the fishes captured were juveniles and their biological parameters are given in Tables 1 and 2.

Between the distance from shore and the

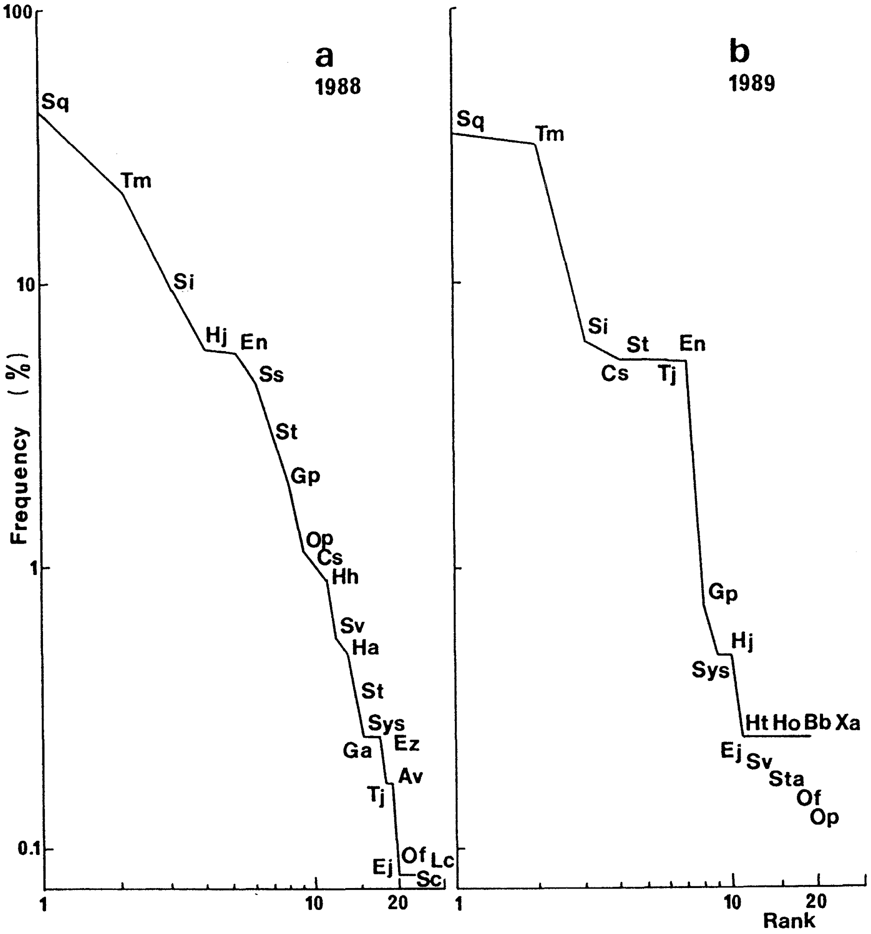

Fig. 5. Cumulative Rank-Frequency Diagrams obtained for the fish communities associated with drifting seaweed in the Tohoku Area in 1988 (a), and in 1989 (b). Species abbreviations as in Tables 1 and 2.

minimum or mean body-length of fish, significant differences were noticed in 1990 with *S. quinqueradiata* (Fig. 6a). The otoliths extracted from these specimens (Fig. 6b) were further proof of the significant differences in the size-growth with the distance from shore, consequently with the drift:

at 70 miles: mean number of rings = 39.25±3.77 with SL = 4.16 ±1.38 cm and Wt = 0.87 ±0.14 g,

at 190 miles: mean number of rings = 46.25 ±4.97 with SL = 3.83 ±0.69 cm and Wt = 1.26 ±0.68 g,

and at 390 miles: mean number of rings = 43.75±5.93 with SL = 2.9±1.15 cm and Wt = 0.63 ±0.35 g.

In 1989, the arithmetic mean for the number of rings counted on *S. quinqueradiata*'s otoliths was equal to 39.71 ±9.41 with SL = 40 ±20.09 mm: while it was 39.5 ±2.29 with SL = 33 ±9.11 mm in *T. modestus*. In 1990, the arithmetic mean for the number of rings in *S. quinqueradiata* was 43.08 ±5.75 with SL = 3.64 ±0.48. No obvious relation could be noticed between the number of rings and the length of the fish (r = 0.445).

Niche relationship

In 1988, most of the 735 stomachs analysed were full:emptiness coefficient was found

Table 1. Biological parameters in fishes associated with drifting seaweed in the Tohoku area in 1988. Symbols are r: correlation factor; a: condition factor or Fulton Index; b: allmetric factor; K: ponderal index ($K = 10^3W/L^3$) in the weight-length relationship ($W = aL^b$). Blank: damaged specimen.

Species	*abbr.*	r	a 10^{-2}	b	K	Length (cm)				Weight (g)			
						Min.	Mean	SD	Max.	Min.	Mean	SD	Max.
Abudefduf vaigiensis	Av												
Cololabis saira	Cs	0.969	0.465	2.779	2.95	2.9	3.32	1.13	4.3	0.07	0.11	1.43	0.24
Enedrias nebulosus	En	0.960	0.338	2.731	2.22	2.9	5.68	1.18	7.4	0.06	0.39	1.61	0.80
Engraulis japonica	Ej												
Erilepsis zonifera	Ez												
Gasterosteus aculeatus	Ga						2.3			0.10			0.12
Girella punctata	Gp	0.845	1.09	3.188	10.55	1.3	1.55	1.08	1.8	0.02	0.04	1.34	0.07
Hexamogrammos agrammus	Ha	0.994	3.375	3.545	11.34	4.2	5.41	1.52	11.4	0.63	1.49	4.47	21.00
Histrio histrio	Hh	0.995	3.53	3.219		1.2	2.62	2.00	11.1	0.09	0.78	9.45	99.45
Hyperoglyphe japonica	Hj	0.995	2.85	2.751	16.33	3.6	7.56	1.55	27.6	0.94	7.44	3.38	262.9
Liza carinata	Lc												
Oplegnathus fasciatus	Of						1.9				0.13		
Oplegnathus punctatus	Op	0.996	1.89	3.154	23.9	1.2	2.64	1.47	4.6	0.04	0.40	3.36	2.40
Sebastes inermis	Si	0.980	1.39	2.939	16.81	2.3	3.53	1.27	6.4	0.20	0.56	2.03	4.50
Sebastes schlegeli	Ss	0.942	0.60	3.538	14.85	0.9	3.16	1.09	4.4	0.01	0.37	1.37	1.36
Sebastes taczanowski	Sta												
Sebastes thompsoni	St	0.952	0.342	5.013	6.32	0.9	1.66	1.33	2.2	0.03	0.04	4.44	0.12
Sebastes vulpes	Sv												
Seriola quinqueradiata	Sq	0.996	0.957	3.039	14.21	1.9	5.97	1.41	15.7	0.10	2.18	2.86	53.53
Stephanolepsis cirrhifer	Sc												
Syngnathus schlegeli	Sys					15.8			20.7	1.01			2.24
Thamnaconus modestus	Tm	0.989	1.29	3.095	15.76	1.7	3.75	1.29	6.8	0.08	0.77	2.21	4.79
Trachurus japonicus	Tj						3.0				0.27		

Table 2. Biolobical parameters in fishes associated with drifting seaweed in the Tohoku area in 1989. Symbols are r: correlation factor; a: condition factor or Fulton Index; b: allometric factor; SCI: stomach contents index. Blank: damaged specimen

Species	*abbr.*	r	a 10^{-2}	b	Length (cm)				Weight (g)				SCI	
					Min.	Mean	SD	Max.	Min.	Mean	SD	Max.	mean	SD
Blepsias bilobus	Bb													
Cololabis saira	Cs	0.517	0.849	1.662	2.0	2.22	1.06	2.5	0.03	0.03	1.20	0.04		
Enedrias nebulosus	En	0.971	0.603	2.465	3.6	5.42	1.21	6.7	0.15	0.39	1.63	0.84	4.92	1.98
Engraulis japonica	Ej					1.60				0.03				
Girrella punctata	Gp	0.902	3.664	1.494	1.5	1.66	1.15	2.0	0.07	0.08	1.25	0.11		
Hexamogrammos agrammus	Ha					7.0				4.33				
Hippocampus takakurae	Ht													
Hyperoglyphe japonica	Hj				5.2	5.35	0.21	5.5	4.35	4.80	0.64	5.25	11.78	3.13
Oplegnathus fasciatus	Of													
Oplegnathus punctatus	Op					1.40			0.07					
Sebastes inermis	Si	0.990	2.897	2.701	1.3	4.03	1.49	6.0	0.08	1.25	2.97	4.03	6.96	1.82
Sebastes taczanowski	Sta													
Sebastes thompsoni	St	0.973	2.328	2.759	1.6	2.19	1.21	3.1	0.08	0.20	1.73	0.50	4.43	1.55
Sebastes vulpes	Sv					2.10				0.16				
Seriola quinqueradiata	Sq	0.992	1.183	3.043	1.0	4.04	1.62	11.4	0.01	0.83	4.36	23.87	6.89	2.70
Syngnatuus schlegeli	Sys					18.3			1.56					
Thamnaconus modestus	Tm	0.988	3.963	2.156	1.0	2.75	1.41	4.2	0.04	0.35	2.12	1.03	5.73	2.52
Trachurus japonica	Tj	0.979	3.228	2.310	1.7	2.48	1.23	3.1	0.12	0.26	1.64	0.49	3.79	1.60
Xanthichthys auromarginatus	Xa													

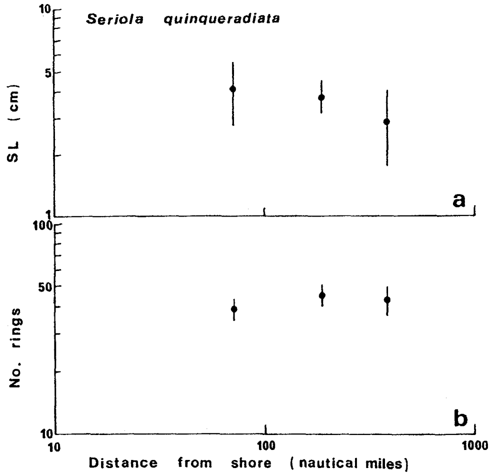

Fig. 6. *Seriola quinqueradiata*: (a) standard length (SL, mean and range), and (b) number of rings counted on otoliths of specimens collected with drifting seaweed in the Tohoku Area at various distances from shore in 1990.

only for *S. quinqueradiata* (6.34), *T. modestus* (10.92), and *H. japonica* (8.82). Except *Enedrias nebulosus*, which fed essentially on gammarid organisms, the dominant food items were copepods in the smallest individuals (< 7 cm) of *S. quinqueradiata*, *T. modestus* and *S. inermis*. No obvious relation was noticed between food organisms of the fish and epiphytal fauna attached to floating seaweed (even if sometimes, some few benthic prey were found in some fish stomachs, their quantity and abundance (< 2%) were not significant compared to the whole diet of the fish). The four species, excluding *E. nebulosus*, were essentially plankton feeders. Some of the fish larvae found in *S. quinqueradiata* were identified as species belonging to the genus *Sebastes*. The food composition of *Hyperoglyphe japonica* was rather complicated and the most diversified, its niche breadth index (H' = 3.385) being the highest. *Pyrosoma* sp. was found in all the stomachs. The other species had relatively simple feeding habit. The smallest niche breadth index was found in *S. inermis* (H' = 1.591), while those of *S. quinqueradiata* (H' =2.211) and *T. modestus* (H' =2.248) were not excessively different. Low similarity values were obtained for all diets when niche overlap indices were high, specially between *S. quinqueradiata*, *T. modestus* and *S. inermis* (values > 0.850; Table 3). In 1989, *Hyperoglyphe japonica* was almost absent from the samples and therefore was not analysed, while *Sebastes thompsoni*, which was among the five dominant species, was studied. All the 271 stomachs were full. Once more again, except *E. nebulosus*, the four species were essentially plankton feeder. The highest niche breadth index was found in *T. modestus* (H' =2.583), and the smallest one in *S.thompsoni* (H' =1.166), while those of *S. quinqueradiata* (H' =1.563) and *E. nebulosus* (H' =1.659) were not excessively different, and the one of *S. inermis* was higher (H' =2.407). Some Gammaridae found in the diet of *E. nebulosus* were identified as *Jassa falcata*, and some Caprellidae as *Caprella penantis*. Some benthic prey were found in the diet of *S. inermis*, the Gammaridae were identified as *Jassa falcata* and represented ca 12% of the whole diet, while some Caprellidae could be identified as *Caprella penantis* and *Caprella danilevskii*, and represented ca 8% of the diet. Similarity values were low (except between *S. quinqueradiata, and S. inermis*: 0.707) though niche overlap indices were high, specially between *S. quinqueradiata*, *T. modestus*, and the *Sebastes* sp. (Table 4).

4. Discussion

Drifting seaweed

The shape of the RFD was almost similar and showed a "juvenile community" insinuating that *Sargassum hornerii* was the pioneer leader of the drifting seaweed in the Tohoku Area. Drifting seaweed found in this Area seemed to have a peak of abundance in May-June and decreased in July. This might be induced by a decrease i temperature caused by the mixing of the cold Oyashio and warm Kuroshio currents, by the occurrence of numerous eddies along the Kuroshio Extension, and by the seasonal change in abundance connected to the life history of the seaweed. The bulk of algae found offshore were smaller than those collected near the coast or in Sendai Bay. Most seaweed were caught in healthy conditions with intact holdfasts and receptacles. Nevertheless, the coastal drifting seaweed

Table 3. Diet similarity obtained by Ochiai Index (1957) and niche overlap estimated by Morisita Index (1959) as modified by Horn (1966) in the dominant species of the drifting seaweed-associated fish community in the Tohoku area, in 1988. Species abbrebviations given in Table 1.

	Sq	Tm	Si	Hj	En	
Sq		0.417	0.354	0.544	0.306	Diet
Tm	0.847		0.589	0.476	0.204	Similarity
Si	0.881	0.864		0.481	0.28	
Hj	0.510	0.627	0.487		0.250	
En	0.491	0.462	0.504	0.339		
	Niche overlap					

Table 4. Diet similarity obtained by Ochiai Index (1957) and niche overlap estimated by Morisita Index (1959) as modified by Horn (1966) in the dominant species of the drifting seaweed-associated fish community in the Tohoku area, in 1989. Species abbrebviations given in Table 2.

	Sq	Tm	Si	St	En	
Sq		0.447	0.707	0.354	0.354	Diet
Tm	0.702		0.527	0.316	0.632	Similarity
Si	0.874	0.823		0.272	0.500	
St	0.897	0.676	0.834		0.250	
En	0.290	0.305	0.532	0.271		
	Niche Overlap					

seemed to be younger and freshly detached from their near substratum, since some of their holdfasts were still attached to some coastal stones. While drifting, seaweed might become fragile and weaker due to their ageing combined with rough environmental and oligotrophic conditions. *Sargassum patens,* which was found offshore in the Perturbed Area, was the only typical southern species, while *Coilodesme japonica,* always associated with *Cystoseira hakodatensis,* was the only typical northern species caught exclusively off Hokkaido. The drifting seaweed found in the Tohoku Area seemed to have drifted mainy from the nearest coast:Sendai Bay and its northern part (the southern coast are mainly made of sand beach). Moreover, few species of the Tohoku community were reported in the southern waters of (and off) Japan, and compared with previous findings off Shikoku (Ohno, 1984), the qualitative similarity was very low (0.361). Most of the species described in this study are listed in Matsushima Bay and in the northern part of Sendai Bay-Kinkasan (Takamatsu, 1936; Segawa *et al.*, 1964). Caprellid fauna associated with floating seaweed, especially *Caprella acanthogaster,* was further proof of drift-origin since this species is characteristic of northern waters and is reported to be from the Tohoku District (Hirayama and Kikuchi, 1980).

Associated ichthyofauna

All the fishes found with the drifting seaweed in the Tohoku area had been previously reported as species with a tendency to associate with drift algae. Concerning the five dominant species of the present community, they belong to a category called resident, either obligatory as for *Thamnaconus modestus, Sebastes inermis* and *Enedrias nebulosus,* or non obligatory like *Seriola quinqueradiata* and *Hyperoglyphe japonica* (Senta, 1965; Ida, 1986). The faunistic list found in the Tohoku community was not different from previous findings reported from southern waters off Japan. The dominant species and the structure were however different. *E. nebulosus,* which fed essentially on gammarid, the dominant species in Sendai

Bay, was essentially found in nearshore water, while *S. quinqueradiata* and *T. modestus* were collected in offshore water along the Kuroshio Extension. *S. quinqueradiata* (40.83 %) was the dominant species in the Tohoku drifting seaweed-associated fish community, and its escort was composed of *T. modestus* (23.99%), *S. inermis* (8.70%), *E. nebulosus* (5.59%), and *H. japonica* (4.54%); all were plankton feeders and found in close cohabitation, but did not show any strong competition which could lead to the exclusion of one of the dominant species.

Seaweed-fish association: floating nursery

The ecological role of drifting seaweed on the distribution of plankton and the movement of larval fishes, as another important source of5 food especially for *Seriola quinqueradiata* (DAMANT, 1921; ANRAKU and AZETA, 1967), could explain their presence. Shadow of drifting seaweed on the sea surface might have an influence on nychthemeral plankton migration by inducing a kind of rheotropism (phototropism) which could attract the organisms during their migration, like rot the fishes (LYON, 1905; KOJIMA, 1957; BOUGIS, 1976; PERES, 1976). Summer set net catches of young *Seriola quinqueradiata* (>15 cm long) were reported by fishermen in Sendai Bay. Juvenile stages were, however, uncommon or never taken. Considering that the spawning ground of this species is located off the southern coast of Japan (south of 34°N) and the role of the Kuroshio warm current on the transportation of the floating objects such as fish eggs and larvae (FUJIMOTO and HIRANO, 1972), juvenile *S. quinqueradiata* presumably used different drifting seaweed, of varying origin according to the spawning season (from March to June), as means of transportation during their migration from south to north along the Kuroshio. When a patch of algae reduced the size, juveniles probably migrated to another fresh, healthy seaweed drifting from the nearest coast, becoming independent and pelagic when reaching to young adult stage. Presence of *Sargassum patens* in offshore samples seemed to support this drift-origin hypothesis form the south. But the most likely hypothesis, taking into consideration the number of rings counted on otoliths, might be a passive drift of eggs and larvae with the warm Kuroshio current from the south to the north. Assuming that the current speed is about 20 miles per day, and that the effective period of survival of fish eggs and larvae floating on the surface of the ocean is about 30 days (FUJIMOTO and HIRANO, 1972), the juveniles of fishes found with the Tohoku drifting seaweed might be probably associated with them since a period of about 10 days, and might have encountered them in the Tohoku Area.

Moreover, *Seriola quinqueradiata*, which was the main catch in May 1990, seemed to be the pioneer species, followed by *Thamnaconus modestus*, and to induce the arrival of the others fishes in this Tohoku community (the "colonization" of this drifting seaweed ecosystem). The mean SL and the mean number of otolith rings of fishes collected remained stable among the drifting seaweeds examined, the significant differences likely showing the origin of different cohorts, thus indicating a type of "turn-over" phenomenon among these fishes. Only juveniles could enter and live around the drifting seaweed, while adults are independent and pelagic ; like if it was a result of a regular flow of individuals passing into the drifting seaweed and replenishing the stocks with juveniles. Moreover, drifting seaweed seemed to play a key role as spawning ground and eggs propagation for the Pacific saury *Cololabis saira* (KIMURA *et al*., 1958).

These results and observations led to the assumption that drifting seaweed are comparable to a nursery ecosystem, i. e. a feeding and growth place (LENANTON *et al*., 1982; SAFRAN, 1987a and b; 1990a), but a drifting one, where juveniles of fishes could find conditions necessary for existence and survival with shelter and protection, like beneath a Fish Aggregating Device (KOBAYASHI, 1989), but a natural one. Finally, a major implication of this study is that the association of fishes with drifting seaweed might have an influence on recruitment patterns (the seasonal change in oceanographical conditions in the Tohoku

Area-due to the seasonal change of the intrusion of the cold Oyashio into the warm Kuroshio, to the numerous eddies, to the different velocities of the currents, etc.-might have an influence on the life history of the seaweed, therefore on their drifting ability and finally on the rucruitment patterns of the fishes).

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APPENDIX

Drifting seaweed found in the Tohoku area

Species	abbr.	order	class	division
Codium fragile	Cf	Coiales	Chlorophyceae	Chlorophyta
Coilodesme japonica	Cj	Dictyosiphonales	Heterogeneratae	Phaeophyta
Desmarestia viridis	Dv	Sporogonales	〃	〃
Laminaria japonica	Lj	Laminariales	〃	〃
Costaria costata	Cc	〃	〃	〃
Ecklonia cava	Ec	〃	〃	〃
Eisenia bicyclis	Eb	〃	〃	〃
Undaria pinnatifida	Up	〃	〃	〃
Cystoseira hakodatensis	Ch	Fucales	〃	〃
Hizikia fusiforme	Hf	〃	〃	〃
Sargassum patens	Sp	〃	〃	〃
Sargassum hornerii	Sh	〃	〃	〃
Sargassum ringgoldianum	Sr	〃	〃	〃
Sargassum confusum	Sc	〃	〃	〃
Sargassum hemiphyllum	Sh	〃	〃	〃
Sargassum duplicatum	Sd	〃	〃	〃
Sargassum serratifolium	Ss	〃	〃	〃
Sargassum fulvellum	Sv	〃	〃	〃
Asparagopsis hamifera	Ah	Nemalionales	Floridae	Rhodophyta
Grateloupia elliptica	Ge	Cryptomeniales	〃	〃
Rhodoglossum pulcherum	Rp	Gigartinales	〃	〃
Ptilota pectinata	Pp	Ceramiales	〃	〃

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Résumé: Algues dérivantes et ichthyofaune associée ont été échantillonnées dans les eaux du Tohoku, Pacifique nord-ouest, en été 1988, 1989 et 1990, pour analyser la structure de ces communautés et les relations écologiques entre les différentes espèces dominantes de poissons. Les résultats obtunus montrèrent: 1) un pic d'abondance en algues dérivantes dans le Tohoku en mai-juin et une décroissance en juillet. *Sargassum hornerii* représentait l'espèce dominante parmi ces algues jeunes et fraiches qui semblaient venir principalement de la côte proche: baie de Sendai et sa partie nord. Les algues commencàrent à dériver, généralement défaunées, pour gagner l'Extension du Kuroshio où elles se mélangèrent à d'autres espèces-certaines venant du sud. 2) L'espèce dominante de la communauté ichthyologique était *Seriola quinqueradiata*, escortée par *Thamnaconus modestus*, *Sebastes inermis*, *Hyperoglyphe japonica* et *Enedrias nebulosus*. *E. nebulosus*, dont le régime alimentaire était composé essentiellement de gammaridés, fut collecté principalement en baie de Sendai, tandis que les autres espèces, trouvées au large et se nourrissant essentiellement de plancton, semblaient cohabiter sans compétition. 3) Des jubéniles de *S. quinqueradiata* semblaient utiliser les algues dérivantes, le long du courant chaud Kuroshio, comme moyen de transport durant leur migration sud-nord. Néanmons, l'hypothése la plus probalbe, tenant compte du nombre d'anneaux de croissance des otolithes, serait une dérive passive des oeufs et larves avec le Kuroshio durant un maximum de 30 jours (période effective de survie), puis les juvéniles auraient rencontré les algues du Tohoku et se seraient associés à elles depuis une dizaine de jours. L'ichthyofaune associée était composée de juvéniles, comme si un flot régulier de juvéniles traversait les algues en permanence, comme dans une nourricerie flottante, et pouvant influer sur le déterminisme du recrutement.

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Prediction of the distribution of settled *Sargassum* propagules*

Satoru TODA**

Abstract: This paper investigated the way to predict the distribution of *Sargassum* propagules settled on the sea bottom using diffusion parameters obtained by current measurements. Solving a vertical transport equation, I estimated the vertical flux of propagules at the sea bottom and assumed that the lateral distribution of drifting propagules is expressed by the Gaussian distribution. Combining the vertical flux of propagules and horizontal diffusion, I proposed a model that predicts the distribution of *Sargassum* propagules settled on the sea bottom.

In order to obtain the diffusion parameters of this model, I made current measurements around *Sargassum* forests in Gokasho Bay, Mie Prefecture, Japan. Using these parameters, I predicted the distribution of settled propagules released instantaneously from the center of a *Sargassum* forest. I compared the predicted distribution with the field data obtained by using artificial substrata. The distribution predicted by the model using these diffusion parameters agreed well with the actually measured distribution of propagules of *S. horneri* around an offshore forest.

1. Introduction

One of the most precarious stage in the life of any benthic organisms is their dissemination phase. For most seaweeds, microscopic propagules with little or no powers of locomotion represent the most important, often the only dispersal mechanism. However, this aspect of algal ecology has been relatively little studied. This paper proposes a method for predicting the distribution of settled propagules of *Sargassum* by using diffusion parameters obtained from current measurements and compares the predicted distribution with the measured distribution of *S. horneri*.

2. Release, settlement and adhesion of propagules of *S. horneri*

S. horneri, a brown seaweed which is popular in central Japan, become fertile in April and May. Eggs are found on the surface of the receptacles, and after few days propagules are released from the surface of the receptacles before development of rhizoids, and sink with their base up. After propagules touch on substratum, the tenacity of adhesion increases with the length of the period for which the propagules have been in residence on the substratum (OKUDA, 1984). After two days the percentage of the propagules of *S. horneri* surviving exposure to a water flow of 90cm/s exceeds ninety percent (IHKURA, personal communication), and they are hardly dislodged from the substratum under ordinary wave conditions in *Sargassum* forests.

3. The model

The purpose of the model is to predict

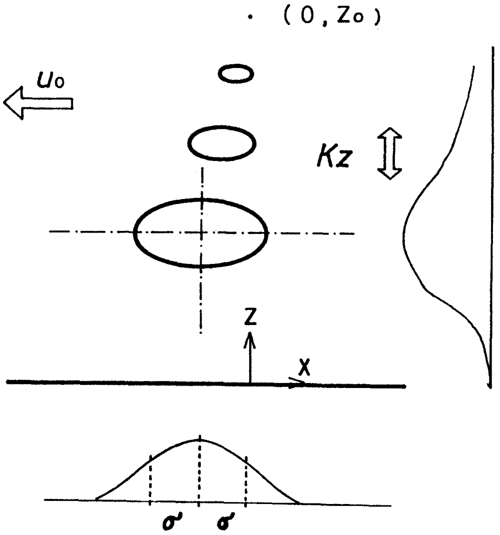

Fig.1. Schematic processes through which propagules released from a single point sink and diffuse in turbulent water.

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**Inland Station, National Research Institute of Aquaculture, Tamaki, Mie, 519-04 Japan the distribution of settled propagules using the diffusion parameters obtained by current measurements. I intend the model to be simple, but capable of realistically predicting the distribution of settled propagules.

I deal with a two-dimensional diffusion problem. Consider the situation shown in Fig. 1. A propagule is shed at a moment ($t=0$) from a single point set at some distance from the sea bottom ($x=0$, $z=z_0$). For simplicity, I deal with vertical and lateral diffusion independently each other.

(1) *Vertical diffusion*

If $p_z(z, t)$ describes the probability that a propagule is at point z at time t, then the equation describing the dynamics of the probability is given by

$$\frac{\partial p_z}{\partial t}+w\frac{\partial p_z}{\partial z}=K_z\frac{\partial^2 p_z}{\partial z^2}, \quad \cdots\cdots\cdots\cdots(1)$$

where w is the sinking velocity of the propagule and is assumed to be a negative constant, K_z is the vertical eddy diffusivity and is assumed to be constant. This equation can be solved if initial and boundary conditions are provided. First, I assume that the initial condition is $p_z(0, z)=\delta(0, z_0)$. The second assumption is that the propagule adheres when it contacts the sea bottom, $p_z=0$ at $z=0$, and the water depth is sufficiently deep to neglect surface effects. Solving Eq. (1), which applies the initial and boundary conditions, we see that

$$p_z=\frac{1}{2(\pi K_z t)^{1/2}}\left[\exp\left\{-\frac{(z-z_0)^2}{4K_z t}\right\}-\exp\left\{-\frac{(z+z_0)^2}{4K_z t}\right\}\right]\cdot\exp\left\{\frac{w(z-z_0)}{2K_z}-\frac{w^2 t}{4K_z}\right\}.$$
$$\cdots\cdots\cdots\cdots\cdots\cdots(2)$$

Calculating the flux at the sea bottom, we see that

$$f_z(t)=\left[wp_z+K_z\frac{\partial p_z}{\partial z}\right]_{z=0}$$
$$=\frac{1}{2(\pi K_z t)^{1/2}}\frac{z_0}{t}\cdot exp\left\{-\frac{(z_0+wt)^2}{4K_z t}\right\}.\cdots\cdots(3)$$

This $f_z(t)$ is the probability that the propagule released from $z=z_0$ at $t=0$ contacts the sea bottom at a time t, and is shown in Fig. 2 for values of K_z. The release height (z_0=5m) and sinking velocity (w=-5mm/s) are typical values for *S. horneri*.

From this figure, we can see that for the

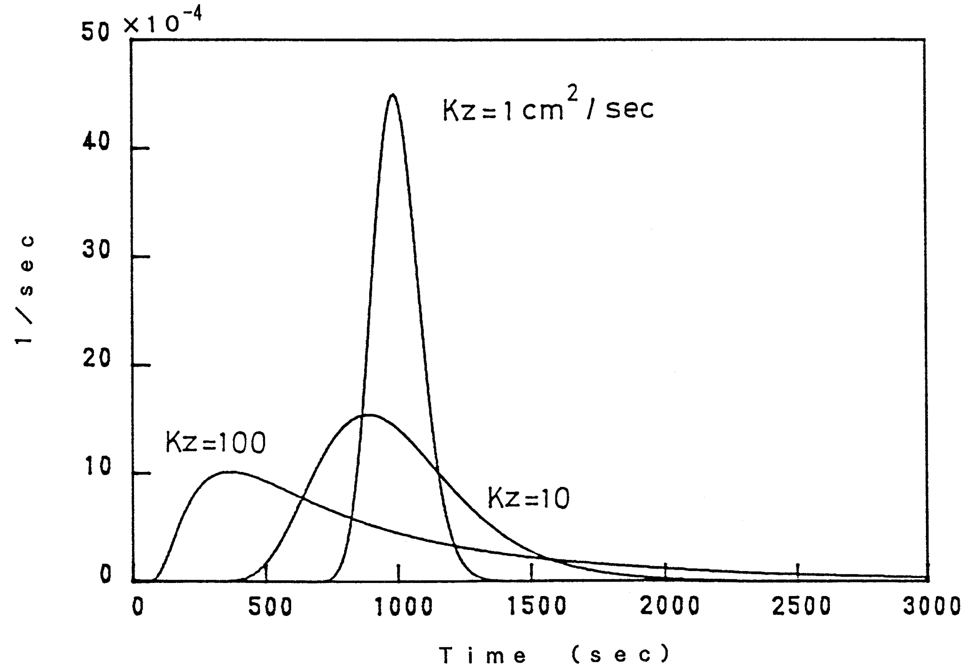

Fig. 2. Vertical flux of *Sargassum* propagules at the sea bottom estimated by Eq. (3) for z_0=500 cm and three values of K_z .

increasing vertical eddy diffusivity most propagules settle more rapidly because of diffusive transport, while some propagules stay longer in the water column.

(2) *Lateral diffusion*

Lateral diffusion is variable due to inherent properties of fields of flow. I assumed that lateral distribution of the propagule is given by

$$p_x(x,t) = \frac{1}{(2\pi)^{1/2}\sigma} \exp\left\{-\frac{(x-u_0t)^2}{2\sigma^2}\right\}, \cdots\cdots(4)$$

where $p_x(x,t)$ is the probability that the propagule is at point x at time t, u_0 is a uniform flow, and σ^2 is the variance about the center of the distribution. The relationship between σ^2 and t is determined from field observations.

(3) *Distribution of settled propagule*

The probability that the propagule released from a point $x=0$, $z=z_0$ settles finally at a distance x is then given by

$$P(x) = \int_0^\infty f_z(t) \cdot p_x(x,t)dt. \cdots\cdots\cdots\cdots\cdots\cdots\cdots(5)$$

If we know the values of vertical diffusivity K_z and can express the horizontal variance σ^2 as a function of time after release, we can predict the distribution of *Sargassum* propagules settled on the sea bottom by using Eqs. (3), (4) and (5). When the source of propagules is not a single point and the release of propagules is continuous, we can predict the distribution of the settled propagules by integrating Eq. (5) for space and time.

4. Estimation of the diffusion parameters

Diffusion in the ocean has been studied by using dye or drifters. This is essentially a Lagrangian approach which provides data related to diffusion processes. However, Lagrangian type field experiments are difficult to carry out for a long period of time around *Sargassum* forests. Hence I adopted the moored current meters, and estimated the diffusion parameters under the assumption that Eulerian process is approximately similar to Lagrangian one.

(1) *Distribution of Sargassum forests*

Field observations were carried out in Gokasho Bay, central Japan (Fig. 3). Figure 4 shows the study site. From April to May

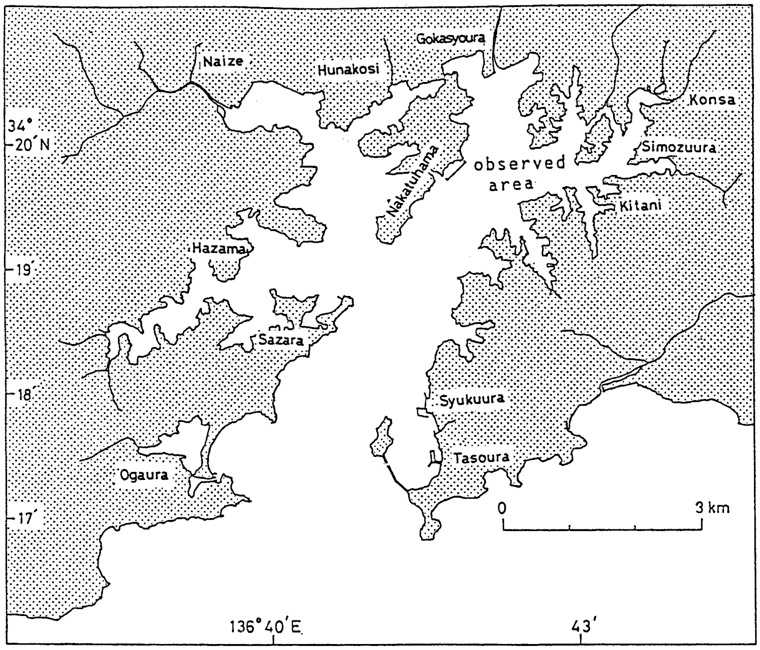

Fig. 3. Map of Gokasho Bay, Mie Prefecture, Japan.

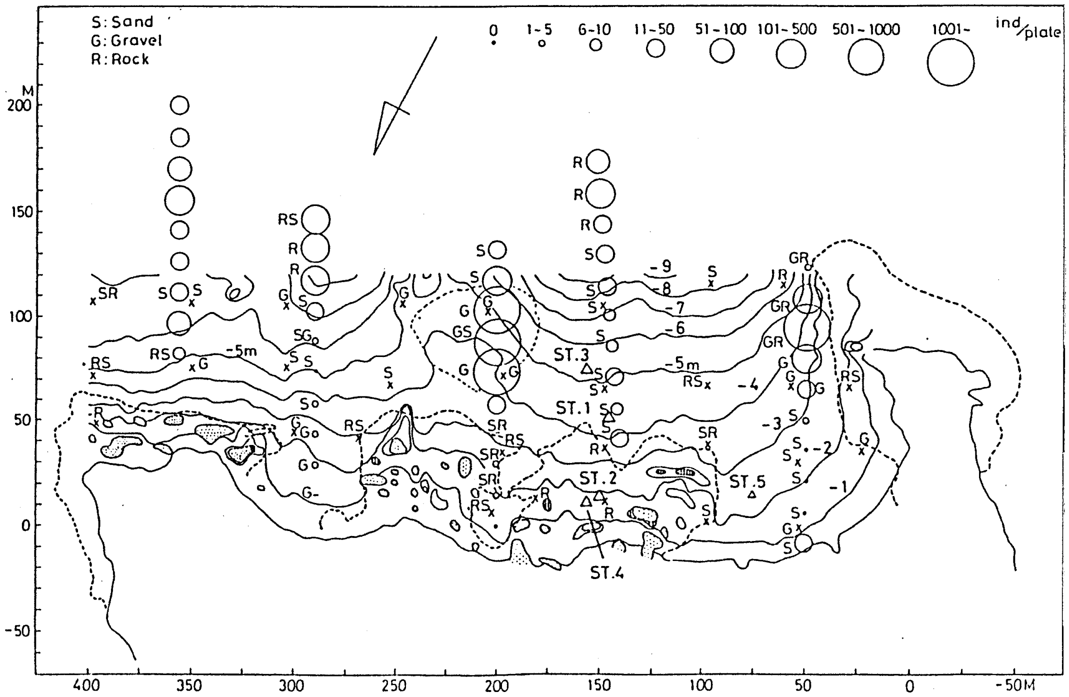

Fig. 4. Study site and numbers of *Sargassum* propagules per plate settled on artificial substrata put out on 9–18 April and sampled on 8–14 May 1985. Broken lines indicate rock or gravel regions determined by aerial photographs. Crosses are stations where bottom substrata were observed. Triangles are stations where water movement were measured.

Sargassum forests mainly composed by *S. horneri* and *S. piluliferum* grow luxuriantly in rock or gravel regions indicated by broken line in the figure. The density of *Sargassum* forests is about 4 kg wet weight per square meter (TODA *et al.*, 1989).

(2) *Vertical diffusivity*

Locations of current measurement sites are shown in Fig. 4. Table 1 lists the bottom depth at the measurement sites, the height at which current meters were fixed and sampling time-intervals. I measured vertical velocity in a *Sargassum* forest (Run 1–1) and offshore (Run 1–2) of it. Waves were visually estimated to have a period of about 6 second, and the power spectra of vertical velocity showed strong peaks of frequency 0.17/s.

Values of vertical diffusivity are obtained by

$$K_z = < w^{'2} > T_* \qquad \cdots\cdots\cdots\cdots\cdots\cdots\cdots(6)$$

and

$$T_* = \int_0^\infty r_w(\tau)\,d\tau\ , \qquad \cdots\cdots\cdots\cdots(7)$$

where $< w'^2 >$ is the mean squares of vertical component of the turbulent velocity obtained by subtracting the running mean from the measured data for 6.6 sec to cut off the effect of wave orbital velocity, and $r_w(\tau)$ is the auto-correlation function. The vertical distribution of K_z is shown in Fig. 5. The mean of K_z was 2.4 cm^2/s at offshore of the *Sargassum* forest and was 1.3 cm^2/s in it.

(3) *Lateral variance as a function of time after release*

I analyzed north component of lateral velocity which was dominant in the study site (Run 2,3; Table 1,2). The lateral displacement of propagules $Y(t)$ is calculated by integrating the measured velocity under the assumption that Eulerian process is similar to Lagrangian one, namely

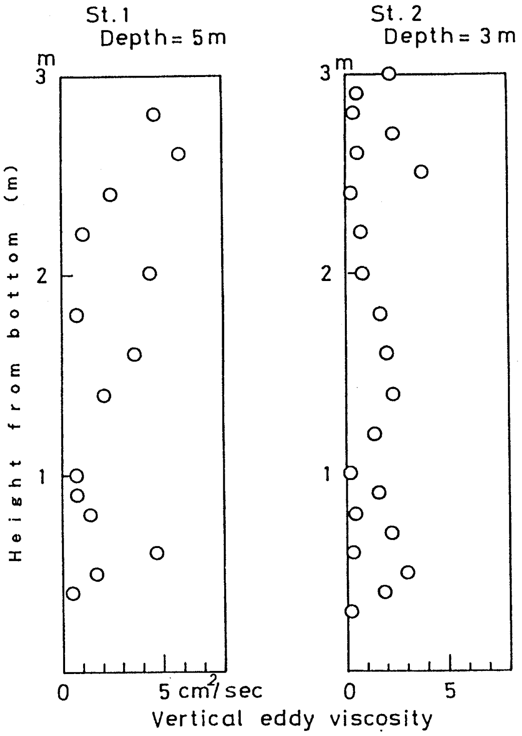

Fig. 5. Profiles of vertical eddy viscosity at St. 1 on 30 April (Run 1-1) and at St. 2 on 2 May (Run 1-2) 1985.

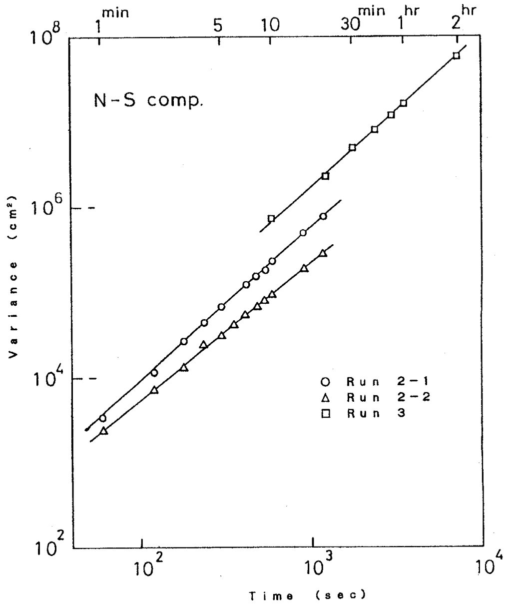

Fig. 6. Regressions of variance (σ^2) of lateral displacement of *Sargassum* propagules vs. time (open circles: Run 2-1, open squares: Run 2-2, open triangles: Run 3).

Table 1. List of current measurements around *Sargassum* forests. Location of the study site is shown in Fig. 4.

Run	St.	Bottom depth (m)	Sensor height (m)	Sampling interval	Length of one record and duration of measurement
Run 1-1	St. 1	5.0	0.4-2.8	0.317 sec	3 min 1985 4/30 13:00-15:00
Run 1-2	St. 2	3.0	0.3-3.0	0.317 sec	3 min 1985 5/ 2 12:30-16:00
Run 2-1	St. 3	6.2	2	1 min	1 day 1987 3/ 9 11:00-
Run 2-2	St. 3	6.2	2	10 min	19 day 1987 4/14 0:00-
Run 3	St. 4	2.5	1	5 sec	1 day 1986 4/23 10:00-

Table 2. Statistics for current measurements.

	Run 2-1		Run 2-2		Run 3	
	E-comp.	N-comp.	E-comp.	N-comp.	E-comp.	N-comp.
Mean (cm/s)	0.13	0.68	0.37	0.30	0.42	-0.35
S.d. (cm/s)	0.80	1.00	1.39	1.67	0.56	0.83
Max. (cm/s)	3.30	5.60	12.70	8.90	2.75	3.04
Min. (cm/s)	-2.60	-3.30	-6.20	-11.80	-2.46	-4.83
a	1.54	2.56	15.37	6.45	1.09	3.42
m	1.78	1.78	1.66	1.80	1.72	1.60

$$Y(t)=\int_0^t u dt, \qquad \cdots\cdots\cdots\cdots\cdots(8)$$

Figure 6 shows the variance (σ^2) of $Y(t)$ plotted against time t. The regression line fitted to the bilogarithmic plot corresponds to $\sigma^2(t)$ proportional t^m.

$$\sigma^2=at^m \qquad \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots(9)$$

Values of the indices a and m are shown in Table 2.

The rate of relative lateral diffusion may be represented by a coefficient of eddy diffusion K_x defined by

$$K_x=\frac{1}{2}\frac{d\sigma^2}{dt}\ . \qquad \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots(10)$$

From Eq. (9), K_x is then given by

$$K_x=\frac{1}{2}mat^{m-1}=c\sigma^r\ , \qquad \cdots\cdots\cdots\cdots\cdots\cdots\cdots(11)$$

where $r=2(m-1)/m$ and c is a constant. Equation (11) represents the dependence of K_x on scale (BOWDEN, 1974). Theoretical treatment of diffusion shows the case $m=1$ is Fickian diffusion with K_x constant while $m=2$ implies that K_x increases linearly with t or σ, corresponding to a constant diffusion velocity. The case $m=3$ corresponds to K_x being proportional to 4/3, which is considered with inertial subrange conditions for locally isotropic turbulence, if σ is identified with the scale of the process.

Values of the index m lay between 1.6 and 1.8, that is a little smaller than 2. Anyway, we can estimate the variance of lateral diffusion by Eq. (9) and Table 2.

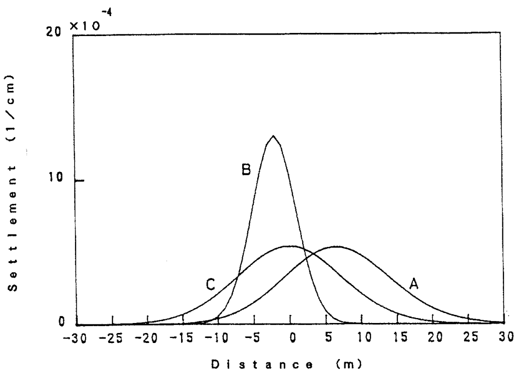

Fig. 7. Distribution of *Sargassum* propagules (1/cm) estimated to settle to the sea bottom by Eq. (5).

A: $z_0=500$ cm, $K_z=2.4$ cm^2/s, $u_0=0.68$ cm/s, $\sigma^2=2.56\ t^{1.78}$.

B: $z_0=300$ cm, $K_z=1.3$ cm^2/s, $u_0=-0.35$ cm/s, $\sigma^2=3.42\ t^{1.6}$.

C: $z_0=500$ cm, $K_z=0$ cm^2/s, $u_0=0$ cm/s, $\sigma^2=2.56\ t^{1.78}$.

(4) *Prediction of the distribution of settled propagules*

Combining the vertical flux and horizontal diffusion, I calculated the probability distribution of settled propagules by Eq. (3), (4) and (5) using the diffusion parameters obtained by current measurements (Fig. 7). The distribution curve A is calculated by using the vertical eddy diffusivity obtained by Run 1-1 and the relationship between σ^2 and t obtained by Run 2-1 at offshore stations (St. 1 and St. 3) of the *Sargassum* forest. The curve B indicates that at St. 2 (Run 1-2) and St. 4 (Run 3) in the *Sargassum* forest. The curve C is calculated under similar conditions with A except uniform flow (u_0) and vertical diffusivity are neglected. The curves A and C are seen to be similar in shape, showing that the effect of sinking velocity of propagule (w) exceeds the one by vertical diffusion in this case.

5. Distribution of settled *Sargassum* propagules

I investigated the distribution of settled *Sargassum* propagules by using artificial substrata (vinyl chloride plate 10 cm ×5 cm, Fig. 8). Artificial substrata were put out on 9-18 April and sampled on 8-14 May 1985 in study site (Fig. 4). The majority of measured propagules was *S. horneri* and the number of propagules settled on the artificial substrata

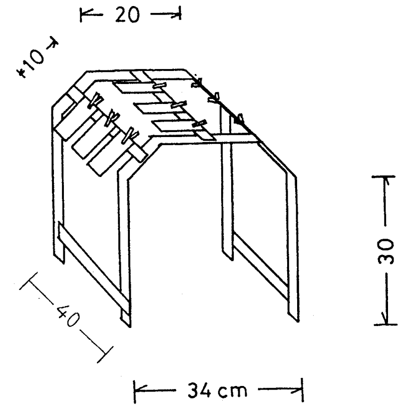

Fig. 8. Artificial substrata (vinyl chloride plate, 10 cm×5 cm) attached to a stainless grid.

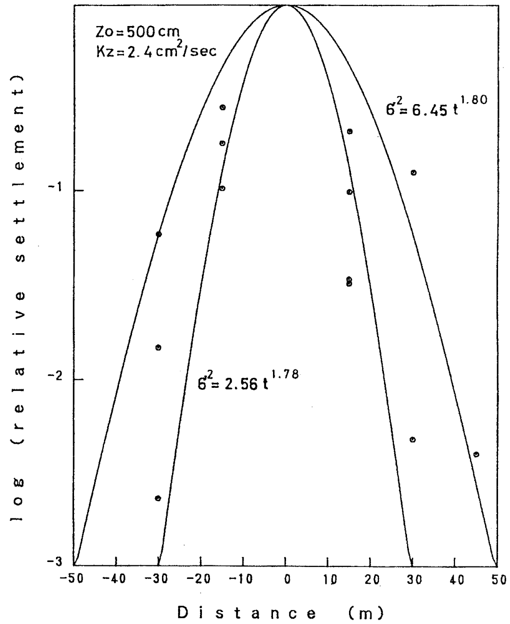

Fig. 9. Comparison of numbers of *Sargassum* propagules estimated to settle to the sea bottom with observed one (open circles). Solid lines show estimated distribution of propagules by Eq. (5).
A: $z_0=500$ cm, $K_z=2.4$ cm^2/s, $u_0=0.68$ cm/s, $\sigma^2=2.56\ t^{1.78}$.
B: $z_0=500$ cm, $K_z=2.4$ cm^2/s, $u_0=0.30$ cm/s, $\sigma^2=6.45\ t^{1.8}$.

ranged from 0 to 2197 individuals/50 cm^2. Numbers of propagule settled on the artificial substrata in a near-shore region were low, while numbers were high around an offshore *Sargassum* forest. These results indicate that wave motion effected the settlement of propagules on the artificial substrata in the following manners (Toda *et al.*, 1989). In a near-shore *Sargassum* forest where wave ray concentrates, the propagules that fell onto the substrata were carried out by wave motion. In a near-shore small bay where wave ray disperses and the sea bottom is muddy, settlement of silt on the substrata inhibited the settlement of propagules. On the other hand, in a offshore region where wave motion has little effect on the settlement of propagules, distribution of propagules reflected the dispersion from offshore mother plants.

I compared the actually measured distribution of propagules of *S. horneri* in a offshore region with the predicted distribution, under an assumption that the propagules are released from the single point set at a distance of 5 m from the sea bottom in the center of the offshore *Sargassum* forest. In Fig. 9, solid curves represent the estimated distribution of propagules using the power law obtained from two observations in a offshore region of *Sargassum* forests, while open circles show the relative number of propagules normalized by the maximum number of propagules in the center of the *Sargassum* forest. The predicted distribution agreed well with the distribution of relative number of propagules of *S. horneri* obtained from the field experiment in the offshore region.

Acknowledgement

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ホンダワラ類幼胚の着底数密度分布の予測

杜多　哲

藻場中心の一定の高さからδ関数的に放出された幼胚が、中心から一定の位置の海底に着底する確率密度分布を予測する手法を提案した。鉛直方向には拡散係数を定数として扱い、幼胚の沈降と拡散を考慮した輸送方程式を解いて、海底面での幼胚フラックスを幼胚放出後の時間の関数として求めた。水平方向への拡散による幼胚の水平分布は正規分布で近似できると考え、その広がりを表す統計的分散は幼胚放出後の時間の関数として観測結果から求めることとした。海底面でのフラックスと水平方向の拡散を組み合わせることによって、幼胚の着底確率密度分布を求める方法を示した。

このモデルの中の拡散パラメーターを求めるために、三重県五ヶ所湾のガラモ場周辺で流れの測定を行い、鉛直拡散係数および水平方向の広がりを表す統計的分散と時間の関係を求めた。これらの拡散パラメーターを用いて藻場の中心からδ関数的に放出された幼胚の着底数密度分布を予測した。また人工的な付着基盤を多数海底に設置することにより、アカモク幼胚の着生数の分布を求めた。波の影響の少ない沖側の藻場周辺では、予測した分布と測定した分布はよく一致しこの手法の有用性が示された。

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Experimental study of swimming activity and orientation of sole (*Solea solea* L.) larvae and juveniles: influence of endogenous rhythm, light, gravity, temperature and feeding*

Gisele CHAMPALBERT, C. CASTELBON, L. LE DIREACH,
C. MACQUART-MOULIN and G. PATRITI**

Abstract: An experimental study of the swimming activity of sole larvae and juveniles was carried out to assess the migratory mechanisms of sole between the spawning areas, often located offshore, and the inshore and estuarine nurseries.

The experiments were carried out in different types of tanks fitted with special devices inducing sudden or progressive variations of external factors. Animal detection was achieved by photoelectric or optoelectronic barriers as well as by visual observations and an infrared converter.

The effects of endogenous rhythm, light, gravity, temperature and feeding are described. Experimental results are compared with *in situ* observations.

1. Introduction

In most areas of the French Atlantic coast and in particular in Biscay Bay, sole (*Solea solea*) spawning areas are located in the open sea but old larvae and early juvenile are mainly found in inshore areas and estuaries.

Hypotheses based on passive drift and spreading processes are inadequate to explain sole transport because of local currents parallel to the coast. Therefore, very likely active vertical and horizontal movements, are involved.

In the framework of the National Programme on the Recruitment Determinism (PNDR), a project focussed on the migratory mechanisms of sole larvae and juveniles was set up to try to predict the recruitment. The effects of internal factors (endogenous rhythm, age) and external factors (light, gravity, pressure, temperature, salinity, sediment, currents, feeding) on the swimming activity and the orientation of larvae and juvelile were experimentally studied. In this paper will be summarized the effects of endogenous rhythm, light and gravity, temperature and feeding.

2. Materials and methods

Most animals came from hatcheries, and a few were caught in the sea. Reared in the laboratory at constant temperature under natural illumination, sole were fed, according to their age on live *Artemia nauplii*, or dead *Artemia*, or pieces of chopped polychaetes. During the experiments, to maintain standard conditions and avoid changes in feeding behaviour, animals were not fed. Experiments concerning the effects of light, gravity and temperature were carried out on the different larval and juvenile stages from hatching to a size of about 40 mm. Experiments dealing with feeding behaviour were performed on metamorphosing larvae and metamorphosed soles.

In short duration experiments, visual observations were done, directly at strong light intensities or with an IR converter under very weak light intensities. In long duration experiments, automatic recordings using actographs and actotaxigraphs based on photoelectric cell detection (MACQUART MOULIN, 1979: CASTELBON, 1987) were made. The experiments involved different types of tanks-cylindrical, U-shape or parallelipipedic tanks-fitted with special devices to vary parameters (MACQUART-MOULIN *et al*., 1976; MACQUART-MOULIN *et al*., 1989; CASTELBON, 1987; CHAMPALBERT *et al*., *in* press). Twotypes of light sources were used: a source giving a beam of parallel rays of white light and a fluorescent tube. Variations of the light intensity were achieved by means of neutral filters.

Data were treated and results expressed on different types of curves: actograms showing

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hourly variations of activity; periodograms derived from William and Naylor periodogram method (1972) or Whittaker and Robinson (1926) method; actotaxigrams describing spatio-temporal variations of soles as a function of time (Castelbon, 1987).

3. Results

3. 1 Endogenous rhythm

In total darkness, stage I larvae did not exhibit a specific rhythmic swimming activity. Subsequently, a circadian rhythm appeared. Most often diurnal activity was high in stage 2 but early during ontogenesis (generally from stage 3), it became mainly nocturnal; from metamorphosis the main peak of swimming activity was consistently nocturnal (Fig. 1).

3. 2 Light and gravity

Due to the interrelated effects of light and gravity on the swimming activity and the migrations of marine animals, two types of experiments were carried out. Experiments in horizontal tanks were performed to study the effects of light on horizontal movements. Experiments in vertical tanks were done to study the effects of light, combined or not to those of gravity, on vertical movements.

Effects of light on horizontal movements; phototaxis in a horizontal plane

Orientation (phototaxis) and activity (photokinesis) were studied during short and long duration experiments on dark and light-adapted animals. This was done in horizontal tanks, light coming in laterally. A phototaxis index was calculated: 0 indicates the neutrality, values comprised between -1 and 0 a negative phototaxis and values between 0 and $+1$ a positive phototaxis. Photokinesis was expressed by an index corresponding to the percentage of soles reaching the wall closest to or farthest from the light source within 10 minutes.

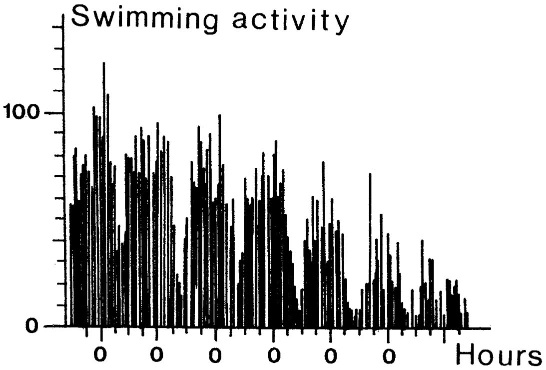

Fig. 1. Swimming activity of juvenile sole kept in total darkness

Moreover, to ascertain a possible role of a phototaxis rhythm, the experiments were carried out at different hours during the day and at night. No obvious rhythm of phototaxis appeared during the daily cycle in larvae. Nevertheless, from metamorphosis until a size of about 30 mm phototaxis index values were maximum for crepuscular or nocturnal illuminations. Figure 2 represents the phototaxis index variations during development. Up to an age of 2 or 3 days, larvae were neutral; then they remained photopositive at diurnal and nocturnal light intensities except for a few days before metamorphosis. During this short period of development, phototaxis decreased at diurnal illumination. From 35 mm, juveniles tended to be photonegative at diurnal illuminations.

The very low kinesis observed at diurnal intensities in larvae after hatching increased in the subsequent developmental stages. Just before metamorphosis there was a marked photoinhibition at diurnal intensities; from then, kinesis became maximum at crepuscular and nocturnal intensities (Fig. 2).

Effects of light and gravity on vertical movements

The effects of gravity and therefore geotactic responses were studied during short and long duration experiments in vertical tanks subjected to natural or artificial light variations. Swimming activity was low during the day. When light intensity was reduced artificially, whatever the time, the number of geonegative reactions increased; consequently an increased number of animals swam near the surface (Fig. 3). The reverse reaction was true: an artificial increase of light intensity reduced the geonegative reactions and increased the geopositive ones. The threshold of the geotaxis reversal varied with age. Close to

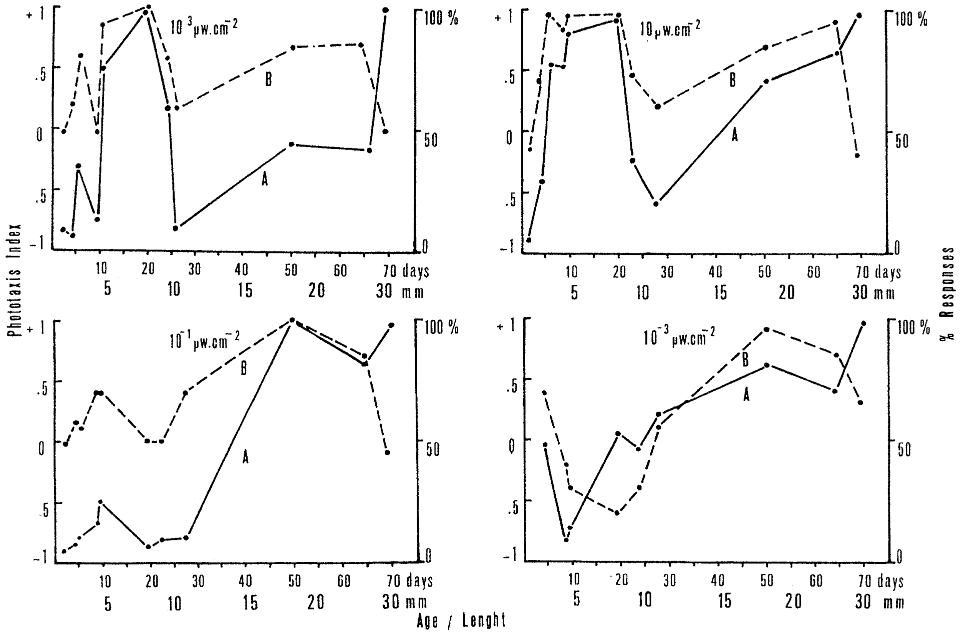

Fig. 2. Evolution of phototaxis and photokinesis of larvae and juvenile sole at diurnal (10^3 μW • cm^{-2}), crepuscular (10 and 10^{-1} μW • cm^{-2}) and nocturnal (10^{-3} μW • cm^{-2}) intensities (from Champalbert *et al.* in press)

10^{-1} μw•cm^{-2} one week after hatching, it was about 10^{-2} μw•cm^{-2} in 12-day-old larvae and reached 10^{-4} μw•cm^{-2} in young juveniles; in older soles (30 mm long) the threshold decreased to values as low as 10^{-6} to 10^{-7} μw•cm^{-2}.

The influence of kinetic variations induced by light and endogenous rhythm was demonstrated in juveniles subjected for several days to natural day-night variations or artificial DL cycles of a 24 h periodicity, phased or inversely phased with the local natural cycle: in these conditions there was an obvious 24 h periodicity with a maximum activity during the dark phase. Figure 4 represents juvenile swimming activity as a function of time in an inverse DL cycle (f=12): There was little or no activity during the light phase (from 6 p.m. to 6 a.m.) and high activity with a main accumulation of juvenile near the surface during the dark phase (from 6 a.m. to 6 p.m.).

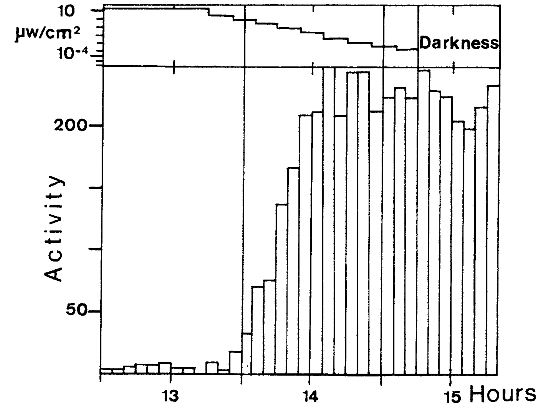

Fig. 3. Swimming activity variations induced by light intensity variations.

The respective effects of geotaxis and phototaxis on orientation reactions were determined in experiments carried out either in U-shape tanks illuminated from one of their surfaces or in cylindrical vertical tanks illuminated laterally or from below.

Figure 5 (top) shows the actogramme of juvenile sole activity respectively near the surface and near the bottom when animals were kept in a cylindrical tank illuminated from below with natural light. During the night swimming activity was low near the bottom and high near the surface. At nocturanal intensities, positive phototaxis should

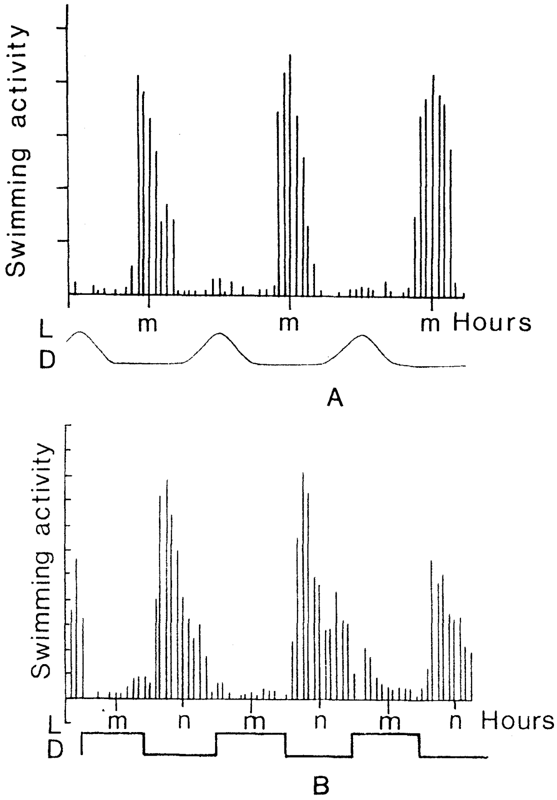

Fig. 4. a) Actogram of juvenile sole in artificial light phased with the local natural cycle; experiment with progressive changes in light intensity.
b) Actogram of sole juvenile in artificial light inversely phased with the local natural cycle; experiment with sharp changes in light intensity.

keep animals in the lower part of the tank. Therefore, the accumulation near the surface was induced by geonegative reactions only; phototaxis and geotaxis were thus antagonistic.

Figure 5 (bottom) shows the activity of sole swimming near the surface in a U-shape tank illuminated from one of the two surfaces. At night, the activity near the surface was higher in the illuminated part of the tank than is the dark one, thus demonstrating the combined effects of geotaxis and phototaxis.

3. 3 Temperature

Three types of experiments were carried out on juveniles: experiments at constant temperatures, experiments with temperature gradients; experiments with cyclic variations of temperature. The effects of temperature on swimming activity, endogenous rhythm and distribution were considered and the combined effects of light and temperature subsequently studied. Activity was increased at high temperatures within the tolerated range. In total darkness, juveniles subjected to 12 h temperature cycles exhibited a rhythmic activity of the same period. Activity increased during the heating phase, and decreased during the cooling phase, whatever the time of day (Fig. 6).

Juveniles subjected to both temperature variations and diurnal light variations tended to exhibit a 24 h rhythmic activity thus demonstrating the major effect of light compared to temperature.

In experiments with temperature gradients, juveniles tended to avoid the warmest surface layer in total darkness as well as in DL conditions. This was particularly obvious when the range of variations was wide.

3. 4 Feeding

The effects of food types and concentrations on swimming activity and fixation of juvenile soles were studied in total darkness and under natural DL conditions. Animals were given different types of food: live pelagic (*Artemia naupii*) or benthic (polychaetes) food, or frozen food (nauplii or adults of *Artemia*, or polychaetes).

About one hour after feeding swimming activity of juvenile sole decreased markedly, but more or less noticeably according the food concentrations they were given. This occurred in DL conditions, as well as in total darkness. Swimming stopped after every feeding and resumed from 1 to 4 days later. Similar results were obtained with live *Artemia nauplii* or polychaetes. No decrease in activity was observed with dead food in animas used to feeding on live food.

4. Discussion and conclusions

Our experiments clearly demonstrate the existence of endogenous rhythm in old larvae and juveniles soles and confirm previous results concerning old juveniles (CHAMPALBERT and CASTELBON, 1989). This agrees with

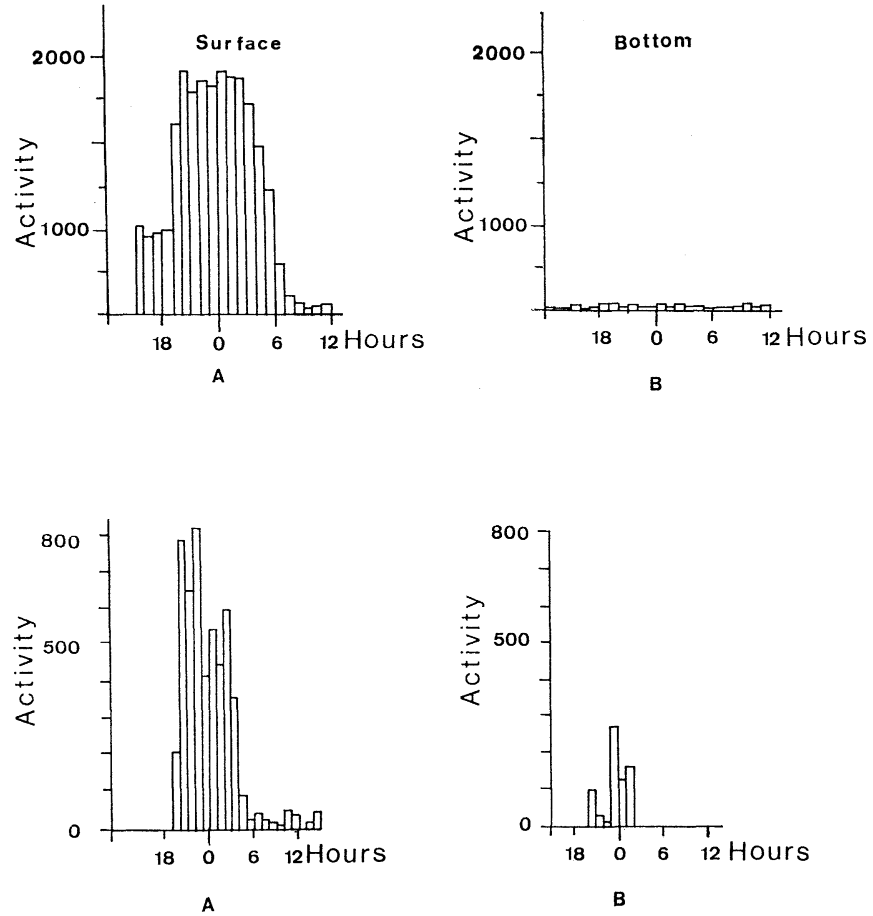

Fig 5. top: Actogram of juvenile sole activity near the surface (A) and the bottom (B) of a cylindrical tank illuminated from below.
bottom: Actogram of juvenile sole acfivity near the surface of a U-shape tank.
A: activity near the dark surface; B: activity near the illuminated surface.

results on flatfish (O' Connor, 1972; Gibson, 1973, 1976).

In old larvae as well as in juveniles the external factors can modify the endogenous circadian rhythm of swimming activity. Some of these factors such as temperature, induce behaviour changes but cannot synchronize a rhythm. Our experiments showed that sole migrations are not prevented by temperature gradients but animals tend to avoid high temperatures. In the same way, Champalbert *et al.* (in prep.) observed that salinity gradients do not constitute a real barrier to vertical movements. These results agree with the penetration of animals into estuarine nurseries and coastal waters where temperature and salinity vary widely (Marchand *et al.*, 1989).

Light and gravity play a greater role than temperature and salinity, in the control of migratory processes of larvae and juvenile soles. The importance of phototaxis reactions on herring and flatfish larvae, noted by Blaxter (1969, 1972) was confirmed by our experiments on sole (Chambalbert *et al.*, in prep.). We also observed that geotaxis, phototaxis and photokinesis have combined or antagonistic actions which vary during development. Important behaviour changes occur a few days after hatching, then during metamorphosis and lastly above a size of 35 mm.

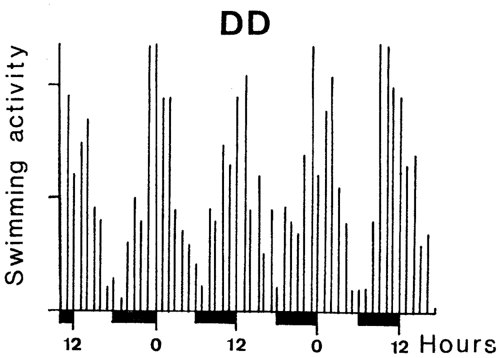

Fig. 6. Swimming activity of juvenile soles subjected in total darkness to 12 htemperature cycles. Dark stripes indicate the heating phases.

From this size on, juvenile behaviour did not seem to differ from the adult one described by Kruuck (1963).

Our experimental sutdies, in agreement with field observations, can explain some migratory processes and characteristic changes of distribution during the ontogenesis. For a few days after hatching (3–4 d) whatever the intensity, geotaxis is positive, phototaxis neutral and photokinesis low. This may explain why early larvae are found in deep waters. In larvae from 7 days to before metamorphosis the number of geonegative increases at diurnal intensities. At this stage, photokinesis is maximum and phototaxis positive. Such behaviour may be responsible for the progressive upward migrations observed in old larvae in the sea. From early metamorphosed to larger juveniles (30–35 mm), the number of geonegative reactions and photokinesis decrease at diurnal intensities; they are maximum at crepuscular or nocturnal intensities. Except in the first stage and metamorphosing larvae, phototaxis remains positive and one can assume that it acts in the horizontal plane, inducing movements towards illuminated shallow areas; its action in the vertical plane is possible only for illuminations lower than the geotaxis inversion threshold. In the sea this juvenile period corresponds to a migration towards the bottom. Finally, positive geotaxis, negative phototaxis and low kinesis characteristic of old juveniles behaviour in the laboratory, agree with the decrease of migration amplitude observed in the sea.

In addition to hypotheses based on physical mechanisms and spreading by diffusion (Koutsikopoulos *et al.* in press) our experiments give new evidence to explain the transport of sole larvae from offshore to inshore areas. Oriented movements and increased activity of juveniles that metamorphose in offshore areas, could enhance the spreading as a result of decreased activity in coastal areas along with a decreased kinesis juveniles may remain temporarily in estuaries.

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Résumé: Une étude expérimentale de l'activité locomotorice des larves et juvéniles de sole a été entreprise pour comprendre les mécanismes migratoires des soles entre les aires de ponte, souvent situées au large, et les nurseries cotières ou estuariennes.

Les expériences ont été effectuees dans différents types de cuves munies de dispositifs permettant de réaliser des variations soudaines ou progressive des facteurs extenrnes tels lumière, température, salinité, pression. La détection des animaux est faite à l'aide de barrages phototélectriques ou optoélectroniques ainsi que par observation visuelle directe ou avec un convertisseur infrarouge.

Les effets du rythme endogène, ceux de la lumière, gravité, température et alimentation sont résumés. Les résultats expérimentaux sont compares avec les observations obtenues dans le milieu naturel.

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Ecology and behaviour of puerulus of spiny lobsters*

Jiro KITTAKA**

Abstract: Because of the difficulty to culture phyllosoma/puerulus in laboratory and to collect puerulus just after metamorphosis, little has been known about ecology and behaviour of puerulus. Recently complete development of phyllosomas has been shown for several species of spiny lobsters: *Panulirus japonicus, Palinurus elephas, Jasus lalandii, J. edwardsii, J. verreauxi* and a hybrid between *J. novaehollandiae* and *J. edwardsii*.

The newly moulted puerulus was transparent at the early stage. It was carried by current and swam rotating with occasional beating of the pleopods. Slight differences were observed in the swimming posture between species. The clinging behaviour was observed one or few days after metamorphosis. A puerulus of *P. japonicus* settled 4 days after metamorphosis. *J. edwardsii* and *J. verreauxi* were observed to occupy the shelter on the following day of metamorphosis. *J. edwardsii* burrowed into the fine silt substratum while *J. verreauxi* showed clinging behaviour on artificial fibre.

No feeding behaviour was observed during the entire period of the puerulus. Without feeding the dark pigmentation developed on the carapace at the advanced stage. The puerulus moulted into the postpuerulus stage about two weeks after metamorphosis for *P. japonicus* and about three weeks for *P. elephas* and *Jasus* spp. Transparent pueruli of *J. edwardsii* were tolerable to high water temperature of 26℃ and low salinity of 26‰.

1. Introduction

Spiny lobsters hatch phyllosoma larvae which disperse by currents into the open ocean. The larval life is estimated as up to about a year. The final stage phyllosomas metamorphose into the puerulus stage, which is the only transitional stage from the phyllosoma to the juvenile. Because of the difficulty to culture phyllosoma/puerulus in the laboratory and to collect puerulus in the ocean, little has been known about ecology and behaviour of the puerulus.

The advanced stage puerulus is trapped by various type collectors. The pueruli of the Western Australia spiny lobster *Panulirus cygnus* were captured by the grass type collector by PHILLIPS (1972). Those of the New Zealand spiny lobster *Jasus edwardsii* were investigated using the crevice type collector by BOOTH (1979). Recently, requirements of the settlement substratum and factors induced molting into the postpuerulus have been investigated on the California spiny lobster *P. interruptus* by SERFLING and FORD (1975), and on the Caribbean spiny lobster *P. argus* by MARX and HERRNKIND (1985a, 1985b).

The stage of the puerulus is identified with the development of hepatopancreas and pigmentation of exoskeleton. However, the early stage pueruli captured by the collectors are lacking the information after metamorphosis until settlement. The information at the early stage could be available through complete development of phyllosoma and puerulus cultured in the laboratory. Recently culture of phyllosoma and puerulus from egg has been shown for several species of spiny lobsters: the Japanese species *P. japonicus* (KITTAKA and KIMURA, 1989), the European species *Palinurus elephas* (KITTAKA and IKEGAMI 1988), the South African species *J. lalandii* (KITTAKA, 1988), the New Zealand species *J. edwardsii*, and *J. verreauxi*, (unpublisherd), and a hybrid between *J. edwardsii*, and the Australian species *J. novaehollandiae* (KITTAKA, et al., 1988). Although the number of pueruli produced was very few, ecology and behaviour of puerulus just after metamorphosis have been revealed in the laboratory.

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2. Materials and methods

Puerulus cultured in the laboratory

Matured spiny lobsters: Matured *P. japonicus* were caught in Japan and *P. elephas* and 4 species of the genus *Jasus* were transported to Japan from their origin countries. Several females and males were reared in a FRP tank (dimensions: 2.5m × 1.2m × height 0.7m) with slowly running seawater and aeration. Water temperature maintained between 12℃ and 22℃ for *P. japonicus* and 10℃ and 20℃ for *P. elephas* and *Jasus* spp. Mussels *Mytilus edulis* were given as food daily. Mating, spawning and hatching occurred once every year. Females carried eggs for 2–3 months after mating.

Phyllosomas: Hatching occurred in February for *P. elephas*, in July and August for *P. japonicus* and *J. verreauxi* and almost all year round for for other *Jasus* spp.. Several thousand first stage phyllosomas were cultured in a 100 *l* circular tank. Seawater treated with a 5 μm ceramic filter and ultra-violet sterilizer was supplied at the bottom through a recirculating system. Cultured microalgae *Nannochloropsis* sp. was added at several million cells/ml to the culture water. Water temperature was maintained at approximately 25–26℃ for *P. japonicus* and at 18–20℃ for other species. The larvae were fed with *Artemia* nauplius at the initial stage and small pieces of mussels at advanced stage. The culture water was exchanged for about 2–4 weeks.

Puerulus: After metamorphosis, the pueruli were kept in the phyllosomas tank for several days. After the pueruli showed settling behaviour, they were transferred into a plastic cage (dimensions: 13 cm × 9 cm × height 11 cm) placed in another FRP tank. A piece of mussel shell was placed in the cage as shelter. Ambient sea water was supplied through a 5 μm cartridge filter. Water temperature was maintained at about the same ramge for phyllosomas. The pueruli cultured from phyllosomas are shown in Table 1.

Puerulus collected in the wild

Collection of pueruli of *J. edwardsii* was made at Castlepoint on the east coast of the North Island of New Zealand during the period from January 17 to February 22 in 1989 (Hayakawa *et al*, 1990) and from January 28 to February 15 in 1991. Collectors were composed of eight plywood sheets (38 cm × 38 cm × 1 cm) to make crevices of 2.5 cm in height at the edge part (Booth 1979) and were placed with concrete weights. The collectors were checked daily and settled pueruli were removed for observation in the laboratory. Effects of water temperature and salinity were tested with 10ℓ plastic containers.

3. Results

Metamorphosis and swimming behaviour of puerulus

Cessation of feeding and retraction of hepatopancreas are signs of approaching moult for phyllosomas of all species observed. Final stage phyllosomas became moveless about 2 days before molting. On the day of metamorphosis the body colour of the phyllosomas became white-turbid, and several hours before moulting eyestalks and pereiopods

Table 1. List of puerulus cultured in the laboratory

Species	Date of hatching	Date of metamorphosis	Final stage of phyllosoma (instar)	Duration of phyllosoma (days)	Duration of puerulus (days)
Jasus lalandii	1 Aug. 1986	3 Jun. 1987	15 (estimated)	306	31
Jasus hybrid	8–13 Sep. 1986	31 Jul. 1987	15 (estimated)	319	
Palinurus elephas	19 Mar. 1987	29 Jul. 1987	9 (estimated)	132	15
	18 Feb. 1988	16 Jul. 1988	9 (eatimated)	148	11
Panurilus japonicus	18 Jul. 1987	22 Jun. 1988	29 (estimated)	340	15
				391	12
*J. edwardsii**	20 Dec. 1989	18 Oct. 1990	17	303	19
*J. verreauxi**	17 Jul. 1990	7 Feb. 1991	17	205	20

*un published.

became flaccid for the majority species except *J. verreauxi*. The latter species occasionally bent abdomen and beated pleopods vigorously like newly mouted puerulus of other species. The puerulus took two or three minutes to emerge dorsally through the thoracoabdominal membrane. The newly moulted puerulus was transparent except in the eyes. It was carried by current and swam rotating with vigorous beating of the pleopods. They jumped backwards occasionally with bending abdomen. Slight differences were observed in the swimming posture between species: the second antennae and five pairs of pereiopods were extended forward for *J. lalandii*, the pereiopods were slightly out-streched for *P. japonicus*, both the second antennae and pereiopods were slightly out streched for *J. edwardsii* and *J. verreauxi* and both were streched wide for *P. elephas*.

Settlement behaviour

The clinging behaviour was observed in the following day about 12 hours after metamorphosis for a puerulus of *P. japonicus*. However, the individual left the substratum and began to swim again. Three days after meta morphosis, this individual was observed to extend appendages wide and cling to the screen net on the recircalatimg system placed in the center of culture container. The individual was observed again to swim in the following morning and to cling in the afternoon 4 days after metamorphosis. The latler case is considered as the settlement because no swimming behaviour was observed after that time.

Another individual of *P. japonicus* showed clinging behaviour 5 days after metamorphosis. For the individual, molting was not done complete at metamorphosis and malformation was formed at one of the second antennae. This may be a possible factor to delay settlement behaviour for the individual.

Clinging behaviour was observed three days after metamorphosis for *P. elephas*. The puerulus clung on the substratum with its wide stretched 5 pairs of periopods. The clinging posture of this species was remarkably different from others: the puerulus lifted the cephalothorax part and supported its abdomen with beating vigorously 5 pairs of pleopods. Sheltering behaviour was not observed for this species. To determine settlement behaviour for precisely *P. elephas*, further observation will be required.

J. edwardsii was observed to occupy the shelter one day after metamorphosis or to burrow into the fine silt substratum. They showed preference on fine silt such as sedimented at Castlepoint rather than fine sand sampled at Sanriku coast. *J. verreauxi* showed clinging behaviour on stones or artificial fibre on the day of metamorphosis, while no burrowing behaviour was observed for this species.

Feeding behaviour

The phyllosomas preyed food particles with the third, fourth and fifth pereiopods, and transferred to the mouthparts with maxillipeds to graze. They have large hepatopancreas which is usually filled with food materials. After metamorphosis, the pueruli showed no appetite on any kind of animal or vegetable foods, and no food materials were found in hepatopancreas. If they took food, the food materials could be visible because the puerulus is transpsrent at its early stage.

The light-coloured hepatopancreas became visible several days after metamorphosis and well develped at the advanced stage of puerulus. No feeding behaviour was observed during the entire period of the puerulus. Rearing condition for the pueruli of *P. japonicus* was summarized in Table 2.

Without feeding the dark pigmentation developed on the carapace at the advanced stage, and the pueruli molted into the post-puerulus 15 and 12 days after metamorphosis, respectively. The first moult post-puerulus begun to feed mussels on the day after moulting.

Effects of water temperature and salinity

Surface water temperature and salinity fluctuated between 16 and 21℃ and between 33.6 and 35.5‰ at Castlepoint during the survey period in January and February in 1989. Collected transparent pueruli were tested in number of 5 each at water temperature

Table 2. Culture condition for the pueruli of *Panulirus japonicus*

Puerulus	1		2	
Date of metamorphosis	22 June 1988		12 August 1988	
Days of phyllosoma stage	340		391	
Period of puerulus (days)	15		12	
Water condition	*Nannochloropsis*	Filtered	*Nannochloropsis*	Filtered
Days	7 (initial)	8 (final)	5 (initial)	7 (final)
Water temperature(℃)	26.4	25.3	25.3	25.1
Salinity (‰)	35.43	35.24	35.37	35.20
pH	8.30	8.30	8.26	8.25
Nannochloropsis ($\times 10^3$ cells/ml)	63	0	70	0
Water exchange (daily %)	0.3	22.5	0.8	2.6

24, 26 and 28℃, respectively. All individuals survived for about 96 h at 24 (range:23.1–25.9) and 26 (24.9–27.1)℃. All individuals died at 27.9℃ within 2.5 h. Lethal water temperature for the early stage puerulus is considered at 27–28℃.

Transparent pueruli were also tested in number of 5 each at salinity 35.0, 31.5, 28.0, 26.3, 24.5, and 21.0 ‰, respectively. All individuals survived at salinity higher than 26.3 ‰. All individuals died at 24.5 ‰ within 7 hours and at 21.0 ‰ within 5 hours. Lethal salinity for the early stage puerulus is considered at 25–26 ‰.

4. Discussion

Pelagic phase of spiny lobsters is composed of the planktonic phyllosoma stage and the nectic puerulus stage. Duration of the pelagic phase is roughly estimated by time difference between hatching season and settlement season. Thus, it is estimated at about one year. To estimate the puerulus period is rather difficult due to lack of sampling of the late stage phyllosomas and the early both stage puerulus. Pueruli at various developmental stages are collected at seashores at Castlepoint (Booth, 1979; Hayakawa *et. al.*, 1990). However, dulation after metamorphosis for them is unclear. Accurate information will be available by complete development in the laboratory.

The puerulus of *P. elephas* (Kittaka and Ikegami, 1988) *P. japonicus* (Kittaka and Kimura, 1989) and *Jasus* spp. showed clinging behaviour relatively short period (1–3 days) after metamorphosis. Clinging behaviour is considered to be the site searching behaviour for settlement. An active puerulus of *P. japonicus* was observed to settle 4 days after metamorphosis (Kittaka and Kimura, 1989). The hepatopancreas became visible several hours after settlement, a V-shaped structure one day after settlement, and bifidness at the anterior parts 2 days after settlement (Kittaka and Kimura 1989). This may suggest that puerulus consumes energy for swimming purpose only during pelagic phase, perhaps including site searching phase. Development of hepatopancreas will commence just after settlement.

The duration of puerulus was 11 days for *P. elephas* (Kittaka and Ikegami, 1988), 12–15 days for *P. japonicus* (Kittaka and Kimura, 1989), 19 days for *J. edwardsii*, and 21 days for *J. verreauxi* under laboratory conditions, respectively. While in the wild the puerulus of *J. edwardsii* is estimated to swim inshore after metamorphosis up to 20–40 days according to the local oceanographic conditions and the width of the continental shelf (Booth, 1989). Assuming that the wild puerulus of *J. edwardsii* takes similar site searching behaviour and developmental stage, the duration of *Jasus* puerulus is estimated at about 40–60 days. This estimated duration of puerulus in the wild will be corrected if metamorphosis occurred rather inshore on puerulus transport mechanism was more efficiently provided in the ocean.

Once culture method was established, ecological and behavioural data obtained in the laboratory would provide more accurate information. Although feeding by puerulus was reported for *J. lalandii* (SILBERBAUER, 1971) and *P. elephas* (ORTON and FORD, 1933) feeding was not observed for both species by our culture experiments. Without feeding the pueruli of *P. japonicus* molted into the postpuerulus (KITTAKA and KIMURA, 1989). The pueruli were kept in the phyllosoma culture tank for initial several days after metamorphosis, which contained microalgae *Nannochloropsis* sp. to control water quality. Morphological observation of the puerulus of *J. edwardsii* showed distinct regression of the mouthparts compared to both late phyllosoma and postpuerulus stage (NISHIDA *et al.* 1990). If the puerulus depended on nutritionally microalgae in the water, the digestive glands would be filled with microalgae intake. No such evidence was realized.

Transparent puerulus just after settlement showed tolerance to higher water temperature and lower salinity which seldom occur in the wild. Thus, the puerulus is very tough animal. However, they require good water quality and sufficient water exchange. An improved device to culture pueruli is required for further behavioural studies.

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Role of temperature and salinity on survival and growth of crustacean larvae*

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Abstract: Growth and survival of marine animals depends on their physiology. Temperature plays an important role on general metabolism, and salinity on osmotic pressure variations, free amino acid content and proteic metabolism. Generally, researches developed on biology of larvae are studying the effect of only one external factor on some biological characters, as growth, respiration, food consumption, etc. In order to develop a better knowledge of the survival rate of crustacean larvae of the species *Palaemon serratus*, several studies have been done in different combinations of salinities and temperatures, leading to a design of tridimensional abacus. These abacus are a characteristic of the species, and they may be used to predict the survival rate of the larvae in their natural environment. The optimal survival is varying at different steps of the larval growth, leading to a beginning of explanation of the migratory processes and behavior. Digestive capacities are also affected by temperature and salinities as well as oxygen consumption, and intracellular free amino acids. Excretion of ammonia and other nitrogen containing molecules are also affected by such variations of external factors of environment. The results of these studies will be very helpful to understand the equilibrium between species in the marine populations in natural ecosystems.

1. Introduction

The study of processes governing recruitment are almost always taking in consideration the number of juveniles entering in a fishery or the number of larvae constituting the phase of prerecruitment. But very seldom the studies take care of the qualitative factors who play a role in the recruitment processes. These qualitative factors play nevertheless an important effect in the survival of larvae, and we have to evaluate them as precisely as possible to understand in detail how the survival rate is affected by these factors.

Two main factors play a role in the survival of larvae:

- the quality of the eggs spawned, especially for the composition of their reserves, and their genetic characters,
- the resistance of larvae hatched, to the external factors as temperature, salinity, oxygen, dissolved organic matter, quality and quantity of food, etc. (CECCALDI, 1982).

It is not possible to understand all the effects of each of these factors, taken separately, and much more difficult to study the simultaneous variations of all of the edaphic factors. Nevertheless, it is possible to study two of these factors, taken in combination, all other factors remained fixed. (COSTLOW, 1967; REGNAULT and COSTLOW, 1970; ZEIN-ELDIN and ALDRICH, 1965).

The survival of larvae and postlarvae depends on the conditions of environment and on trophic factors (CAMPILLO, 1975; FORSTER, 1970). If one take a sample of 100 larvae hatched on the same time, coming from the same female mother, they are growing approximately at the same growth rate. A few of them show a slower growth rate, a few other ones a higher growth rate, even if they are fed the same way. We have developed specific experiments to increase our knowledge in that field.

2. Experiments

Survival and Growth

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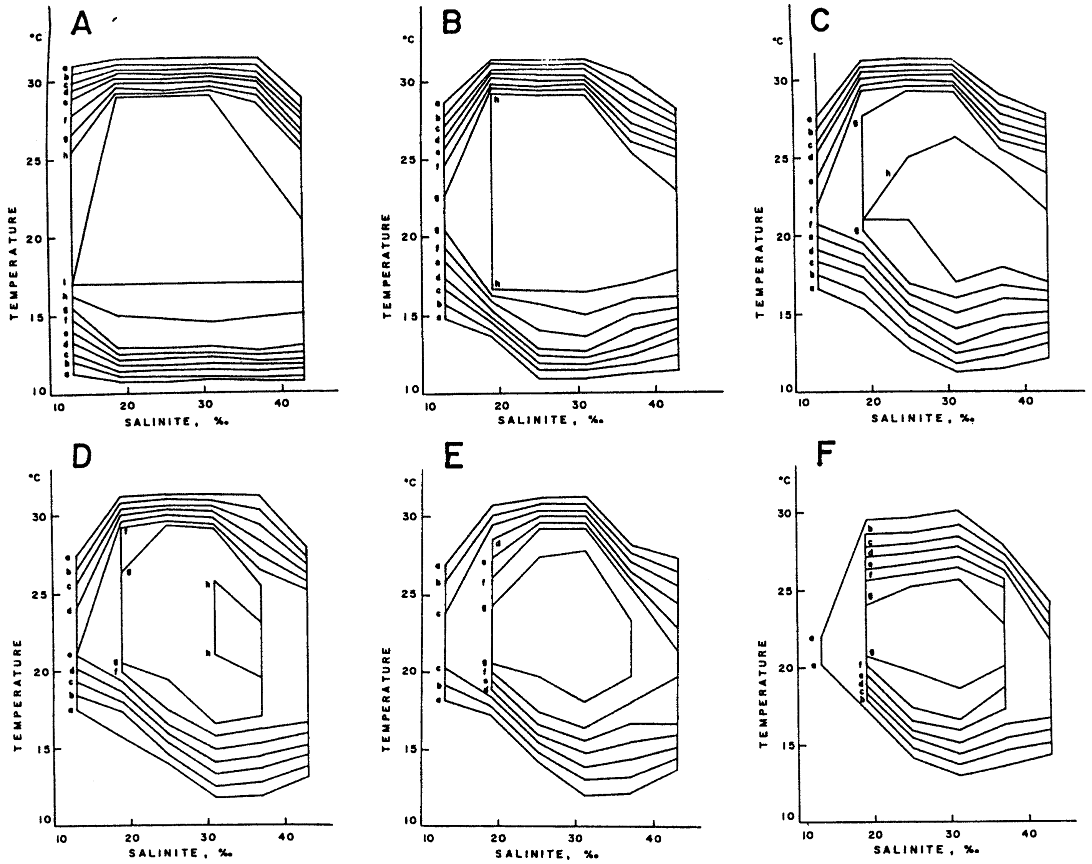

Fig. 1. Estimates of survival patterns between larval stages of *Palaemon serratus* as a function of different temperature-salinity concentrations. a, 20%; b, 30%; c, 40%; d, 50%; e, 60%; f, 70%; g, 80%; h, 90%; i, 100%. A, from ZI to ZII; B, from ZI to ZIII; C, from ZI to ZIV; D, from ZI to ZV; E, from ZI to ZVI; F, from ZI to PL (Post larve).

In order to study the variability of the survival and the growth rate, we have studied samples of 50 larvae of *Palaemon serratus* just hatched (YAGI and CECCALDI, 1985; YAGI *et al.*, 1990).

The rate of survival and the duration of the intermolt were established for each of the six zoea stages and also the rate of metamorphosis and total duration in thirty different temperature and salinity combinations. Postlarvae were obtained in 24 combinations. The rate of survival for each larval stage was influenced significantly by salinity as well as by temperature. The values of the combinations allowing 50% survival decrease during larval development. Mortality is particularly high for thresholds of low temperature – low salinity and high temperature – high salinity. It is remarkable to note that survival is better in conditions of high salinity and low temperature or low salinity and high temperature (Fig. 1).

Temperatures allowing 50% survival range between 11.7 and 30.5 ℃, up to the third molt, from 14.1 to 30.3 ℃, up to the fourth molt, from 14.7 to 30.0 ℃, up to the fifth molt, and from 15.1 to 27.8 ℃, up to metamorphosis. In the same way, salinity ranges from 13‰ to 43‰ from the first stage and from 19‰ to 43‰ beyond this stage. Rate of survival decreases by half between the first larvae and the postlarvae.

The first postlarva appeared on the fifteenth day in combinations of 25 ℃–19‰ and 21 ℃–25‰. Q_{10} values, according to Van't Hoff"s formula for speed of growth during

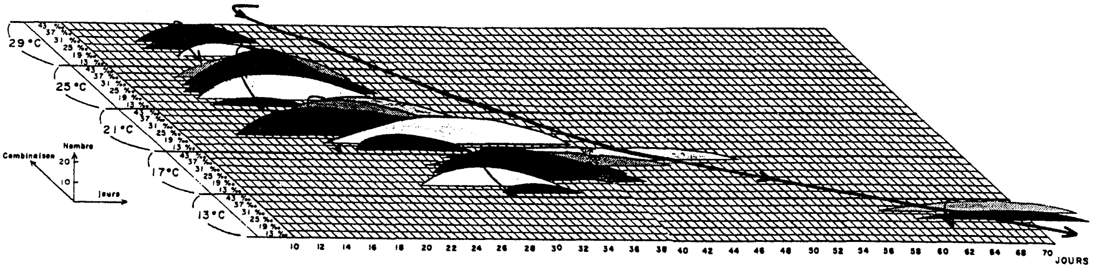

Fig. 2. Perspective model to show the combined temperature-salinity effects on the number of daily incidences of metamorphased postlarve of *Palamon serratus*.

their larval development up to metamorphos is, vary from 1.78 minimum for a salinity of 19‰ to 2.52 maximum for a salinity of 43‰.

Three-dimensional perspective model were also drawn to improve knowledge of the combined influence of temperature and salinity on larval development and the number of appearances of postlarvae during metamorphosis (Fig 2).

Oxygen consumption

The oxygen consumption of the six successive zoeal stages of *Palaemon serratus* reared in 30 different combinations of temperature and salinity was measured. Oxygen consumption per individual, R, increased with the age (or the dry weight, W) of the larvae according to a power function $R=a\cdot Wb$ but no significant relationship was found between the specific respiration, R′ (respiration rate per dry weight unit), and the dry weight of successive larval stages. Nevertheless, highest rates were always observed in the Zoea IV, for all temperature and salinity conditions. These maxima were probably related to a large nutritional changes occurring at this period of development.

Temperature affected according to a linear funtion $R'=a'+b'\cdot T\cdot Q_{10}$ values varied between 1.50 and 2.58 according to the larval stage and the salinity, except for the Zoea I at the lowest salinity where a very high value of 5.89 was recorded. The respiration rate decreased at the lowest and highest salinity values. The salinity effect on metabolic rates is described by a quadratic equation $R'=a''+b''S+cS2$. The combined effect of temperature and salinity on the respiration of the six successive larval stages is tllustrated using tridimentional models. respiration rates were recorded at salinities between 25 ‰ and 31‰ and at the highest temperature (29℃), as shown by Yagi *et al.* (1990) (Fig 3).

Free amino acid

From our another studies, we have shown that free amino acid composition is varying very much at different steps of the larval growth in the shrimp *Penaeus japonicus* (Marangos *et al.*, 1990). Free amino-acid content increases from 83 to 687 micromoles/g dry weight from egg to post larval stage (20 days old: P20). There is a sharp increase between zoea and mysis stages, and another one between one day post-larvae (P1) and P20. After the mysis stage, free essential and non-essential amino-acid evolve in a different way: the non-essential free amino-acid content, mainly glycine, increases continuously whereas essential free amino-acids content decreases (about 40%) from the mysis stage to metamorphosis in post-larvae (P1).

Free amino acids content evolution during larval development exhibits the same trend as the variation of the digestive enzyme activity. These experiments show that the osmoregulatory processes of crustacean larvae are varying at different steps of the larval growth.

But we have to point out that the amino-acid content depends also on salinity and on temperature. These results show the complexity of the regulatory processes, as they occur in nature, if we are considering only temperature and salinity.

Essential amino-acid in that species show a diminution at mysis and following stages. It

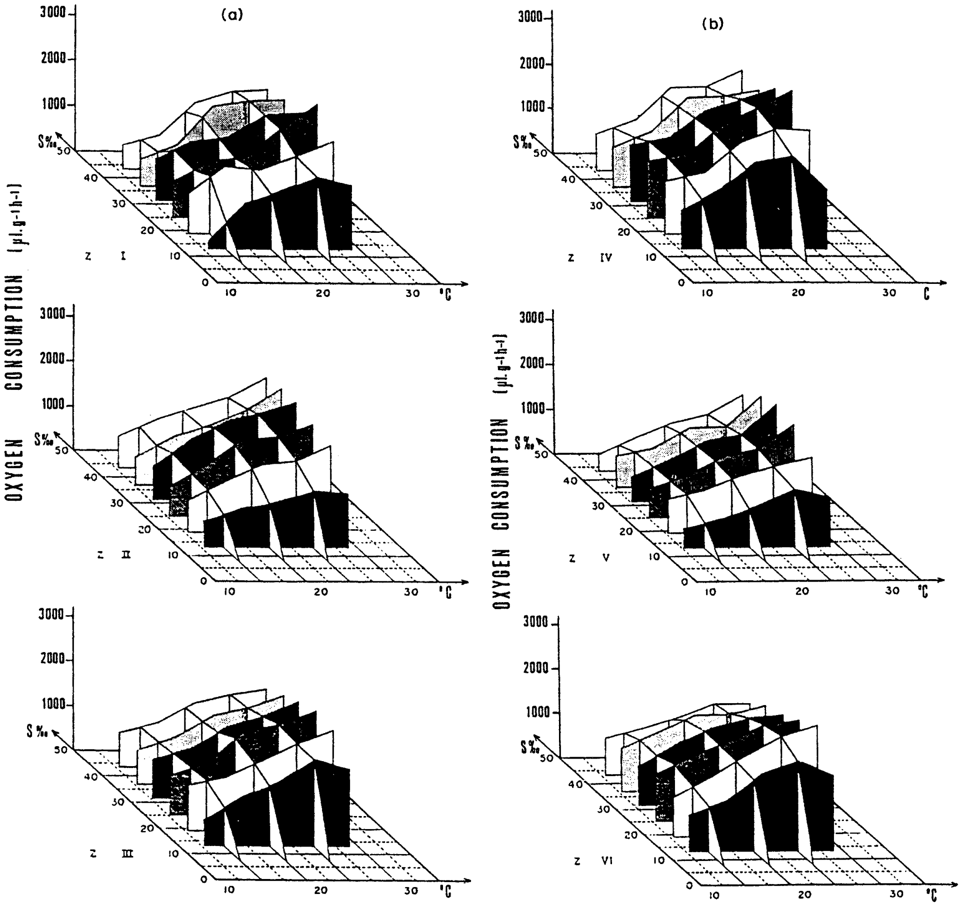

Fig. 3. Three-dimentional models of the influence of combinations of temperature and salinity on the consumption of oxygen per unit of dry weight of the larvae of *Palaemon serratus*: (a) stages ZI–ZIII; (b) stages ZIV–ZVI.

seems also that the potential of protein synthesis, which is in connection with essential free amino-acids, is in opposition with the capacity of osmotic regulation of these larvae.

There is a link between the age of the larvae, the food they are consumed, and their capacity to survive; this could be explained as zoea and mysis are living in desalted water of estuaries, as other *Penaeids*, and post-larvae are settled in the bottom located at a higher distance than the first larvae.

Detailed analysis of such amino acid show large variations of each one; the integration of all of them conduct to the osmoregulatory capacity of the larvae.

The evolution of amino-acid content on the passage of zoea stage to mysis stage, then to following stages, should have some straight relation to the competition of the food eaten, and the capability of the larvae to adapt these physiology to that composition.

The quality of food plays also a prominent role in crustaceans. For instance, in *Penaeus vannamei*, for biochemical analyses, nine individuals per treatment were used for the determination of the hepatosomatic ratio, proteins, proteases, amylases and trypsin. The results show that a high level of soya bean of fish meals in the diet strongly depresses growth without any apparent effect on the digestive enzymes or the hepatopancreas parameters. No effect of soya bean meal type or geographical origin on the fish meal was detected. The results suggest that the incorporation of both soya bean and fish meals in the diet should be restricted to low concentrations and only with the aim of diversifying the protein sources (GALGANI *et al*, 1988). These results concerns adults but the same situation exist in larvae, who are rather selective for their food, at different steps of their growth.

3. Discussion

It appears, from the results obtained, that it is necessary to draw specific abacus, for each species, and for each larval stage.

Resistance of first stages: The younger stages are less sensitive to large variations of temperature, and salinities than the older ones.

This could be interpretated as an advantage for the species; when the eggs are layed and when the first larvae are hatched, they are transported passively by currents. As the adults are living on shallow water, the eggs and larvae may enter in estuaries or desalted waters,without great damages.

The aged larvae adcquire regulatory processes in the same time than their swimming capacities.

Seasonal variations of survivors: Of interest also are the observation of tridimensional models showing the survival rates at various combinations of an optimal zone of survival. But if the external temperature and salinity are changing, some mortality appears in the group who was able to survive in the optimal combination of external factors.

The original sample of the larvae was not genetically homogenous, and a selective mechanism appears when the external condition are fixed for a long time. If several successive winters are very cold, an evolution process begins, as the most resistant larvae to cold survive better to the other larvae. They will grow, giving adults who are better survivors in cold conditions than the "usual" or "ordinary" adults.

Year after year, there is a genetic play, favorising one part of the population or another one depending of the meteorological conditions and of the hydroclimat.

Daily incidences of metamorphosed postlarvae: For high temperatures, between 25 and 29℃, the apparition of metamorphosed post-larvae occurs 15 days after hatching and the last one several days after. The whole sample metamorphoses in a short period of time, but the molts are not simultaneous. They appears at different days from the first incidence of metamorphosed post-larvae.

For the combinations, temperature 17℃, salinity 31‰, that period of time is very long, reaching almost one month. That characteristic represent an evident advantage for the species because the dissemination of the post-larvae will be much longer that for high temperatures and high salinities conditions.

Metamorphosis and salinity

One more surprising fact appeared in the study of that results: the optimal survival is better in rather desalted water, (salinity 31, 25 and even 19‰) than in sea water (salinity 37‰). It seems that, for sea water species, the salinity of sea water is too high, at least for the species we have studied; this could be of great help in aquaculture for instance, if one wish to obtain a population of larvae metamorphosing in the same time for aquaculture, to have a large range of sizes of post-larvae.

4. Conclusion

The role of temperature and salinity on survival and growth of crustacean larvae is more more complex than expected.

Survival rate depends on both factors taken simultaneously as it occurs in nature. But the results obtained in aquaculture tanks may give us interesting results in a rather short period of times. They have to be completed by physiological and biochemical works, then by genetical and molecular biology studies. These three ways of reseach remains open.

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Co-ordination of the pelagic and benthic life history phases in marine benthic invertebrates: two examples from the Polychaeta.*

Michel BHAUD** and Anthony J. GREHAN**

Abstract: An introduction is presented of work carried out in the French marine station at Banyuls (Mediterranean coast) within the framework of the French national programme (PNDR) concerned with determining the factors that effect recruitment. Two terebellid polychaete species have been chosen as suitable models for recruitment studies: *Eupolymnia nebulosa* (Montagu) producing spawning egg masses and larvae with a short pelagic phase, and *Lanice conchilega* (pallas), free spawning with a long planktonic stage. The suitability of these species particularly for laboratory experimentation is discussed. Laboratory and field observation of the recruitment processes in these two species shows that: a) *E. nebulosa* larvae have weak dispersion capabilities which promote retention of the larvae in the vicinity of the adult habitat, and at least at one location, the synchronisation of the release of spawning egg masses with appearance of macroalgae which provide nursary areas for young juveniles appears to be important in controlling recruitment suceess; b) *L. conchilega* larvae with long planktonic development appear to be retained close to the adult habitat by local hydrodynamic mechanisms.

1. Introduction

The success or failure of larval settlement on the bottom is a critical feature in the maintenance of benthic invertebrate populations and to a large extent controls the temporal and spatial variability of the adult stages. Experiments in the field are, however, of limited value in the description of the actual events occurring during settlement. In-laboratory experimentation is therefore obligatory, to interpret the likely effects, on the small scale, of hydrodynamics and biological processes.

This paper provides a brief introduction to, and temporary synthesis of, work carried out by researchers in the French marine station of Banyuls (Mediterranean), in collaboration with the marine station of Archachon (Atlantic coast) and within the framework of the PNDR (a national program concerned with determining the factors that effect recruitment). More detailed results of this work are contained in the following publications; BHAUD and DUCHÊNE, 1989; BHAUD and DAUVIN, 1990; BHAUD, *et al*., 1990.

One major programme directive requires the study of model species preferably species which are well known in term of their ecology and reproductive biology. In the two laboratories above, work is being carried out on the Polychaeta, more specifically, two species of Terebellidae: *Eupolymnia nebulosa* (Montagu) which produces spawning egg masses and larvae with a short planktonic stage (3–15 days), and *Lanice conchilega* (Pallas) which is free spawning and has a long planktonic stage (>3 weeks). Information on the basic biological features of these species can be found in BHAUD (1988 a and b; 1990 a and b).

In addition to work on model species, a project to provide quantitative and comparative field data on recruitment of the principal species in a muddy sand *Nephtys hombergii* community and in a fine sand *Spisula subtruncata* community in the bay of Banyuls, is in progress. The aim of this study is to tract settlement and early post-settlement recruitment in a number of species, especially with regards to post-settlement mortality rates. A pluridisciplinary approach has been adopted with the intention of producing an integrated model of the main physical and biological processes occurring during the spring recruitment period in the study area.

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The following results obtained from the study of *Eupolymnia nebulosa* and *Lanice conchilega*, are presented to highlight some of the more important recruitment processes in the two species.

2. Suitability of *Eupolymnia nebulosa* and *Lanice conchilega* as model species for study.

Eupolymnia nebulosa.

A laboratory study of the settlement behaviour of *Eupolymnia nebulosa* on different sediments has been carried out both in still water and using a hydrodynamic canal (Bhaud, 1990b; Cha, 1990). Laboratory experimentation on *E. nebulosa* has several advantages: a) the number of available larvae for each experiment is always high enough to allow the utilization of a container with a large volume of water, approx. 60 litres; b) this container, in the form of a self-circulating canal, facilitates the passage of water over removable plates which can be covered with various substrates; c) the duration of each experiment, 2 to 5 days, show final settlement distribution patterns and not just the initial arrival of larvae at the bottom; d) easy observation of larval tubes facilitates accurate monitoring of settlement; e) synchronisation of settlement produces individuals of the same age for experimentation; f) the short duration of planktonic larval life facilitates more rapid experimentation; g) photography of the substrate in the canal enables rapid counting of tubes without disturbing the test plates.

Lanice conchilega.

The larvae of *Lanice conchilega* are present in the plankton of the bay of Banyuls from November to February. Adult densities are never high as indicated by diver survey (<1 ind. $5m^{-2}$). *L. conchilega* is an associated species in the fine sand *Spisula subtruncata* and the muddy soft sediment *Venus ovata*. community (Guille, 1970), and is also found in *Posidonia* sp. beds (eel grass) in the bay of Banyuls (Laubier et Paris, 1962). Larvae for experimental use are obtained by plankton sampling. While the number of available larvae obtained is much less than for *E. nebulosa* (often less than 50 individuals per tow), sufficient material is obtained for canal experimentation (Bhaud *et al*., 1991). In nature, the long duration of the planktonic stage of *L. conchilega* permits the determination of spatial distribution and thus permits study of the species larval dispersion ability.

3. Results and Discussion

To examine the interaction between larvae and sediments at settlement, several experiments were developed to assess:

- the ability of larvae to use several types of sediment in terms of the nature and size of grains,
- the ability of larvae to use a heterogeneous sediment,
- the effect of current on larval sediment choice capabilities,
- the application, if possible, of these results to explain observed variability in the field.

Eupolymnia nebulosa

A) The ability of larvae to construct primary tubes with respect to the grain size and the nature of sediments

This experiment was carried out in still water containers and concerns the ability of the larvae to manipulate a sediment (Table 1). The results show that larvae are best able to utilize decanted silt (No. 6 and 7) and microbeads (No. 5) while clay particles (No. 8) although of sufficient size are not utilized due to their morphological unsuitability for manipulation.

B) Settlement choice in the presence of two different sediments

Two of the substrates used in (A) above (N° 2 and 6, respectively FS and DS in Table 2), were deposited individually in ten separate petri-dishes arranged in two rows of five in the same aquarium. The two sediment types were presented in alternating pattern in each row and between rows. Free swimming larvae released from an egg mass were introduced to be aquarium and gave the following tube distribution after settlement five days later:

Table 1. Main biological features and recruitment characteristics examined in the two species.* The time lag between the appearance of *Lanice conchilega* larvae at Banyuls (B) (Mediterranean sea) and Arcachon (A) (Atlantic coast) increases the period of possible study.

	*L. conchilega**	*E. nebulosa*
Biological features:		
Larval availability	B: December->March A: April->July	B: March->June
Fertilization and spawning	free spawning no egg masses	benthic egg masses
Length of larval life	3 weeks in the plankton	3-15 days between release of eggmasses and settlement
Number of larvae available	30-50 per plankton tow	5,000 to 20,000 per egg mass
Recruitment processes examined:		
In-laboratory	buoyancy, floatation: role of secretion	interaction with sediment
	influence of flow: lengthening of planktonic life	influence of flow: multiplication of contacts during short period
In-field	dissemination in connection with physical structures	dissemination over a short distance; co-ordination of the life cycle.

Table 2. The preference of *E. nebulosa* larvae for several different types of sediment. The ability of these larvae to use the sediment and to construct or attempt to construct tubes is assigned a value from 0 (grains not displaced) to ++++ (well constructed tubes). FS: Fontainebleau sand; MB: glass microbeads; DS: decanted silt; PC: pure clay.

	sediment	size (mm)	strength of use
1	FS	250-200	0
2	FS	200-160	+
3	FS	160-100	++
4	MB	150-105	+++
5	MB	60-45	++++
6	DS	<60	++++
7	DS	<40	++++
8	PC	5a40	0

FS (160-200 mm): 445 375 355 370 340
DS (<60 mm): 195 230 50 245 265

There were significantly (Student's t: 4.25, $p>0.05$) less tubes on the silt, which seems to be contrary to the results in Table 2. A grain size of 160-200 μm seems to be too large to allow tube building. Closer inspection revealed that the tubes were not built from grains of fine sand but from small quantities of silt present in the running seawater supply (even after double decanta decantaion) or from contamination by neighbouring silt containing petri dishes. This experiment, in effect, shows that sediment heterogeneity may produce higher rates of settlement, i.e. the availability of small amounts of manipulable particles can render an otherwise unusable sediment suitable for settlement. After five days of this experiment, all newly constructed tubes were occupied but after a further six days approximately 2/3 of the tubes in the dishes containing sand were empty while all the tubes in the dishes containing silt were occupied. A new factor became important, i.e. food availability.

In summary, the 160–200 mm fraction of Fontainebleau Sand appears to be unsuitable for larval settlement (result in Table 2). However, by the addition of a small amount of silt, the resulting silt/sand aggregate is capable of supporting initial settlement but ultimately is inadequate for the maintenance of juvenile stages. The fine sand particles provide a firm support for settlement but are inadequate for feeding, therefore, development is quickly halted. This also indicates that the larvae possess sufficient intrinsic energy reserves to attain the benthic existence and that during the initial settlement phase, external energy supplies are not required.

The larvae have three basic requirements during early settlement: a need for a solid support, material for tube building and a food source for nutrition. Larvae may be fooled by certain sediment categories (e.g. 4 and 5 in Table 2). Individuals satisfy short-term needs as they arise, they do not recognise whether a sediment is compatible with the later requirements of the juvenile, and do not search for organic material on arrival at the sediment surface. This contrasts with the results obtained by Butman *et al*. (1988) for other species, as it can't be show, in this case,that larvae initially settle on a substrate commensurate with the adult needs and particularly, the need for food material.

C) The influence of current flow on settlement

The influence of sediment type and thickness on the settlement of the larvae of the polychaete *E. nebulosa*, was examined as a function of near bottom current flow. The number of larvae settling on 2 different sediment types (mud or artificial microbeads) with different thicknesses (thin layer: 60–100 mm and thick layer: 2 mm) were compared (Fig 1). Larvae showed a preference for this layered sediment which permitted access to the hard bottom. When only thick layers of the two sediment types were offered, the larvae preferred microbeads to mud. Current flow favoured settlement in terms of sediment thickness but didn't affect settlement in terms of sediment type. The effect of current flow is much more marked when the substrate is suitable. This is understandable because the current causes an increase in lateral advection and thus in the number of potential visits to the sediment surface by the larvae.

D) Observations of spatial and temporal variability in the field

Four stations with different depths have been examined in the vicinity of Banyuls. In 1990, the appearance of spawning masses in January at the shallowest station (1m) was much earlier than usual. This may have resulted from rapid growth of oocytes during the autumn coincident with higher than

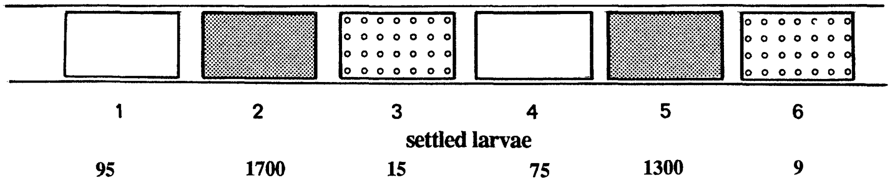

Fig. 1. Settlement by larvae of *Eupolymnia nebulosa* on a series of plates containing different sediments. The results show that there is: 1) good selection in the canal with alternating sediment choice, and 2) a larval settlement requirement for both hard and soft substrates. The current speed (2 cm over the bottom in the direction of the long axis of the canal) is 7.5 ±0.7 cm s^{-1} which does not result in resuspension of the test sediments. Plate dimensions: 17×9 cm (After Cha, 1990). 1 and 4 = bare plates, 2 and 5 = natural mud (<60 μm) in a thin layer (permitting access to the hard bottom), 3 and 6 = natural mud (<60 μm) in a thick layer (not permitting access to the hard bottom).

normal water temperatures due to the persistence of the summer thermocline. Early spawning at the shallow station may be disadvantageous due to an apparent dependance on macro-algae for the provision of juvenile nursary sites. These algae first appear in April, therefore, larvae which are released before this date have much higher probability of dispersion away from the adult locality. The degree of synchronisation between spawning and macro-algal appearance seems to determine to a large degree, inter-annual fluctuations in density at this location.

The variation in the maximum number of spawn masses observed at a shallow water station during a period of 7 years was as follows:

1982	1983	1984	1985	1986	1987	1990
125	190	85	85	130	92	156

The small interannual variability in adult (female) density of *E. nebulosa* at this location may be due to the following characteristics: 1) the importance of larval retention by the macro-algae; 2) pulsed spawning which ensures the success of, at least, a small number of larvae; 3) high settlement success (observed in the laboratory); and probably, 4) weak interspecific larval and adult (decreased sediment collecting activity) competition; and 5) a relatively long life span of at least 4 years.

E) Settlement on a natural sediment

If larval settlement requirements identified by experimental observations, reflect the needs of the adults in the adult location, then the larvae should be collected from soft substrates more easily than from hard substrates. A simple experiment confirmed that the silty sands of a *Nephtys hombergii* community represents a potential substrate for *E. nebulosa* larval settlement even though adults of this species are not found in any of the soft substrate populations in the bay of Banyruls (GUILLE, 1970).

The absence of adults of *E. nebulosa* in this community is potentially explained by 2 hypotheses which concern the larvae or juveniles; i) larval dispersion from adult brood stocks, located close to the shore, is sufficient to colonise the silty sand community in the middle of the bay, but after settlement other factors inhibit further development; ii) larval dispersion is insufficient to reach the *Nephtys hombergii* community. The absence of larvae in the plankton or juveniles in epibenthic sledge samples collected in the vicinity of this community tend to support the second hypothesis: i.e. current advection is too weak to transport larvae from nearshore to the *Nephtys hombergii* ground in the middle of the bay. Larvae remain close to the areas occupied by the adults which is consistent with the mode of larval development, i.e., short pelagic, lecithotrophic development,serving to limit dispersion.

Lanice conchilega: *dispersion capabilities of the planktonic larvae*

A) Buoyancy observed in the laboratory

Observation of the aulophore larva of *L. conchilega* has been made in a sufficiently large volume of water for the conditions of displacement to be similar to those occurring in nature (Fig. 2.). The position and the stability of these larvae in the water column depends on the secretion of a mucus thread and not on the circulation of the water between the body of the larvae and the wall of the larval tube (BHAUD and CAZAUX, 1990). After initial settlement the larvae still retains its ability to return to the water column. This suggests that the conditions which permit larvae to re-enter the pelagic sphere may be as important as those which control the sinking rate in determining the eventual settlement location.

B) Field observation of the larvae

In spite of the long duration of the planktonic life, the local hydrodynamic conditions in the bay of Banyuls do not necessarily have a dispersive action: regular planktonic sampling at the same location recovers successive different stages of development, i.e. the primary detritic benthic tubes and mucus planktonic tubes occupied by larvae having between 1 and 5 tentacles (MARCANO, 1991).

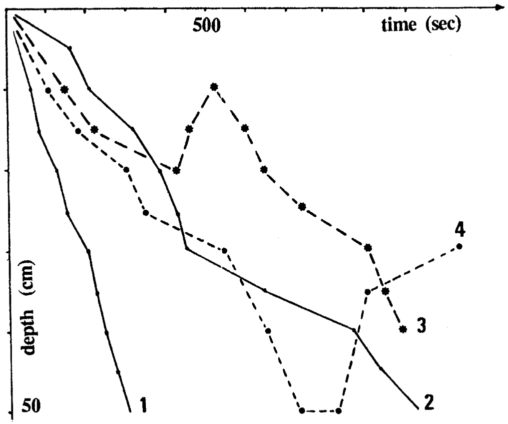

Fig. 2. A study of the buoyancy characteristics of *Lanice conchilega* larvae in an experimental chamber with still water.
1: An example of the vertical all profile of an empty tube; mean time (s^{-1}) for a 50 cm descent (n=6, m=516, s=62).
2: An example of the vertical fall profile of a larva without a tube; mean time (s^{-1}) for a 50 cm descent (n=7, m=804, s=119).
3 and 4: Vertical displacement profiles of aulophore larvae. After observations of 2500s, larvae were still in the water column after a more or less short passage at the bottom.

However, this observation doesn't definitely prove larval retention in the bay of Banyuls. It is likely that some exchange occurs between larvae inside and outside of the bay; but the extent of this possible exchange hasn't been quantified. Preliminary biological data (quantitative differences between material recovered from stations of 25m and 60m depth in the bay, and differences in the age of the larval stages) indicate that there is at least partial isolation between the bay and the exterior. Wind and wind driven currents have been studied. Two directions predominate; i) a westerly wind which causes a circular current movement which when combined with the residual north-south moving current results in the retention of the larvae in the bay; and ii) an easterly wind (coming from off-shore) which causes large disruption of the water mass. The hydrodynamic features in the bay of Banyuls are source of variability which have a direct influence on the amount of competent larvae available for settlement and can in part explain the success of failure of recruitment in *L. conchilega* (Sinclair, 1988). The degree of retention controls directly the quantity of larvae arriving at the end of their development and capable of settling in the bay.

4. Conclusions and prospectives.

Important factors controlling the availability of competent larvae and the success or failure of recruitment in the two polychaete species studied in the bay of Banyuls are as follows: A) *E.nebulosa*. The weak dispersion capabilities of the larvae promote retention in the vicinity of the adult habitat and perhaps serve to prevent larvae from reaching the middle of the bay where the substrate is suitable for initial settlement (laboratory results) but would result in subsequent high mortality of juveniles. The synchronisation of the release of spawning egg masses with the local appearance of macro-algae (at least at one shallow location) concurs with weak larval dispersion potential. Further work will be carried out to determine the cause of early spawning in the shallow water population. The potential link between the rate of oocyte development and the degree of summer thermocline persistence (with the consequent prolongation of high water temperature) will be investigated experimentally. B) *L.conchilega*; Large scale retention structures, rather than variation in fecundity, seem to play the most important role in determining the variation in the abundance of *L. conchilega* larvae in the bay of Banyuls. Future expeimental work with this species will focus on the effects of microscale hydrodynamic processes. Observations on the effects of near bottom turbulent flow on the settlement ability of component larvae will be assessed through flume studies.

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Changes in biochemical composition and otolith microstructure of larval common soleas, *Solea solea* (L.) under experimental starvation*

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Abstract: Experiments on starvation were carried out at 12 and 19℃ on larvae of *Solea solea* (L.), in order to investigate indices of nutritional state through their biochemical composition and a potential storage of informations thanks to modification of their otoliths.

At 19℃ the increase of dry weight and biochemical compounds during the early ontogeny of fed larvae was more speeded up than at low temperature, and protein deposition was more promoted than storage of energetic lipid. Dry weight and actual amounts of proteins, free amino acids and triglycerides quickly decreased in starved fish and could be used as nutritional indices for reared larvae. Nevertheless, as the essential to non-essential amino acid ratio, they were too dependent upon ontogenetic stages to be used in the field. Because sterols remain constant under starvation, the triglyceride to sterol ratio appears to be a very sensitive and more reliable indice, provided that age is roughly estimated.

Both temperature and starvation modified the larval and sagittal growth parameters, resulting in variable larva-otolith size relationships. Low temperature produced smaller otoliths for equal-sized larvae while, at the same temperature, otoliths were bigger for starving larvae. In early starved larvae, somatic growth was arrested, whereas deposition of low-contrast increments, as observed before first-feeding, was generated. Identified to stress marks, low-contrast increments increased variability of age estimates, although a daily rate of deposition was verified after the onset of exogeneous feeding. Observed in sea-caught larvae, they represent complementary informations on he larva story prior to capture.

1. Introduction

Among all the factors controlling fish recruitment, starvation during early life and duration of the larval and juvenile phases have been suspected for a long time to be two of the main components influencing survival (MAY, 1974). In the field, starved larvae have been detected (e.g. THEILACKER, 1986) and differences in growth rate have been pointed out (BUCKLEY and LOUGH, 1987; HOVENKAMP, 1990). But stunting larvae may be quickly eliminated by predators (BAILEY and HOUDE, 1989), and methods have to be sensitive enough for early diagnosis of starvation and as simple as possible for sea-sample use. Starvation has been known not only to lead to protracted larval life, but also to modify the deposition rate of otolith increments for larvae reared under suboptimal conditions (GEFFEN, 1982). Reliability of age estimates for slow-growing larvae has been opened to questions (RICE, 1987) and changes in otolith microstructure have been investigated under light and electron microscopy (JONES and BROTHERS, 1987; CAMPANA *et al*., 1987).

The common sole is serial spawner and, on the French Atlantic coast, lays its eggs from late winter to spring (ARBAULT *et al*., 1986). Seawater temperature and food availability may vary enough during the spawning season to significantly modify the sole larval condition and consequently their growth rate. Therefore, the first step of our studies was to identify the effects of starvation in early life through changes in biochemical contents and otolith microstructures in order to define biochemical indices unabling us to state, as early as possible, the quality of any larva caught from the sea, and to investigate a potential storage of information relative to fasting on the otoliths (RICE *et*

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al., 1985). Besides, we also need to appraise how microstructural alterations conflict with validation of the ageing technique for otliths of this species.

2. Materials and methods

Experimental conditions

Experiments were carried out in the aquaculture facilities of IFREMER Center, in Brest, Sole larvae were reared under two thermal regimes (19-12℃) and constant photoperiod (LD 18:6), and were fed *Artemia nauplii*. Control larvae were fed once a day as soon as their mouth opened, i.e. on day 2 and 4 at 19 and 12℃, respectively. Larvae were submitted to starvation at early ontogenetic stages; either complete starvation (19 and 12℃ experiments) or delayed first-feeding of 2 to 5 days (point of no return determination at 19℃). The sampling methodology is detailed in LAGARDERE (1989), BOULHIC and GABAUDAN (in press), and RICHARD *et al*., (in press).

Dry weight estimations

Dry weight estimations were carried out individually for protein and amino acid analyses (RICHARD *et al*., in press), and on pools of 50 to 5 larvae for lipid analyses. In this case, the larvae were counted, rinsed with an ammonium formate solution, and deposited onto a clean, pre-weighted glass-fiber filter. The samples were then freeze-dried and weighted on a microbalance.

Biochemical analyses

Total proteic content was determined after acid hydrolysis and derivatization with an OPA reagent on single larva homogenates through spectrofluoremetric measurement of primary amines (RICHARD *et al*., in press). After extraction by trichloroacetic acid on the same homogenate, amino acids were derivatized either with OPA for primary amino acids (LINDROTH and MOPPER, 1979) or with FMOC-Cl for secondary ones (EINARSSON, 1985), and measured by HPLC and spectrofluorometry.

For lipid analyses, pools of 50 to 5 larvae were extracted according to FLOCH *et al*. (1957). Concentrated aliquots of the extracts were deposited onto Chromarods, and total lipids were measured with a Iatroscan TH10 (TLC-FID). Lipid classes were separated on Chromarods using different mixtures of hexane, diethylether and formic acid, and then determined on the Iatroscan (PARRISH, 1987).

Larval and otolith measurements

Larvae were staged and SL measured to the nearest 0.1 mm under a biocular microscope. The gut content was examined in order to evaluate the efficiency of feeding. Otoliths were removed from their otic capsules and were mounted whole on ultrathin cover slips, in a drop of PERMOUNT. They were observed and measured under light microscopy with a magnification of x1,250 and the use of immersion oil. The resolving power was in the 0.2-0.5 μm range. Micrographs were taken with an additional green filter (546nm). Increments were counted from micrographs of otoliths from the 12℃ reared larvae only (N=145). Some comparisons were made between those counts and the results of blind readings obtained by image analysis (N=26). This method, developed at the IFREMER Brest Center, utilizes a technique of pattern recognition where the growth dynamic is taken into account via a structuring function, θ, defined as the reciprocal growth function (H. TROADEC, unpublish. data).

3. Results

Survival and food intake

Disregarding temperature and first-feeding dates, survival varied (41-94%) but declined drastically after the point of no return PNR (0-2.6%). In the 19℃ experiment, the PNR was reached at day 7, i.e. 5d after first-feeding of the control or 2d after yolk resorption (Fig. 1B). The PNR was not determinated at 12℃ but it may be estimated as double because larvae survived 9d (19℃) and 18d (12℃) of complete starvation.

The intake of food immediately followed the *Artemia* supply, even when first feeding was delayed in the 19℃ experiment. First feeding did not start before day 6 in the 12℃ experiment, although food was provided at day 4. Low temperature had probably reduced the activity of early larvae, and

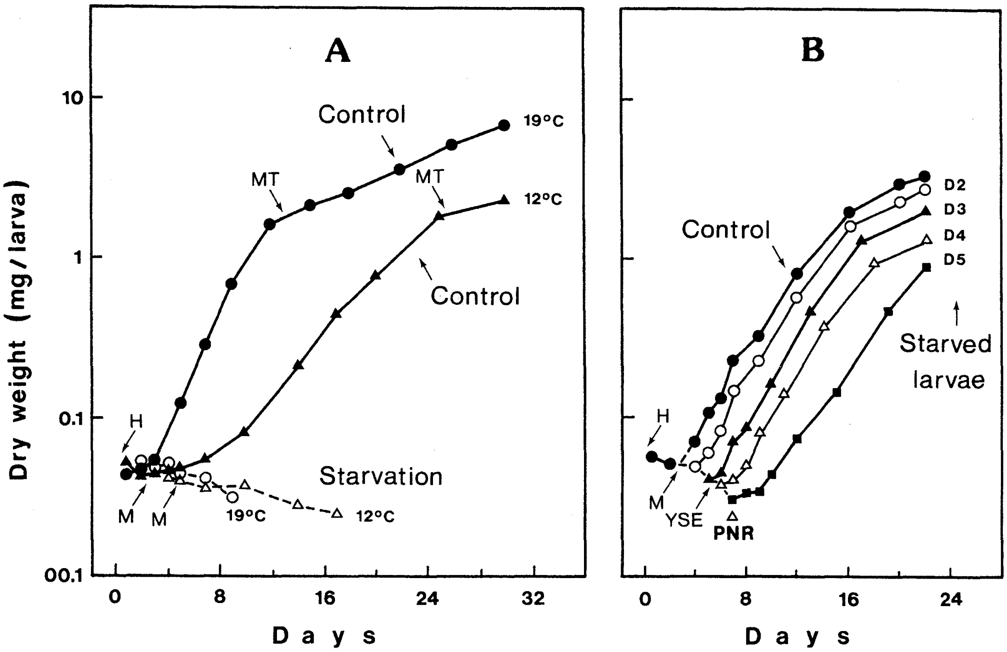

Fig. 1. Variations of individual dry weight in *Solea solea* fed and starved larvae at 12 and 19℃ (A), and effect of delayed feeding at 19℃ (B). H: hatching, M: mouth opening, YSE: Yolk-sac exhaustion, MT: metamorphosis.

thus their feeding ability on preys of large size, so that those larvae were not a good control (LAGARDERE, 1989).

Dry weight variations

The individual dry weight of control larvae increased following the onset of feeding. This increase was two fold quicker at 19℃ than at 12℃ (Fig. 1). Growth curves indicated that experiments lasted long enough to produce juveniles at 19℃. Even if soles began swimming as flatfish at 12℃, their transformation was not completed. Change in swimming behaviour occurred around days 12-13 at 19℃ and days 24-26 at 12℃. A reduction of the growth rate was then observed.

Starved larvae lost weight more rapidly at 19℃ than at 12℃. When larvae were submitted to a late first-feeding, the weight increased just after the first food intake, except for the survivors of the 5d-starved group. However, the initial delay in growth caused by starvation was not recovered, especially in the last group.

Total protein and free amino acid variations

During total starvation experiments (Fig. 2A), protein content per larva dropped till day 2 at 19℃ as vitellus was resorbed. It increased soon after mouth opening in fed larvae while it went on decreasing in starved ones. The larvae still alive on day 9 at 19℃ lost half of the protein content they had on hatching. Protein content rise was slackened upon metamorphosis in fed larvae. The same trends were noticed at 12℃, with some staggering on the longer time: proteic content was equivalent at 12 and 19℃, for a same ontogenetic stage. Relative to dry weight (not shown here), protein content was always lower in starving larvae than in fed ones after yolk sac exhaustion. During PNR experiments (Fig. 2B), protein content restoration after feeding showed that there was no compensatory effect: the batches of larvae kept the same differences all along the experiment. The recovery seemed good even for the 4d-starved larvae but not for the 5d-starved group: protein content restoration started only on day 12 and the large variability noticed thereafter occurred at the same time as high mortality.

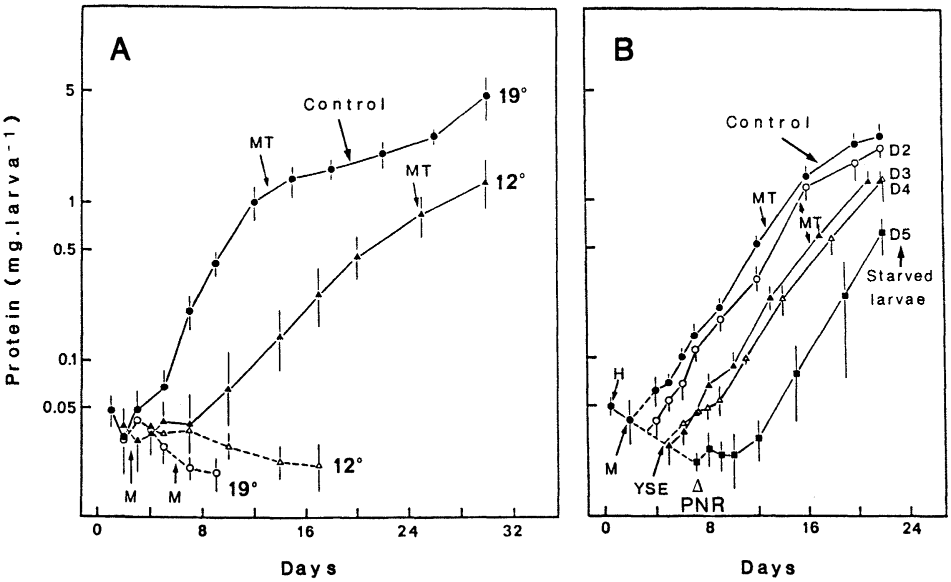

Fig. 2. Variations of total protein content in *Solea solea* fed and starved larvae at 12 and 19℃ (A), and effect of delayed feeding at 19℃ (B). Further specifications as in Fig. 1.

Total free amino acids were strongly lowered by starvation. As essential amino acids can only be taken from food, they were very sensitive to starvation and therefore the essential to non-essential amino acid ratio was also very quickly affected (Fig. 3). It decreased during starvation from 0.85 to 0.27 and to 0.35 at 19℃ and 12℃ respectively. However, it showed large variations during the normal early ontogeny of sole: at 19℃ it decreased sharply during the 5 first days, then rose and decreased again to a very low level after metamorphosis. At 12℃, the peak before metamorphosis was delayed and was higher but there was also a large decrease thereafter.

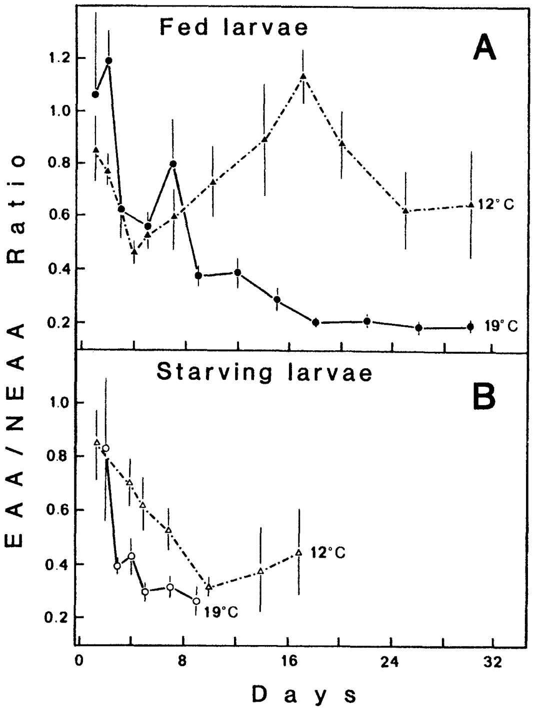

Fig. 3. Variations of essential to nonessential amino acid ratio in Solea solea larvae, fed (A) and starved (B) at 12 and 19℃.

Variations in lipid composition

The triglyceride level showed a decrease linked to the utilization of yolk reserves (Fig. 4). After the onset of feeding, the level quickly increased up to a maximum value corresponding to metamorphosis. This value is much higher at 12℃ than at 19℃. When no food was ingested, the triglyceride level decreased dramatically. The minimum of the curves corresponded to the yolk-sac exhaustion. After a delayed first-feeding, 2d and

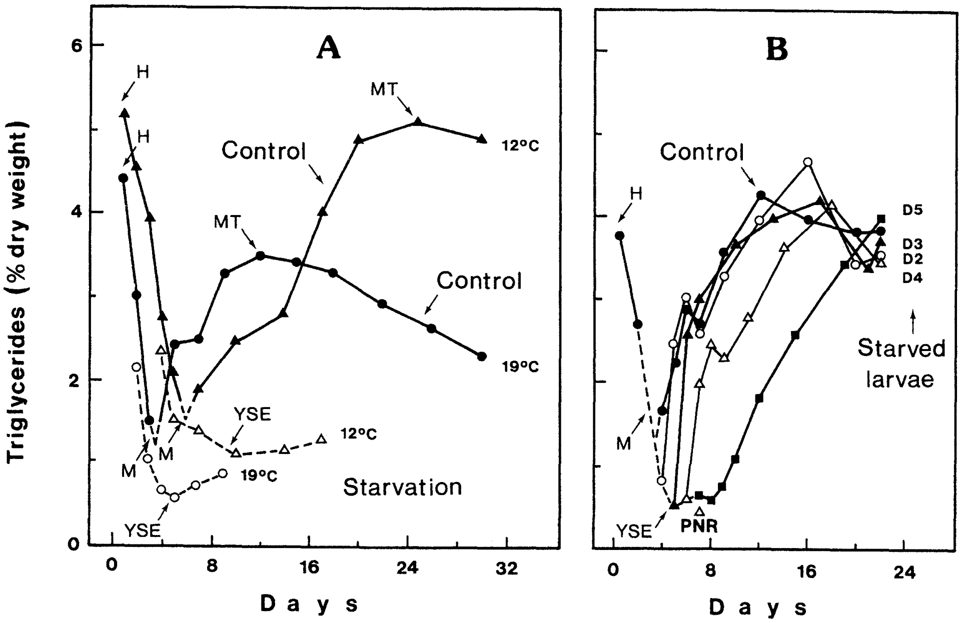

Fig. 4. Variations of triglyceride level in *Solea solea* fed and starved larvae at 12 and 19℃(A), and influence of delayed feeding at 19℃ (B). Further specifications as in Fig. 1.

3dstarved larvae quickly recovered normal levels of triglyceride and then, showed no clear differences as compared to the control group. 4d-starved larvae had some difficulties in recovering normal values, while the survivors of 5d-starved group could not reach the level associated with metamorphosis during the experiment. Total lipid variations, not reported here, showed approximately similar trends, but they were not so accute.

Replenished larvae always showed a higher triglyceride content than the sterol one, the contrary occurring in starving larvae (Fig. 5). If the amount of triglyceride could be related to feeding or starvation, sterol content was less dependent on the larval nutritional state, and this pattern was not affected by temperature. The largest difference between triglyceride and sterol contents corresponded to the PNR. Hence, a triglyceride to sterol ratio can be calculated. Just following hatching, values higher than 2 were observed. The ratio dropped to 1 before first feeding of the control. For this group, it quickly increased up to 2.6 (19℃) or 3.1 (12℃) before metamorphosis. In starved larvae, the ratio fell dramatically to 0.6 (12℃) or even to 0.4 (19℃), when the PNR was reached.

Changes in the incremental pattern of the sagitta

Larval and sagittal growth curves allowed within-temperature comparisons between specific growth rates (b parameter, Table 1a). Subdaily rings were discriminated when increment width increased (Fig. 6A-B and 7A-B). The larva-sagitta length relationships varied significantly, according to the temperature, with a steeper regression in the 12℃ experiment (Table 1b, slopes were significantly different, *t*-test, $p<0.05$), i.e. smaller otoliths for equal-sized larvae. When food limitation reduced the growth rate at the same temperature (19℃ experiment of delayed first-feeding), inverse consequences arose from these relationships, slowly growing larvae (survivors of the 5d starved group) having bigger otoliths than equal-sized larvae from the control (Lagardere, 1989). Otolith measurements of early larvae under starvation demonstrated their continuous but decreasing daily growth until death, while somatic growth was arrested and larvae shrunk through stress.

The incremental pattern of otoliths from the 19℃ reared larvae indicated that except

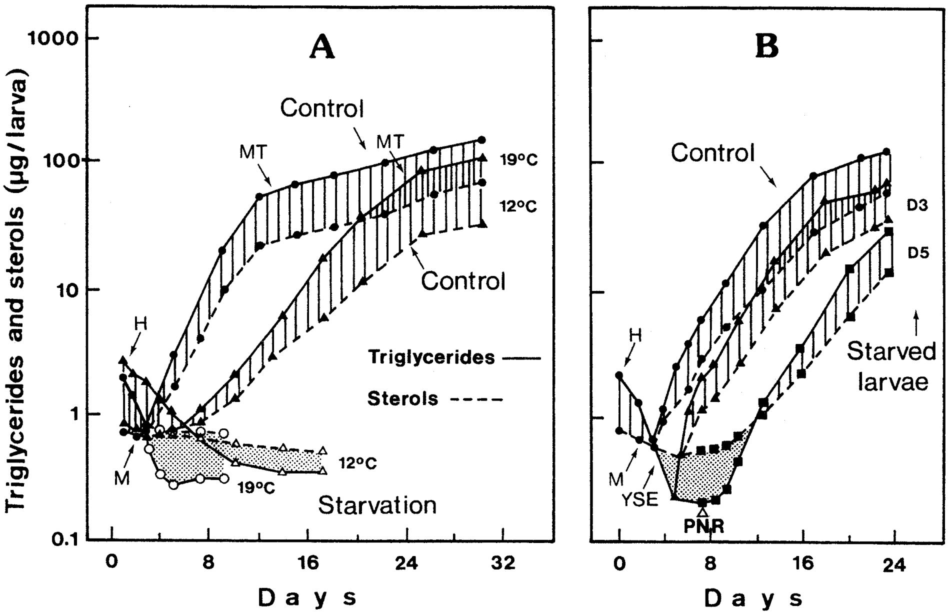

Figure 5. Variations of triglyceride and sterol amounts in Solea solea fed and starved larvae at 12 and 19℃ (A), and influence of delayed feeding at 19℃ (B). Further specifications as in Fig. 1.

for ontogenetic checks, the formation of well-defined increments followed the onset of exogeneous feeding (Fig. 6A). Only hyaline material (i.e. without clear daily increments) was deposited during embryogenesis (Fig. 6 C, band 1) and this pattern was extended during starvation as long as larvae had endogeneous supplies to use (Fig. 6C, band 2 and 3). A significant reduction in width of daily deposits interfered once the yolk-sac was exhausted (band 3). Those deposits were developed into stress bands until somatic growth resumed (Fig. 6D). They contributed to enhance checks, previously identified (LAGARDERE, 1989) at the time of hatching (h), mouth-opening (m) and yolk-sac resorption (y). Low-contrast increments were observed in otoliths of the supposed control larvae from the 12℃ experiment (Fig. 7A-B), and they were related to a delay in first-feeding of 2 to 4d.

The use of the ageing technique was validated

Table 1. Influence of rearing temperatures on the somatic and sagittal growth relationships of sole larvae.

(1a) Specific growth rates (in percent as derived from exponential growth curves of pelagically swimming control larvae (see for further details LAGARDERE, 1989)

	larval length	sagittal diameter
12℃ experiment (days 1-26):	3.45	7.25
19℃ experiment (days 0- 9):	9.23	16.63

(1b) Summary statistics of the larva-sagitta length relationships (in transformed date of control larvae from both experiments)

lnSL = a lnSAG+b:	Regression parameters						
	intercept	se	slope	se	N	R	R2 percent
12℃ experiment	−0.0779	0.0267	0.4753	0.0064	172	0.98	96.99
19℃ experiment	0.0091	0.0468	0.4490	0.0112	95	0.97	94.53

through counts of increments deposited in the otoliths of the 12℃ reared larvae because of their close resemblance with those of field-sampled specimens (Fig. 7 A-B and D-E). Counts were processed from the m check, whose age at formation depended upon temperature (day 4), while initiation of uninterrupted daily increment deposition varied with age at first-feeding (Lagardere, 1989). Reliability of age estimates (i.e. count +3) was tested because of the low contrast of unit increments, and to compare readings from micrographs or image analysis. The regression of increment counts against days was best fitted by a linear model ($y=-0.5601+1.0052x$; $N=145$ $R=0.99$). The deposition

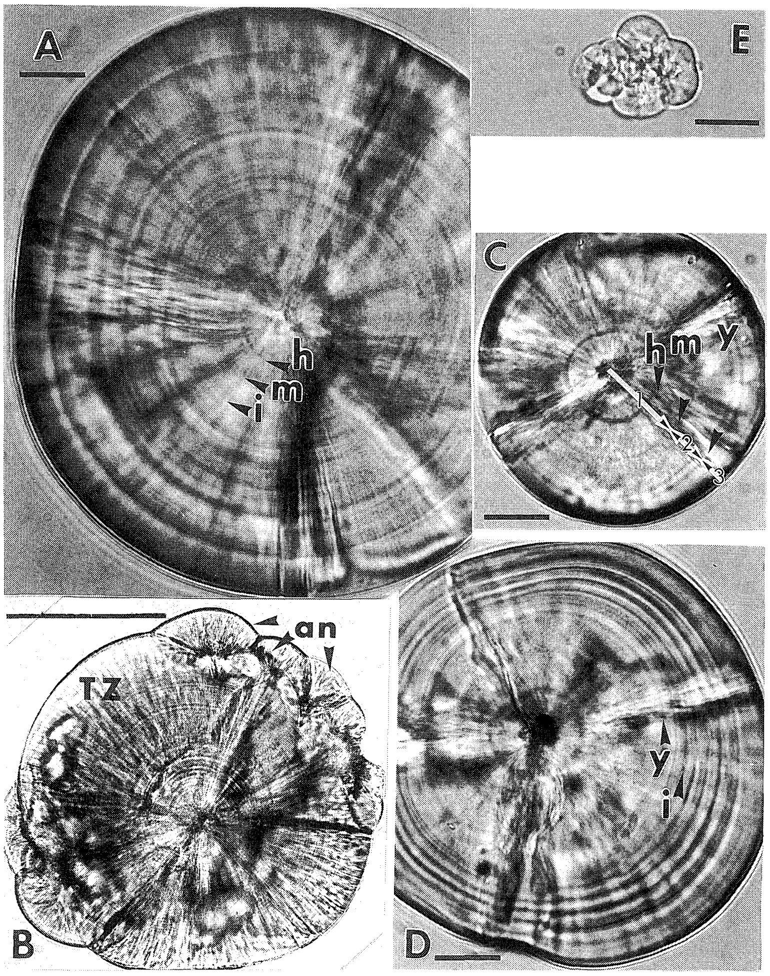

Fig. 6. Sagittal otolith of larval sole (Scale bars: ACDE = 10 μm B = 100 μm).

A-D (19℃ rearing experiment) - A: 10d old control larva, the first defined increment (i) indicates yolk absorption and day 5; B: 14d control larva; C: 10d old larva of the 5d-starved group, low-contrast bands correspond to increments deposited during embryogenesis (1), before yolk absorption (2) and before growth resumption (3); D: 15d old larva of the 5d-starved group.

E: sea-sampled larva at hatching, see multiple primordia of the nucleus coalescing. (an: accessory nuclei; h, m, y: hatch, mouth-opening and yolk-sac exhaustionch ecks; i: first well-defined increment, N: nucleus; TZ: transition zone of metamorphosis)

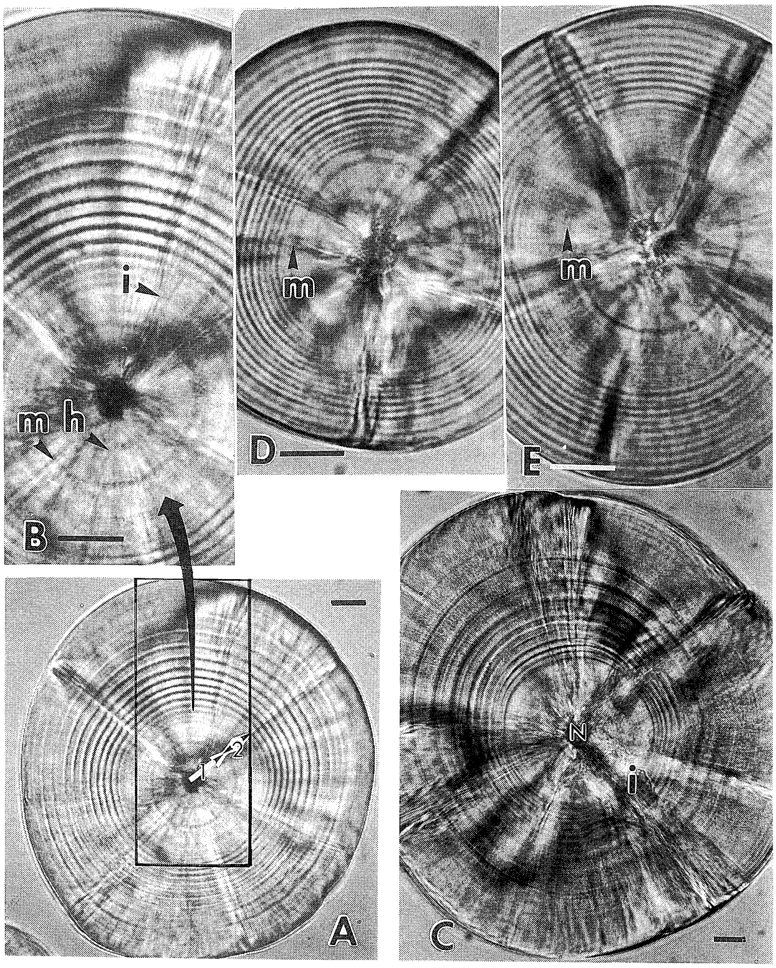

Fig 7. Sagittal otoliths of laval sole (Scale bars: 10 μm)
A-B: 22d old control larva (12℃ experiment)
C : 22d old larva from the 5d-starved group (19℃ experiment)
D-E: Sea-sampled larvae with an increasing development of faint increments deposited after the m check (see Fig. 7 for further explanations).

rate calculated from its slope was not significantly different from one increment per day (t-test: with α : 0.05, $t' = 0.54$, 143 df). However, the intercept was significantly different from 0 and showed a slight but constant underestimation of age. The sources of errors were double, low-contrast increments of the first-feeding stage and subdaily rings of the transition zone. The first might include 2-4 low-contrast increments $\geq 1\,\mu$m in width, as calculated from differences in size of otoliths at known-ages. However, overestimation, due to subdaily rings of the transition zone, had probably reduced this tendency to underestimate ages. Comparisons between the mean of errors on ages, as derived from micrographs and from image analysis (LAGARDERE and TROADEC, unpublish. data) allowed to evaluate the reliability of estimates. They were less precise but more accurate from image analysis (0.2±3) than from micrographs readings (−0.5±2).

4. Discussion

Morphological and behavioural changes occurring during the ontogeny are also reflected in the biochemical composition of sole larvae. Tissue reorganization, during vitellus resorption, setting up of the digestive tract or metamorphosis, leads to variable needs for the different biochemical compounds. This was clearly shown by the variations in the ratio of essential to nonessential free amino acids during the early stages of development: free amino acids, involved in many different biochemical pathways, are extremely sensitive to any metabolic change. Therefore they undergo wide variations during larval development (GATESOUPE, 1986). This was also seen but in a lesser extent in the lipid changes of sole larvae. Despite wide differences in lipid utilization during the development of marine fish, it is well established that those compounds constitute the most important energy source for the larvae in many species (SARGENT *et al.*, 1989) . Variations of triglyce rides are of particular interest, because these components play an energetic role and show simple accumulation or utilization patterns. They dramatically drop during the yolk-sac resorption, since a large part of them are used as an energy source by the larvae (e.g. herring, FRASER *et al*., 1987). When fed, sole larvae accumulated large amounts of triglyceride as larvae of atlatntic herring do (GATTEN *et al*., 1983). At metamorphosis, the increase of amounts in biochemical components is clearly slackened. The onset of metamorphosis seems to require a high level of triglyceride to cover the energetic needs linked to the anatomic and metabolic changes. The trigly ceride level slightly decreased after metaphosis, as also shown in plaice (EHRLICH, 1974a) and pacific herring (FUKUDA *et al*., 1986).

Starved larvae can be distinguished from fed ones of the same batch after one or two days of food deprivation through dry weight, protein or total amino acid measurements. These biochemical compounds decrease steadily and much more quickly in the youngest larvae or at high temperature. The triglyceride content of a sole larva seems to be the most sensitive to the nutritional state. In starved larvae, triglycerides were immediately mobilized and quickly decreased to a very low value which was associated to high mortality. This pattern was also observed in other species (EHRLICH, 1974a, b; TANDLER *et al*., 1989; HAKANSON, 1989a). The sterol content followed the increase in weight for the control larvae, but it did not change much during starvation, as also pointed out for anchovy larvae (HAKANSON, 1989a). Sterols are mainly membrane constituents and are preferentially conserved. So the ratio triglyceride/sterol appears to be a good index of the nutritional condition for field larval fish, as it would be relatively independent of changes in other biochemical compounds (FRASER *et al*., 1987; HAKANSON 1989a, b).

Except sterols, all the components we studied reached a critical level at yolk absorption. This shows that the yolk reserve is not sufficient to ensure growth and hence confirms the critical importance of early food availability (BLAXTER and STAINES, 1971; BUCKLEY, 1980). Larvae starved 2 to 4 days after mouth-opening recovered and survival was not affected. Once on the PNR day, mortality in these batches was very high. The survivors could not recover a good growth before day 12, as also shown by otoliths. In case of severe fasting, metamorphosis was delayed if the amount of triglyceride previously accumulated was not large enough. Contrarily to the studies on other fish (DABROWSKY *et al*., 1986; MIGLAVS and JOBLING, 1989), we did not observed any compensatory effect on weight and on biochemical components. Ontogenetic changes were delayed by a period equal to the length of the starvation interval.

Temperature affected differently the increase of each biochemical compound in fed larvae, and therefore their relative biochemical composition. The final level of percent protein was lower at 12° than at 19°, while it was just the reverse for triglyceride content relative to dry weight and for the mean ratio between essential and non-essential free amino acids. These disparities depending on the biochemical component indicated differences in the effects of temperature on their metabolism. High temperature enhanced the general metabolism, but promoted protein catabolism rather than energetic lipids storage. This temperature effect can lead to completely different changes in starved larvae, as shown by the essential to non-essential amino acid ratio. Thus temperature influence needs to be considered in studying nutritional state (STRUSSMANN and TAKASHIMA, 1989).

It is admitted that starved larvae produce either low-contrast increments (RICE *et al*., 1985) or no increments because of uncountable discontinuous zones. But the term "increment" implies two structures which are together measured and counted, the incremental and discontinuous zones respectively, and otoliths continue to grow even when larvae are starving at early stage. During the 19℃ experiment, otolith growth appears clearly once somatic growth resumes in the survivors of the 5d-starved group, as matarial deposited into the perinuclear area. It was made of poorly defined increments mor and more narrow, and it was identified to stress marks (sensu RICE *et al*., 1987). Lowcontrat increments were first observed in some otoliths of sea-caught larvae (LAGARDERE and CHAUMILLON, 1988; this paper, Fig. 7 D-E). They are a classic feature of early growth (e.g. herring) and associated with slow-growing larvae at the first-feeding stage (CAMPANA *et al*., 1987). This incremental pattern is linked to conservative properties of otoliths and shows more dependence upon metabolic activity than somatic growth (HOVENKAMP, 1990). Sagittal growth, on the form of low-contrast increments whereas somatic growth was arrested, involves significant variations between the larval-otolith size relationships (e.g. REZNICK *et al*., 1989; SECOR and DEAN, 1989; LAGARDERE, 1989). The use of these regressions as shrinkage estimator (RADTKE, 1989), as well as backcalculation of previous length at age (CAMPANA, 1990), if done without caution, may underestimate larval size.

The low contrast of unit increments in the central part of larval otoliths causes the main difficulty in using optical microscopes and therefore image analysis, insofar as the resolving power may be limited by increment width and contrast between incremental and discontinuous zones (CAMPANA *et al*., 1987; LAGARDERE and TROADEC, unpublish. data). Moreover, extensive use of electron microscopy for field studies is not realistic (RADTKE, 1989). In the case of the 12℃ reared larval sole, the low-contrast increment width (≧1 μm) was not a limiting factor. The lack of definition led to a slight underestimation of ages, well-corrected by image analysis. Further improvements are needed to gain more precision, but it appears nevertheless that low-contrast increments were correctly interpreted, if not discriminated, by this image analysis methods. It would be helpful in reading larval otoliths as long as the sagittal growth is detectable. However, errors and uncertainties of ages for sea-caugth larvae are to be suspected when their when their otoliths have stress marks. There are probabilities that their age estimates will not justify the same precision level as the one of known-age larvae reared in a more favorable thermal and trophic environment.

In conclusion, most of the biochemical parameters can work well when applied as nutritional indices for *reared* larvae, when age, stage and history are known. However, some of them, as proteins, total free amino acids, total lipids and triglycerides, are closely linked to the weight (age), which is difficult to measure accurately on the youngest larvae. Moreover, in recruitment studies, larvae caught in the same water mass could have different histories. It is better to precise the variability within a population and thus preferable to analyze individuals. Use of biochemical indices, such as the triglyceride to sterol ratio, less dependent on the larval ontogeny, may be promise to development, once calibrated for sea-sampled specimens. This ratio is more reliable, very sensitive to denutrition and less dependent on ontogenetic changes. Triglyceride and sterol contents may be now estimated on a single sole larva by means of TLC-FID analysis, with satisfactory accuracity and reproducibility. It would provide an instantaneous diagnosis of the larval nutritional state, while saving the possibility of otolith examination (HAKANSON, 1989b). The conservative structure of otoliths account not only for age. Links between dated increments or dated marks and environmental factors are to investigate and may complete the larval history with data existing before capture.

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Effets du jeune expérimental sur la composition biochimique et la microstructure des otolithes chez les larves de la sole commune, *Solea solea* (L.)

Robert Galois, Françoise Lagardere et Pierre Richard

Résumé: Des larves de sole, *Solea solea* (L.), ont été soumises à des jeûnes expérimentaux à 12 et 19℃, afin de rechercher des indices biochimiques de leur état nutritionnel et d'éventuelles marques de jeûne sur les otolithes.

L'accroissement du poids sec et l'accumulation des divers composés biochimiques pendant les premier stades ontogéniques est plus rapide à 19 qu'à 12℃, avec une augmentation plus marquée du taux protéique que des lipides énergétiques à température élevée. Le poids sec et les quantitiés absolues de protéines, acides aminés libres totaux et triglycerides diminuent proportionnellement à la durée du jeûne et peuvent donc etre utilisées comme indices de l'état nutritionnel pour des larves en élevage. Cependant, leurs variations, comme cells du rapport acides aminés essentiels sur non-essentiels, sont trop dépendantes du stade de développement pour que ces paramètres puissent servir à caractériser l'état nutritionnel de larves capturées en mer. Par contre, les sterois demeurant constants au cours du jeûne, le rapport triglycérides sur sterols est un indice tràs sensible et plus fiable, qui demande cependant une estimation approximative de l'âge.

La température et le jeûne modifient les paramétras de croissance des larves et des otolithers, de telle sorte que les relations existant entre la taille des larves et celle des otolithes sont variables. Pour une même taille de larves, une baisse de température produit des otolithes plus petits, alors qu'à température égale, les otolithes sont plus gros pour les larves qui jeunent. Quand le jeûne suit l'ouverture de la bouche, la croissance somatique s'arrete, alors qu'on observe des accroissements á faible contraste, tels qu'ils se forment avant la premiere alimentation. Identifiées à des marques de stress, ces structures augmentent la variabilité des estimations de l'âge, même, si le dépôt d'accroissements journaliers se vérifie apràs le début de l'alimentation exogéne. Observes sur des larves captureées en mer, ils fournissent des informations complementaires sur l'histoire de la larve avant sa capture.

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Changes in lipid accumulation of young red sea bream, *Pagrus major* released into the Inland Sea of Japan (Setonaikai)*

Javier VILLA-NAVARRO**†, Heisuke NAKAGAWA** and Minoru TAKABA***

Abstract: Physiological condition of young red sea bream, *Pagrus major*, released into the Inland Sea of Japan (Setonaikai) were monitored in terms of lipid stores comparing to the 0-age wild fish.

The wild fish accumulated lipids in muscle and intraperitoneal fat body during autumn, then exhausted the lipid reserves during wintering. In the released fish, however, there found two critical periods which were just after release and wintering within one year. The released fish lost lipid reserves soon by perturbation caused by environmental change, then recovered the lipid reserves during autumn to provide for the severe wintering. Therefore high ability of accumulating lipid may be advantageous to survive in the Setonaikai.

1. Introduction

Rearing technique for red sea bream is well established and mass production is being carried out by many organizations in Japan. In order to propagate fishery resources, more than 15,000,000 young red sea bream have be released into the coastal region every year. Nevertheless, while many factors would be responsible for the recovery (IMABAYASHI *et al.*, 1975, 1977; KISO, 1980; OMORI, 1980; MORI, 1980; MATSUMIYA and KISO, 1982), little work has been conducted on the recovery and assessment of fish released into the natural environment.

In this study, adaptation process of young red sea bream released into the natural environment were monitored in terms of biological and biochemical parameters.

2. Materials and Methods

Three groups of young fish (6-10cm in body length) which were produced under different conditions were released from several points of the center of Setonaikai, as shown in Fig. 1. These groups were discriminated by tagging or fin-clipping. The fish were caught by seine netting of a Fisherman's Association in the area shown in Fig. 1.

In Hiroshima Prefecture (Hiroshima Fish Farming Association and Fisherman's Association) the fish were produced by artificial feeding in floating net cages (Group O). The number of released fish was 1,168,000 in 1986 and 1,238,000 in 1987. In Momoshima Experimental Station of Japan Sea Farming Association (JASFA) fish larvae were semi-extensively reared in 9000 m^2 pond (2.5m in maximum depth) with natural organisms and supplemental feeding (Group M). The fish of Hakatajima Experimental Station of JASFA (Group H) were intensively produced, as the Group O. The released number of Group M and H was 50,000 each in both years.

Muscle, liver and intraperitoneal fat body (IPF) obtained from 2 to 10 fish were throughly mixed for proximate composition and lipid analyses. Crude protein was measured by Kjeldahl method. Lipid was extracted with methanol-chloroform. The lipid class composition was determined by an Iatroscan TH-10. For fatty acid analysis, lipid classes isolated by preparative TLC were converted into their fatty acid methyl esters by HCl-methanol. Similarity of fatty acid compositions was evaluated according to TAMURA and OSAWA (1969). In the case where two patterns are the same, pattern similarity value will be 1.

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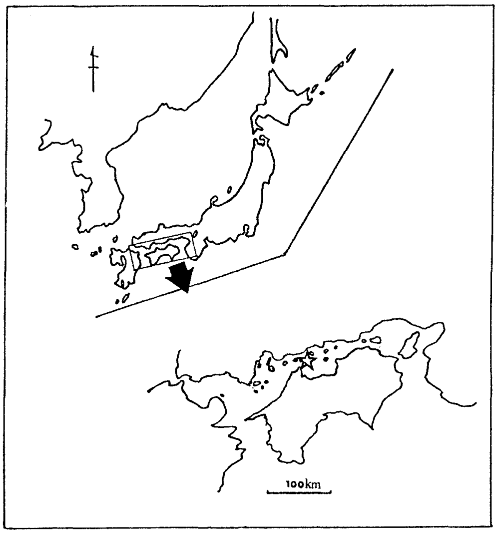

Fig. 1. Location of experimental field in red sea bream. Star is the figure indicates capture area. Fish were released into ca. 40 points within a radius of 50km from capture area.

3. Results

water temperature was maximum in August (26℃) and reached to minimum at March (11℃) in both years. According to observation of stomach content, 33-71% of individuals had the loaded stomach by some crustacean species. There was little or no difference in the major food composition between the released and wild fish, but the released fish seemed to ingest a little more quantity than wild fish. Body length of recovered fish ranged from 4.1 to 12.3 cm. In the Group M and H of 1986, body length decreased significantly within the first 30 days after release and increased thereafter. In winter time, growth was not found in the released groups, nor in the wild fish.

The mode of body weight shown in Fig. 2 resembled that of the body length. Both wild fish and Group O gradually increased body weight till November, then slightly decreased. However, the Group M and H showed a little different mode during autumn. Condition factor showed a little variation during wintering.

IPF, a main energy reserve was fairly different among three released groups (Fig. 3). The Group H having high IPF ratio lost markedly IPF during the following days after release. IPF in wild fish and Group O increased at the end of autumn. During wintering, IPF was exhausted in all the groups, as well in wild fish.

Changes in proximate composition of muscle after release are shown in Table 1. Initial values of muscle crude protein and lipid ranged 19.4-21.6% and 1.0-1.6%, respectively. The Group H was higher in protein and lipid than Group M. The lipids were preferentially consumed after release and the protein was relatively constant till autumn. Although the wild fish retained higher lipid till the end of winter, the Group H exhausted almost of the lipid reserves (0.1%).

More than 90% of muscle lipid consisted of triglycerides (TG). The initial amount of TG in 100g of muscle was not different among the released group, as shown in

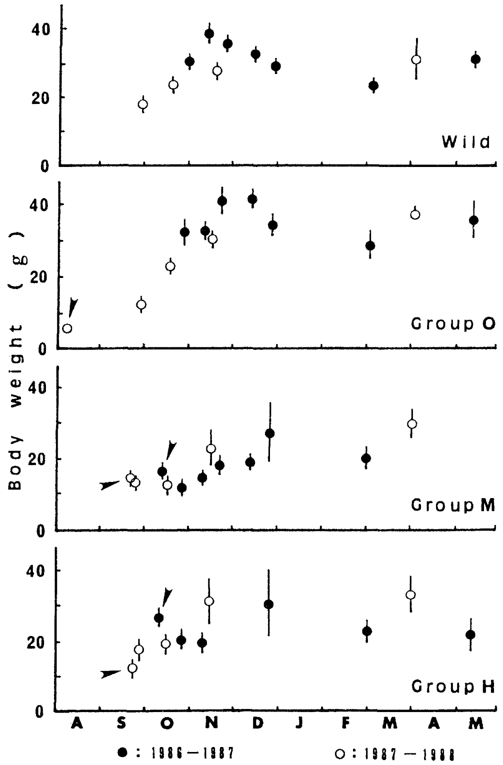

Fig. 2. Changes in body weight of wild and released red sea bream (mean & SE). Arrow indicate release time.

Fig. 4. TG were soon depleted within 50 days after release, then temporarily increased in autumn and decreased again in winter. While phospholipids (PL) were kept at constant level in muscle, slight decrease after exhaustion of TG was found during wintering.

The change of HSI after release was characteristic in each group. The values of Group O, M and wild fish ranged from 1.0 to 1.5. HSI of Group H (2.3 in 1986, 1.8 in 1987) decreased fairly just after release (1.6 and 1.2) and thereafter kept the value constant during wintering.

Main fatty acids of muscle TG are shown in Table 2. The wild fish was relatively low in $C_{18:2}$. While ther appeared some changes in the fish released in 1986, no remarkable variation was found in the fish in 1987 and wild fish. Accumulation of $C_{20:5}$ and selective mobilization of $C_{18:2}$ during wintering were found in the fish released in 1986. The changes in the fatty acid composition of the released groups were highly different among the groups and also between two years.

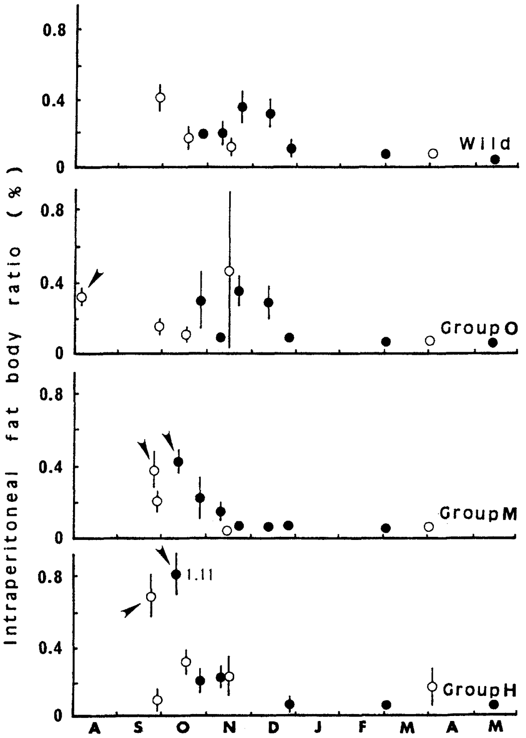

Fig. 3. Changes in intraperitoneal fat body (IPF) ratio of wild and released red sea bream (mean & SE).
IPF ratio = IPF / body weight × 100
Symbols refer to Fig. 2.

Variation of fatty acid composition of IPF was not as high as that of muscle TG. As seen in muscle TG, IPF of wild fish was relatively low in $C_{18:2}$. Muscle PL were characterized by high proportion of highly unsaturated fatty acids, and did not change the proportion.

The similarity of fatty acid compositions between wild and released groups was high in the values before release (>0.87), and decreased with the passage in the natural environment in the 1986-released class(<0.49). However, the fish released in 1987 showed high similarity with the wild fish (>0.88). The similarity in fatty acid composition of IPF was high and always over 0.80, regardless of the released year.

4. Discussion

Wild red sea bream is generally lower in lipid reserves than cultured fish. The lipid amount of surviving coho salmon released into a stream closely approximated that of wild fish (Wood *et al.*, 1960). The high divergency of initial lipid level would be highly dependent on rearing condition. While high lipid reserves are not essential for cultured fish, the energy accumulation in released fish might play an important role in the natural environment.

When young red sea bream are released into the natural environment, they spend at least 7 to 10 days without feeding (Koshiishi and Yasunaga, 1980; Matsumiya and Kiso, 1982). Thereafter feeding could be commenced, but not sufficient to provide for required energy or to grow (Nakagawa *et al.*, 1991). The environmental change would cause serious perturbation which might draw hormonal imbalance and elevation of glyconeogenesis. Depression of HSI which is a good indicator in assessing environmental impact (Heidinger and Grawford, 1977; Barnes et al., 1984) implied purturvation by environmental change.

The fish grew until the beginning of winter, probably due to active feeding. However, temporal

Table 1. Changes in muscle protein (P) and lipid (L) of red sea bream after release (%)

Capture	Wild		Released group Group O		Group M		Group H	
	P	L	P	L	P	L	P	L
Oct. 9, 1986					20.2	1.1 (0)	21.6	1.3 (0)
Oct. 25,	21.1	0.8	21.7	0.9 (82)	21.4	0.9 (14)	19.6	0.9 (14)
Nov. 8,	20.8	1.0	20.6	0.9 (96)	20.4	0.7 (28)	20.0	0.7 (28)
Nov. 20,	21.4	0.9	21.6	1.0 (108)	20.1	0.7 (40)		
Dec. 11,	21.8	1.1	22.1	0.9 (129)	19.9	0.8 (61)		
Dec. 24,	20.1	1.0	20.1	0.8 (142)	19.7	0.8 (74)	18.7	0.8 (74)
Feb. 28, 1987	20.5	0.8	19.8	0.7 (208)	18.1	0.7 (140)	19.5	0.6 (140)
May. 10,	18.8	0.6	18.3	0.5 (279)			17.0	0.1 (211)
Aug. 5, 1987			19.4	1.6 (0)				
Sep. 25,					19.7	1.1 (0)	21.3	1.4 (0)
Sep. 26,	20.3	1.0	18.0	0.8 (50)	19.7	0.9 (1)	19.8	1.1 (1)
Oct. 15,	20.7	1.0	18.3	0.5 (70)	19.6	0.9 (20)	19.2	1.1 (20)
Nov. 13,	20.4	1.0	20.7	0.9 (99)	18.9	0.9 (49)	19.6	1.0 (49)
Mar. 3, 1988	20.8	1.0	20.4	0.7 (237)	19.9	0.8 (189)	20.4	0.8 (189)

Parentheses mean days after release.

decrease in fish size seen in both Group M and H released in 1986 at the end of autumn may be partly explained by the temporal shortage of available food organisms.

Marked body weight loss during wintering would be resulted from exhaustion of body constituents due to decline of feeding activity and of available feed organisms. The red sea bream is a non-migratory, but low availability of food and low water temperature induce the dispersion from nursery grounds to depth. Therefore migration of larger fish from the field could partly account for the marked decrease in body weight just after release. It could be said that sufficient lipid reserves supported by active feeding during autumn would be essential to pass throughout the winter under poor energy intake.

Although all the fatty acids were equally mobilized in the wild fish, specific fatty acids were selectively consumed by the survivors after release. The mode of fatty acid selectivity might be derived from the dietary history which affected TG structure and lipid mobilization. However, the survivors were thought to adapt well themselves in the natural environment. Therefore the fatty acid utilization of survivors released in 1986 might indicate

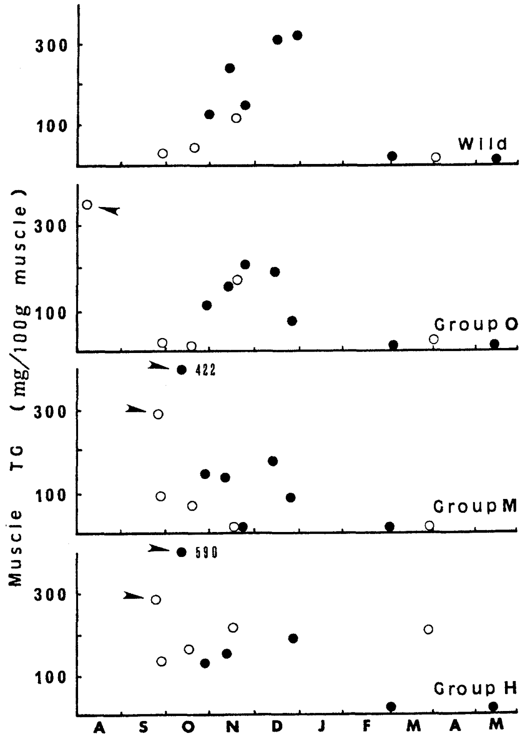

Fig. 4. Changes in muscle triglycerides (TG) of wild and released red sea bream (mean & SE). Symbols refer to Fig. 2.

Table 2. Changes in fatty acid composition (%) of muscle triglycerides of red sea bream after release in 1986

Group/Capture	Fatty acids						
	16:0	18:0	16:1	18:1	18:2	20:5	22:6
Wild							
Oct. 25, 1986	21.6	9.0	7.6	19.7	1.6	12.5	10.2
Nov. 20	20.6	11.2	7.3	27.3	1.6	7.2	6.2
Dec. 24	20.4	7.9	8.8	25.6	1.8	11.5	8.5
Feb. 28, 1987	22.2	9.1	8.0	20.3	2.4	11.5	14.5
May 10	17.6	9.2	7.5	22.4	1.6	14.5	7.3
Group O							
Oct. 25, 1986	21.5	9.6	6.4	32.2	7.9	3.5	6.7
Nov. 20	23.6	9.9	7.4	23.8	1.5	8.4	9.2
Dec. 24	15.6	6.0	6.4	16.9	2.3	30.4	7.5
Feb. 28, 1987	3.2	1.2	1.0	2.3	tr.	88.5	1.1
May 10	10.7	4.6	4.3	10.3	1.8	46.5	7.7
Group M							
Oct. 9, 1986	20.6	6.8	6.3	21.0	3.7	9.1	15.7
Nov. 8	18.8	7.3	6.0	20.8	4.4	9.3	13.2
Dec. 24	17.2	6.9	7.6	20.2	3.4	15.4	11.4
Feb. 28, 1987	9.7	4.0	3.5	13.3	2.2	50.1	5.0
Group H							
Oct. 9, 1986	23.0	7.8	5.4	24.5	6.8	5.8	11.1
Nov. 8	22.2	8.6	5.0	26.5	5.9	2.6	9.3
Dec. 24	19.7	8.0	6.3	22.7	7.0	6.5	9.2
Feb. 28, 1987	15.3	5.9	5.8	18.8	1.9	31.6	7.3
May 18	4.4	1.3	1.9	5.8	1.4	76.0	2.6

insufficient adaptation in feeding habit in the environment.

Retardation of release time would result in defficient lipid stores for wintering on account of insufficient period for recovering lipid reserves. Accordingly, the ability to elevate lipid reserves would be essential for survive in the natural environment.

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瀬戸内海に放流したマダイ体成分の変化

Javier Villa-Navarro・中川平介・高場　稔

要旨：異なった飼育方法で生産した３群のマダイを瀬戸内海に放流した後、採捕してマダイの体成分、主として蓄積脂質を測定し、天然環境における生理状態を、同時に採捕された天然マダイと比較した。放流後の環境の変化により筋肉、腹腔内脂肪組織の脂質が減少したが、秋に活発な摂餌により脂質量に回復傾向がみられた。しかし、水温が低下する冬季は絶食状態にあり蓄積脂質の枯渇がみられた。この現象は天然マダイにおいても観察された。これらの現象から脂質の蓄積能の高いことが冬季の水温の低い瀬戸内海で生残するための重要な条件の１つと推定される。

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Numéro 4

Proceedings of the FranceJapan Syumposium on Determination of Biological Recruitment in the Sea

General theme 1 : Ecology in natural environment

General theme 2 : Experimental biology and recruitment

第4号

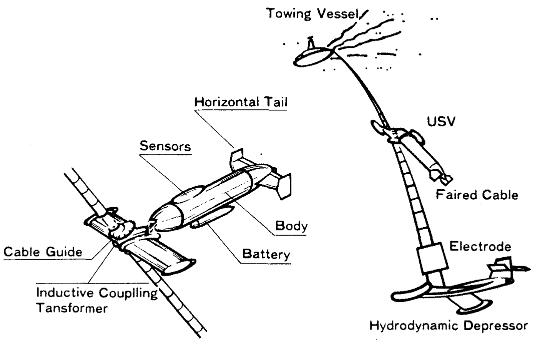
日仏シンポジウム
「海洋における生物加入の決定について」

テーマ１：自然環境中の生態

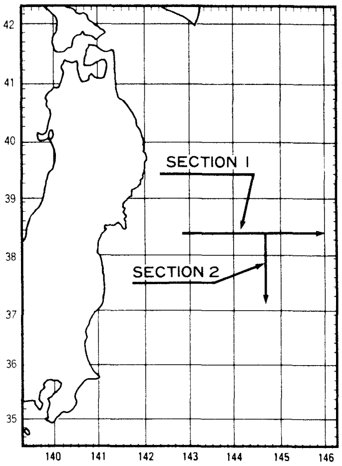
テーマ２：加入に関する実験生物学

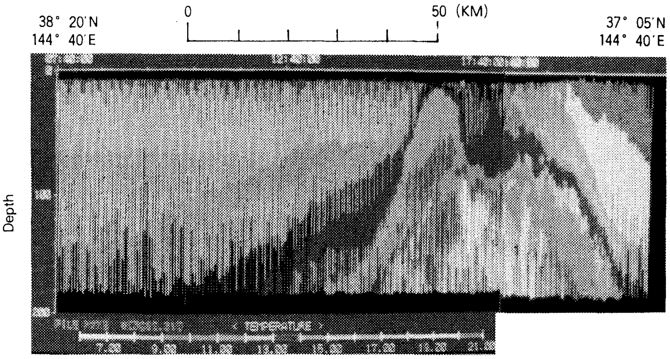
スライド式高速曳航体 JAMSTEC TSK方式
Underwater Sliding Vehicle System (USV)

○本システムは海洋科学技術センター殿の御指導によって開発されました。
○USVは小型かつ軽量で極めて優れた水中運動性能を有しております。
○電磁誘導伝送方式を使うことにより船上からのUSVの昇降運動制御及びリアルタイム信号モニターリングを行うことができます。
○取得データはFD及びハードディスクに記録し2次電算機処理に供します。



The USV system





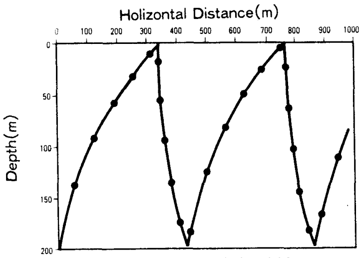
T.Sスライド式高速曳航体によって得られた三陸沖の水温鉛直分布のカラー画像。
(海洋科学技術センター殿から資料を御提供頂きました。)

SPECIFICATIONS

Towing Speed :0〜8knots
Operation Dapth:Max.400m
Tow Cable :8mm hydrodynamically fared stainless steel wire rope with polyurethane coating

Sensor	Range	Accuracy
Conductivity	20〜70ms	±0.05ms
Temperatune	−2〜35℃	±0.05℃
Depth	0〜400dbar	0.5%FS

Data Transport :Inductive Coupling Data Communication System
Sempling Rate :5times per second
Sensor Battery Life :50hours



Trajectory of the USV

T.S.K

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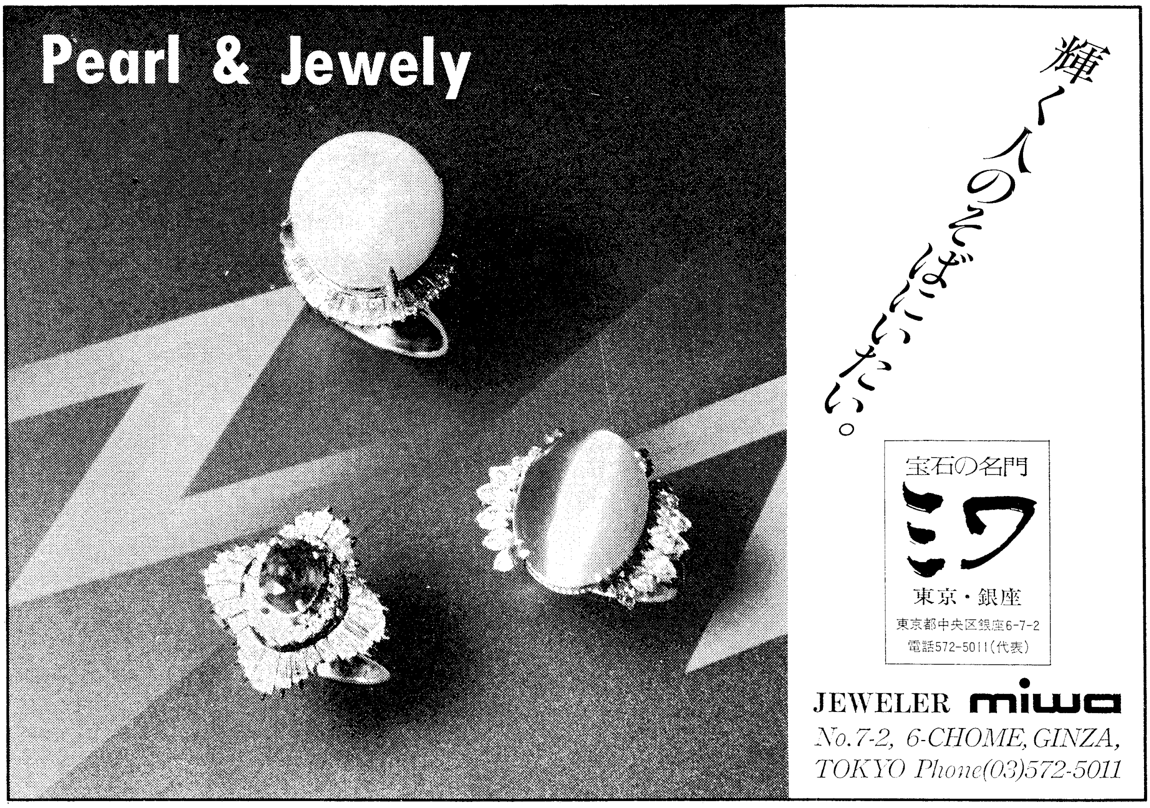
Pearl & Jewely
輝く人のそばにいたい。

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テーマ1：自然環境中の生態

テーマ2：加入に関する実験生物学

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Tome 28 N° 4

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General theme 1 : Ecology in natural environment

General theme 2: Experimental biology and recruitment