OCEANOLOGICA ACTA - VOL. 19 - N° 3-4

Recruitment and year-class segregation in response to abiotic and biotic factors

Physical instability
Biological interactions
Echinoderm populations
Brittany (France)

Instabilité physique
Interactions biologiques
Populations d'échinodermes
Bretagne (France)

Michel GLÉMAREC and Monique GUILLOU

Université de Bretagne Occidentale, URA 1513 du C.N.R.S., Océanographie Biologique, Institut d'Études Marines, 6, avenue Le Gorgeu, B.P. 809, 29285 Brest Cedex, France.

Received 16/02/95, in revised form 23/11/95, accepted 30/11/95.

ABSTRACT

Do post-larval recruitment and year-class segregation constitute a response to abiotic and biotic factors? Avoiding the traditional controversy about conditions in rocky and soft bottom conditions, the authors describe several examples where year-class segregations are evident in soft bottoms, taken from different trophic guilds of echinoderm populations on the coast of Brittany: suspension feeders, herbivorous and carnivorous populations. Physical factors such as fronts or gyres can concentrate larvae and nutritive particles for suspension-feeder populations. These factors are, on the other hand, conducive to the establishment and persistence of stable populations in time. The cohorts being long-lived, the oldest classes are very abundant and, as a result, no place is available to recruits. Negative interactions can appear between adults and juveniles and populations can be considered as closed to recruitment. On the other hand, unstable physical conditions can promote high mortality in adult cohorts and the population can be considered as open to recruitment.

In herbivorous and carnivorous guilds, recruitment occurs in places other than those occupied by the oldest year-classes. Ontogenic trophic migration explained by a change in diet from juvenile to adult is observed. In this case, no truly negative interaction between adults and juveniles appears to occur.

RÉSUMÉ

Recrutement et ségrégation des classes d'âge en réponse aux facteurs abiotiques et biotiques.

Le recrutement des post-larves et la ségrégation des classes d'âge sont-ils une réponse aux facteurs abiotiques ou aux facteurs biotiques ? Les auteurs tentent de répondre à cette question à l'aide d'exemples choisis au sein des populations d'échinodermes des côtes de Bretagne et qui ont déjà fait l'objet de publications. En évitant l'opposition habituelle qui est faite dans la littérature entre les fonds rocheux et les fonds meubles, les auteurs considèrent ces populations selon leur appartenance à des guildes trophiques différentes. Chez les populations de suspensivores, ce sont les structures physiques, les fronts, les circulations cycloniques, les haloclines qui, en concentrant les larves et les particules alimentaires, déterminent la possiblité pour une population de recruter ou non les post-larves. En effet, lorsque les structures protègent les populations, en n'abaissant pas suffisamment le taux de mortalité, les populations sont dites fermées au recrutement. L'interaction entre facteurs physiques et facteurs biotiques, comme la compétition intraspécifique, apparaît alors évidente. Chez les herbivores et les carnivores les recrutements apparaissent le plus souvent dans un secteur différent de celui où vivent les adultes. Des migrations ontogéniques interviennent, mais les interactions négatives entre juvéniles et adultes ne semblent pas apparaître.

Oceanologica Acta, 1996, **19**, 3-4, 409-414.

INTRODUCTION

For several decades, community ecology has been based mainly on the evidence that community structure can be determined by physical and biotic processes. In the widely debated topic about the role of competition among these structuring processes, marine ecologists have emphasized the differences that exist between hard and soft substrata (Dayton, 1984). Hard substrata, notably in the intertidal zone, have produced considerable evidence that, in these space-limited systems, the populations are strongly influenced by biological interactions between functionally important species, but that recruitment is relatively unpredictable (Paine, 1984).

In contrast, soft substrata communities exhibit little evidence of competition. Ecologists have focused their attention on biogenic structures, such as polychaete tubicolous worms (Woodin, 1978). Today it has become evident, from experimental studies, that biotic interactions – particularly between adults and juveniles – have been largely underestimated in soft bottoms (Bachelet *et al.*, 1992).

After Strong *et al.* (1984), we are convinced that "good population ecology is a basis for good community ecology". Taking its examples from echinoderm populations in Brittany, the purpose of this paper is, tentatively, to explain recruitment and year-class segregation as responses to biotic and abiotic factors. The examples belong to different trophic guilds inhabiting rocky or soft bottom environments.

Year-class segregation in suspension-feeder populations

Some populations concentrated as beds constitute permanent features of the sea bottom. The location of these permanent beds can be explained by the existence of physical structures which favoured concentration of the nutritive part of the seston and act as a retention system for planktonic larvae (Hill, 1993). A very clear instance of this is provided by the beds of *Ophiothrix fragilis* in the centre of the Bay of Brest (Hily *et al.*, 1988), where strong instantaneous tidal currents create a cyclonic vortex. This gyre creates optimum conditions for the exploitation of nutriments by brittlestars and the settlement of recruits in its central part.

The persistent character of stable and stricly localized populations of *Amphiura filiformis*, another suspension feeder, has recently attracted the attention of benthologists in the Northeast Atlantic.

In the inner Galway Bay, the presence of a gyre based on a residual flow pattern coincides with the highest *Amphiura* densities (Harte *et al.*, 1982; O'Connor *et al.*, 1983). In the North Sea, at the southern margin of the Oyster Ground, high densities coincide with a frontal structure between stratified and mixed waters established in summer. Creutzberg (1984) showed the current velocities dropped below a critical value and detritus was deposited on the bottom. In the Bay of Concarneau (Glémarec and Ménesguen, 1980; Bourgoin and Guillou, 1988), the *Amphiura filiformis* population is located in low-turbulence conditions where detritus can be deposited at the boundary between fine sands and the muddy central area of the Bay. In Swedish fjords such as Gullmar Fjord (Rosenberg and Moller, 1979; Sköld *et al.*, 1994), different recruitment conditions can be explained by the physical conditions, which are stable under the halocline and more unstable above the halocline.

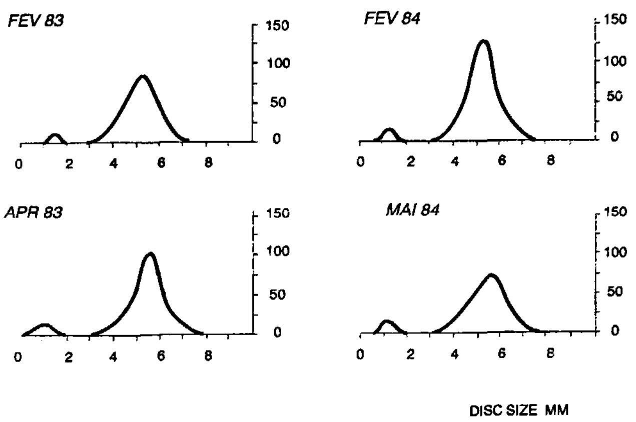

Figure 1

Disc size-frequency of Amphiura filiformis *on the Oyster Ground. Adapted from Duineweld and Van Noort (1986).*

All these situations reveal that the physical instability acts on the population density, on recruitment and, ultimately, on the demographic strategy. In the centre of a gyre or under low residual currents maintaining a halocline or thermocline, adult populations persist over pluriannual periods and recruitment is low. Galway Bay, Oyster Ground and Gullmar Fjord under the halocline illustrate this situation (Fig. 1).

Conversely, in the Bay of Concarneau (Glémarec and Ménesguen, *op. cit.*), off the Northumberland coast (Buchanan, 1963) and above the halocline in Swedish fjords (Rosenberg and Moller, *op. cit.*), the hydrodynamic actions are sufficiently important to be responsible for adult mortalities, so that large fluctuations occur in population densities. The sea bed is available for new recruits which generally account for more than 20 % of the population (Fig. 2). Populations are always maintained under their carrying capacities and no negative interaction between adult and juveniles can appear.

The concept of populations "open" or "closed" to recruitment has been transferred to *Acrocnida brachiata* population studies in the Bay of Douarnenez, where Bourgoin *et al.* (1991) compared unstable intertidal populations with more stable subtidal environments. This concept permits the explanation of some differences in biological variable estimates for *Amphiura filiformis* populations in the Northeast Atlantic (summarized in Tab. 1).

Table 1

Differences of biological variables estimated in Amphiura filiformis *populations in the Northeast Atlantic.*

	Physical instability	**Physical stability**
Recruitment	open: 10-20 %	close: 5%
Rate of growth	decreasing	
Mortality	decreasing	
Density	< 200 ind.m^{-2}	≅ 1 000 ind.m^{-2}
Biotic interactions	Low	High
Longevity	2-4 years	≅ 20 years
Maximum size	increasing	

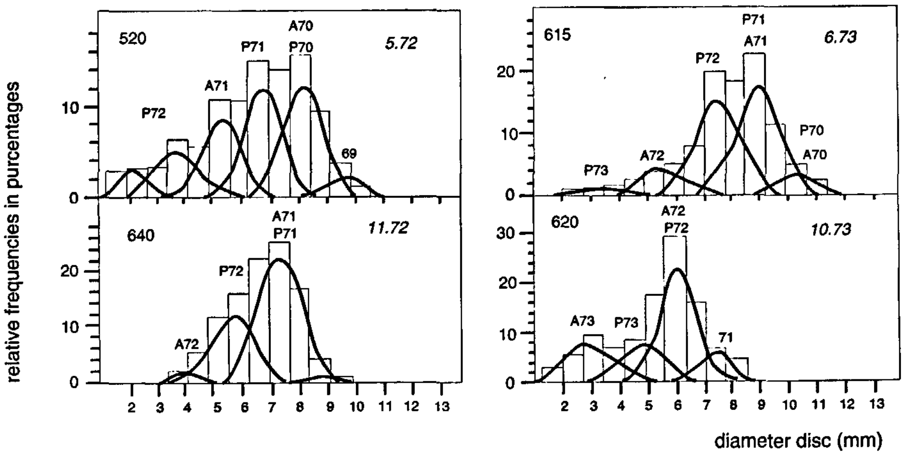

Figure 2

Disc size-frequency of Amphiura filiformis *in Concarneau Bay in spring and autumn 1972 and 1973. Cohorts are identified as modal components by a letter and a number corresponding to the period of recruitment (A: autumn, P: spring, number: year). After Bourgoin and Guillou, 1988.*

So, with these different suspension-feeding populations it is relatively easy to interpret year-class segregation as a function of abiotic and biotic factors, and their relative roles can be estimated.

Year-class segregation in herbivorous and carnivorous echinoderms

Sphaerechinus granularis populations

In the Glenan archipelago in south Brittany, populations of *S. granularis* have been studied from 1988 to 1992 (Guillou and Michel, 1993 *a*, 1993 *b*). Pearce and Scheibling (1991) suggest that the coralline algae maerl (*Phymatolithon*) can induce the metamorphosis of urchin larvae. In the Glenan archipelago, juveniles settle massively with an aggregative distribution on the maerl beds, where they inhabit at several centimetres depth and consume the algae. Progressively an ontogenic migration linked with modifications in the feeding behaviour of this herbivorous species occurs in the direction of *Zostera* beds and rocks. In the kelp beds, the oldest individuals can be responsible for barren grounds (Fig. 3).

Asterias rubens populations

A. rubens, in the Bay of Douarnenez, also demonstrates a measure of ontogenic migration (Guillou, 1983). In the intertidal rocky area, the smallest seastar individuals eat barnacles and small mussels. With growth, their food gathering capability increases and they migrate to more deep soft bottom areas where they consume the endogenous bivalve populations. Predation by such a large echinoderm on the mollusc stock of the macrofauna has been suggested as one of the reasons for the decline of local fishing (Bodin *et al.*, 1985).

Asterias rubens is generally found in dense aggregations, and if their localization can be linked with the distribution of prey in various sediment types, these aggregations must also be interpreted against the larger scale of ontogenic migration from rocky shore to nearshore sediment habitats (Fig. 4).

In these two examples of urchins and asteroids, year-class segregation is the consequence of an ontogenic migration linked with a dietary modification during the life span. Currents can concentrate larvae as suspension-feeders but the presence of prey should be the first condition to determine a definitive settlement.

Anseropoda placenta populations

The population of *A. placenta* has been studied in the Bay of Brest (Guillou and Diop, 1988), on a transect across the Aulne Channel river. The presence of a gyre favours recruitment on the southern bank (Fig. 5). Recruits appear each year in summer (station D), in relatively large numbers (5 m^{-2}). They stay for 8 to 10 months, and then migrate through the channel (stations C and B) and colonize the northern bank (station A). The oldest individuals are located on this bank, while planktonic larvae are caught in the gyre circulation and can settle on the southern bank. This life-history develops over a period of three years.

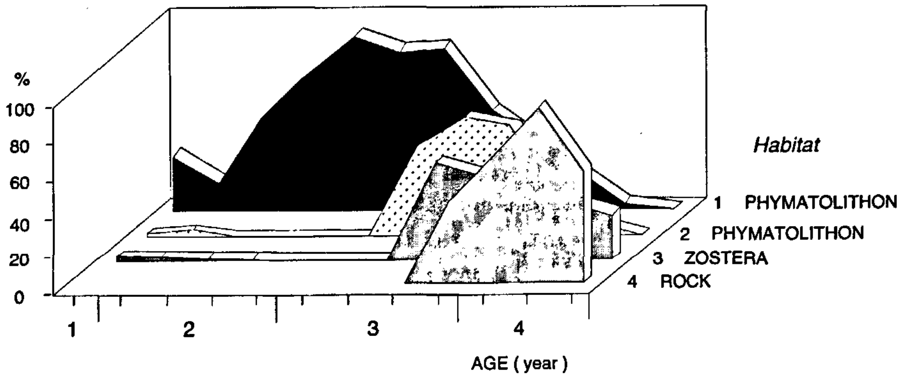

Figure 3

Temporal change of the relative frequency of a year-class of Sphaerechinus granularis *at each station along the sampled transect. The young (2-year old) recruited on* Phymatolithon *bed account for 90 % of the total population, the oldest (4 year old) represent 90 % of the total population sampled on the rocky area. Adapted from Guillou and Michel (1993).*

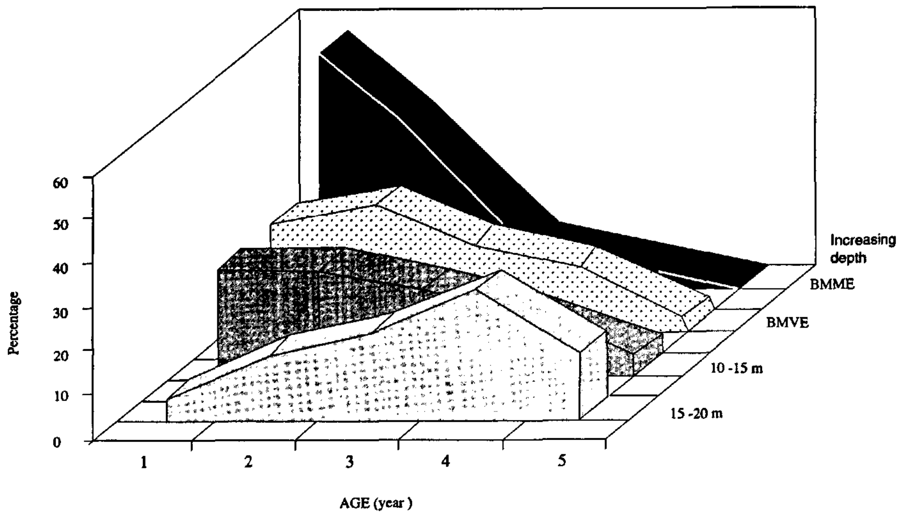

Figure 4

Temporal changes of the relative frequency of a cohort of Asterias rubens *along the bathymetric gradient in Bay of Douarnenez. Adapted from Guillou (1983). LWNT = Low water neap tide (BMME). - LWST = Low water spring tide (BMVE).*

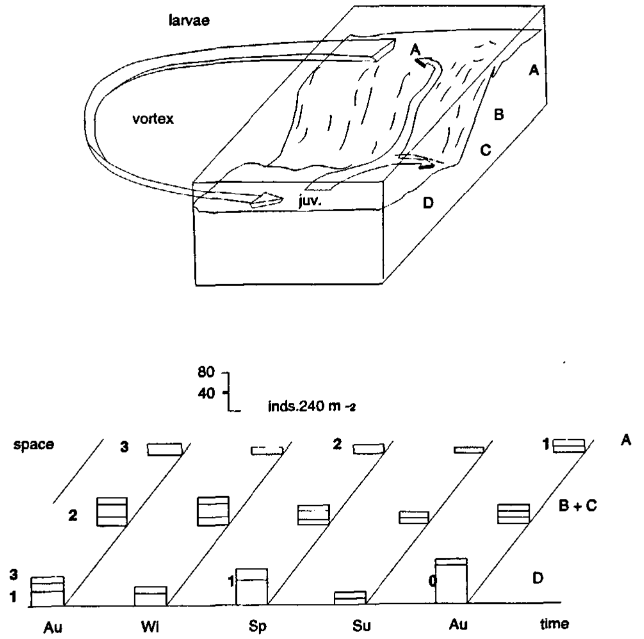

Figure 5

Spatial and temporal distributions of Anseropoda placenta *year-class: 0 recruitment in autumn 1986, 1 recruitment in 1985, 2 and 3 respectively in 1984 and 1983. Numbers give the mean density by 240* m^{-2}. *Arrows illustrate the migrations on the bottom and the planktonic dispersion in the anticyclonic vortex. Sampling station A to D (Fig. 1). Adapted from Guillou and Diop (1988).*

A diet specificity is observed in the individuals of every studied area. *A. placenta* juveniles feed preferentially on small crustaceans (stations D and C). As they grow, their preferred prey becomes small bivalves (station B) and finally small crabs, *Porcellana* and Ophiuroids, *Ophiotrix* (station A). The stomach contents of *A. placenta* reveals a prey-size selectivity (Guillou, 1987). As all the present species coexist in the different stations studied, the quest for the preferred diet would not here appear to be a cause of the observed migrations, which could rather be explained by unfavourable seasonal physical conditions and interspecific competition (Guillou and Diop, 1988). But, as in the case of the two previous examples, it seems that biotic interactions between juveniles and adults are relatively non-existent.

DISCUSSION

Recent developments in cooperative research programmes in Europe have shown scientists to have focused their attention on permanent stations where they can easily collect abundant samples of benthic populations. Special emphasis has often been placed on the population dynamics of pilot species which structure assemblages. Surprisingly, the size distributions in certain patches of high density are stationary in time, with an evident and permanent segregation of year-classes.

Physical factors are evoked as maintaining these biological structures in time. Populations structured by physical processes, such as a front or a gyre, tend to be predictable in space and time. In such populations, abiotic factors do not perturb the adult population to an extent that opens it to new recruitment.

In soft substrata, the suspension-feeding populations appear to be either open or closed to recruitment, so biotic interactions must be reevaluated when physical structures are not sufficient to perturb the environment. The result is space-limited systems with high intrapopulation competition. Rowe *et al.* (1987) with adequate experiments showed that high densities of *Amphiura filiformis* inhibit recruitment. In such high-density soft-sediment communities, the inhibition model best explains the majority of cases of adult-larval interaction. As predicted by Thorson (1966), newly settled larvae may suffer greatly from the feeding activities of adults.

Abiotic factors favour competition, developing a negative interaction between adults and juveniles. This constitutes a clear answer to the question posed by Barry and Dayton (1991): do physical factors modify the biotic interactions? A real connexion between these two kinds of factors seems obvious and the description of the modifications of biological parameters, under the forcing of physical factors should be able to bring the long debate about the *Amphiura filiformis* longevity to an end, by explaining why *Amphiura filiformis* longevity varies from four years in the Bay of Biscay to twenty years in Galway Bay (O'Connor *et al.*, 1983). Longevity does not correspond to a latitudinal gradient, but to the local environment.

After Paine (*op. cit.*), it has become usual to consider that grazers have complicated competitive and mutualistic relationships. Probably this concept can be enlarged to predators. These relationships mainly concern interspecific competitive interactions in space limited systems (Menge, 1982; Guillou, 1990).

In Brittany, examples of herbivorous and carnivorous echinoderm guilds have shown year-class segregation in relation with ontogenic migration. A great deal of informations on asteroids (Sloan, 1980) and echinoids (Vadas, 1977) has shown that their diet and feeding behaviour may vary according to their size. Most of these species become selective feeders as they grow. Changes in their morphology, in their mobility and in their ability to locate algae of prey, allow them to move to the preferred food. When prey is abundant, food preferences probably reflect adaptations, genetically determined, for increasing the intake of food that enhances fitness (Vadas, 1977; Himmelman and Nédélec, 1990). Coexistence of numerous adults with juveniles had little occasion to be described and intrapopulation competition seemed to be avoided. This paper has taken account of extreme situations along two opposite gradients of controlling factors: abiotic and biotic, so that it has been able to propose relatively clear responses. But it may be considered that the structures of most of the populations in benthic macrofauna are a consequence of the mixed influences of both kinds of factors and are situated on the median part of these two gradients. In such cases, identification of the relative influence of each may be expected to be very difficult.

Acknowledgements

The authors are cordially grateful to Paul Tyler and Brian Featherstone for help with the translation.

REFERENCES

Bachelet G., J. Guillou, P.J. Labourg (1992). Adult-larval and juvenile interactions in the suspension-feeding bivalve, *Cerastoderma edule*: field observations and experiments. In: *Marine Eutrophication and Population Dynamics*. G. Colombo, I. Ferrari, V.W. Ceccherelli et R. Rossi, eds. Olsen and Olsen, Fredensborg, 170-175.

Barry R., P.K. Dayton (1991). Physical heterogeneity and the organization of marine communities. In: *Habitat Structure*. S.S. Bell, E.D. Mc Coy and M.R. Mushinsky, eds. Chapman and Hall, London, 270-320.

Bodin Ph., D. Boucher, J. Guillou, M. Guillou (1985). Structure of benthic communities in the Bay of Douarnenez (Brittany). *19th European Symposium on Marine Biology*. Publ. Cambridge University Press. Ed. P.E. Gibbs, 361-370.

Bourgoin A., M. Guillou (1988). Démographie d'*Amphiura filiformis* (Echinodermata : Ophiuroidea) en baie de Concarneau (Finistère - France). *Oceanologica Acta* **11**, 79-88.

Bourgoin A., M. Guillou, M. Glémarec (1991). Physical environment instability and demography variability of the species *Acrocnida brachiata* (Echinodermata: Ophiuroidea) in the Bay of Douarnenez (Brittany). *P.S.Z.N.I. Marine Ecology* **12**, 89-104.

Buchanan J.B. (1963). The bottom fauna communities and their sediment relationships of Northumberland. *Oikos* **14**, 154-175.

Creutzberg F. (1984). A persistent Chlorophyll *a* maximum coinciding with an enriched benthic zone. In: *Proceedings of the 19th E.M.B.S.*, ed. P. Gibbs, Cambridge University Press, 97-108.

Crowe W.A., A.B. Josefson, I. Svane (1987). Influence of adult density on recruitment into soft sediments : a short-term *in situ* sublittoral experiment. *Mar. Ecol. Progr. Ser.* **41**, 61-69.

Dayton P. (1984). Processes structuring some marine communities : are they general?, 181-197. In: *Ecological communities: Conceptual issues and the evidence*. Eds. Stron G.D., L. Simberloff, L. Abele, A. Thristle, Princeton, New Jersey.

Duineveld G.C.A., G.J. Van Noort (1986). Observations on the population dynamics of *Amphiura filiformis* (Ophiuroidea : Echinodermata) in the Southern North Sea and its exploitation by the Dab, *Limanda limanda*. *Neth. J. Sea Res.* **20**, 85-94.

Glémarec M., A. Ménesguen (1980). Functioning of a muddy sand eco-system: seasonal fluctuations of different trophic levels and difficulties in estimating production of the dominant macrofauna species. In: *Marine Benthic Dynamics*, ed. by K.R. Tenore et B.C. Coull, University of South Carolina Press, Columbia, South Carolina, 49-67.

Guillou M. (1983). Les populations d'*Asterias rubens* L. (Echinoderma: Asteroidea) en baie de Douarnenez (Finistère). *Ann. Inst. Océanogr.* Paris, **59**, 141-154.

Guillou M. (1987). Étude du régime alimentaire d'*Anseropoda placenta* (Asteroidea : Echinodermata) en rade de Brest (Finistère ; France). *Bull. Soc. Sc. Nat. Ouest-France*, **Suppl., H.S.**, 133-140.

Guillou M. (1990). Biotic interactions between predators and superpredators in the Bay of Douarnenez, Brittany. In: *Trophic Relationships in Marine Environment*, M. Barnes and R.N. Gibson, eds. Aberdeen University Press, 141-156.

Guillou M., M. Diop (1988). Ecology and demography of a population of *Anseropoda placenta* (Echinodermata: Asteroidea) in the Bay of Brest, Brittany. *J. Mar. Biol. Ass. U.K.* **68**, 41-54.

Guillou M., C. Michel (1993 *a*). Reproduction and growth of *Sphaerechinus granularis* (Echinodermata : Echinoidea) in Southern Brittany. *J. Mar. Biol. Ass. U.K.* **73**, 179-192.

Guillou M., C. Michel (1993 *b*). Impact de la variabilité du recrutement sur le stock d'oursins commercialisables de l'archipel de Glénan (Sud-Bretagne). *Oceanologica Acta* **16**, 423-430.

Harte A.M., J.P. Gilroy, S.F. Mc Namara (1982). A computer simulation of water circulation in Galway Bay. *Eng. J.* **35**, 6-8.

Hill A.E. (1993). Seasonal gyres in shelf seas. *Ann. Geophysicae.* **11**, 1130-1137.

Hily C., J.P. Girardot, B. Quéguiner (1988). Rythme journalier d'activité trophique d'*Ophiothrix fragilis* selon les variations à court terme des conditions hydrologiques. *C.R. Acad. Sci. Paris*, **307**, 265-270.

Himmelman J.H., H. Nédélec (1990). Urchin foraging and algal survival strategies in intensely grazed communities in Eastern Canada. *Can. J. Fish. Aquat. Sci.* **47**, 1011-1026.

Menge B.A. (1982). The role of asteroid predators in benthic marine communities. In: *Echinoderm Nutrition*, M. Jangoux and J.M. Lawrence, eds. A.A. Balkema, Rotterdam, 521-551.

Pearce C.M., R.E. Scheibling (1991). Effect of macroalgae, microbial films and unspecifics on the induction of metamorphosis of the green sea urchin *Strongylocentrotus droebachiensis* (Müller). *J. Exp. Mar. Biol. Ecol.* **147**, 147-162.

O'Connor R., T. Bowner, A. Grehan (1983). Long-term assessment of the population dynamics of *Amphiura filiformis* in Galway Bay. *Mar. Biol.* **75**, 279-286.

Paine R.T. (1984). Ecological determinism in the competition for space. *Ecology* **65**, 1339-1348.

Rosenberg R., P. Moller (1979). Salinity stratified benthic macrofaunal communities and long-term monitoring along the west coast of Sweden. *J. Exp. Mar. Biol. Ecol.* **37**, 175-203.

Sköld M., L. Loo, R. Rosenberg (1994). Production, dynamics and demography of an *Amphiura filiformis* population. *Mar. Ecol. Prog. Ser.* **103**, 81-90.

Sloan N.A. (1980). Aspects of the feeding biology of asteroids. Oceanography and Marine Biology. *An Annual Review* **18**, 57-124.

Strong D.R., J.R. Simberloff, L. Abele, A. Thistle (1984). Preface in Ecological communities: conceptual issues and the evidence. Princeton, New Jersey.

Thorson G. (1966). Some factors influencing the recruitment and establishment of marine benthic communities. *Neth. J. Sea Res.* **3**, 267-293.

Vadas R.L. (1997). Preferential feeding: an optimization strategy in sea urchins. *Ecol. Monogr.* **47**, 337-371.

Woodin S.A. (1978). Refuges, disturbance and community structure: a marine soft-bottom example. *Ecology* **59**, 274-284.