Biotic and abiotic interactions controlling starfish outbreaks in the Bay of Douarnenez, Brittany, France

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ABSTRACT

Massive outbreaks of starfish (Asteridae) occur periodically in European coastal waters. The origins of these irregular population increases are poorly understood. In the subtidal zone of the Bay of Douarnenez, Brittany, France, the occurrence of several species of Asteridae and the polymodal size distribution differentiate these aggregations from the single year-class and monospecific intertidal infestations. An echinoderm population survey from 1982 to 1988 showed an increase in carnivorous starfish (principally *Asterias rubens* and *Marthasterias glacialis*) from 1981 to 1984, when the population reached carrying capacity. At this time, a trophic imbalance between starfish and bivalves was observed. From 1985 onward, the total echinoderm biomass decreased coincidentally with an increase in the two super predators the starfish, *Luidia sarsi* and *Luidia ciliaris*. From 1986 to 1988, the primary carnivorous echinoderm biomass appeared insufficient to meet the food requirements of the *Luidia* species. The role of the different factors controlling these starfish population changes is discussed. Whereas the hypothesis of regulation by *Luidia* predation fits the observations, it is also possible that direct or indirect temperature effects are also involved in population changes.

RÉSUMÉ

Interactions biotiques et abiotiques contrôlant les explosions d'étoiles de mer dans la baie de Douarnenez, Bretagne, France.

Les explosions de populations d'étoiles de mer sont des phénomènes périodiques courants dans les eaux côtières européennes. L'origine de ces agrégations saisonnières est complexe et encore mal connue. Par rapport aux invasions d'étoiles couramment observées dans la zone intertidale, les accumulations subtidales d'étoiles de la baie de Douarnenez (Bretagne, France) présentent des caractères originaux, dont la persistance dans le temps de plusieurs espèces et de plusieurs classes d'âge. Un suivi des populations d'échinodermes de 1982 à 1988 y montre un accroissement des étoiles carnivores primaires (principalement *Asterias rubens* et *Marthasterias glacialis*) de 1981 à 1984. Un déséquilibre trophique est alors observé entre les étoiles et leurs proies potentielles, les bivalves. A partir de 1985, la biomasse totale en échinodermes décroît tandis qu'augmentent les densités de deux super-prédateurs d'Asteridae, *Luidia sarsi* et *Luidia ciliaris*. De 1986 à 1988, la biomasse d'échinodermes prédateurs primaires est largement insuffisante pour répondre aux besoins alimentaires des deux espèces de *Luidia*. Le rôle des différents facteurs susceptibles de contrôler ces concentrations massives d'étoiles de mer est discuté. Si l'hypothèse d'une régulation par les super-prédateurs semble justifiée par les présentes observations, le rôle direct ou indirect de la température ne peut cependant pas être négligé.

INTRODUCTION

The importance of asteroid predation in structuring benthic communities was first demonstrated by Paine (1966) and later reviewed by Sloan (1980) and Menge (1982). In European benthic communities, predatory asteroids are numerous and include both secondary and tertiary carnivores. The most important primary species appears to be *Asterias rubens*. This species limits bivalve numbers in soft subtidal communities and also seasonally invades the low rocky intertidal zone, causing devastation of mussel beds (Forbes, 1841; Chadwick, 1923; Spark, 1932; Vevers, 1949; Hancock, 1955, 1958; Vinberg, 1967; Brun, 1968; Larsson, 1968; Mileykovskiy, 1968; Seed, 1969; Dare, 1973; Gulliksen and Skjaeveland, 1973; Rasmussen, 1973; Dare, 1976; Korringa, 1976; Anger *et al.*, 1977; Warner, 1979; Briggs, 1980; Sloan and Aldridge, 1981; Dare, 1982; Guillou and Guillaumin, 1984; Moore and Campbell, 1985; Guillou, 1990; Naumov and Buryakov, in press).

Little is known about the origin of sporadic asteroid invasions (Sloan, 1980) although most authors report that they are related to feeding activities. Reese (1966) suggests they involved complex interactions, reactions of individuals to environmental stimuli. Both internal factors (prey preferences, olfactory ability, reproductive condition and strategy for survival) and external environmental stimuli (temperature, weather, quality and quantity of prey) may act synergistically to cause the formation of these aggregations. That little is known about the origin of these formations is due to a lack of knowledge of factors affecting the behaviour of seastars and of their population dynamics (in time and space).

In the Bay of Douarnenez, western Brittany, aggregations have been observed in the subtidal zone over a period of several years. They are unusual in that asteroids of different trophic levels coexist and control the structure of local communities (Bodin *et al.*, 1984) through their predation and competitive interactions (Guillou, 1990). The aim of this study was to describe changes in local asteroid aggregations over time. Over eight years, we determined the density of secondary carnivores and prey availability. Further, we examined how higher-order predation, a factor which has been rarely considered in the studies on starfish outbreaks, might affect the population increases.

MATERIALS AND METHODS

The largest densities of Asteridae (*Asterias rubens, Marthasterias glacialis*) along the Atlantic coast of France are found in the Bay of Douarnenez (Bodin *et al.*, 1984). The most impressive aggregations are located in the centre of the bay, in an area where a current gyre has produced a heterogeneous muddy sand bottom (Chassé and Glémarec, 1976) (Fig. 1). The mean grain size of the sediment varies between 125-500 μm silt content (particles < 63 μm) ranging from 1 to 10 %.

Annual surveys were carried out in this area from 1981 to 1988 to quantify the abundance of large epibenthic echinoderms, mainly ophiuroids and asteroids. The temporal changes in the densities of the species collected was follo-wed using the observations made each autumn, except in 1982. The samples were collected using a 1.8 m scallop-dredge without teeth, equipped with a 2 cm-mesh net. The catch of each species was estimated from the ratio of the number of individuals collected to the length of the haul on the bottom. In each haul the dredge was towed for three minutes to prevent the dredge from over-filling. To calculate the density by area swept, the percentage of seastars remaining in the path of the dredge must be known. So a survey was carried out on the same bottoms, using a video camera over a known surface area. On the heterogeneous muddy sand, the dredge took 43.5 ± 4.2 % of the seastars present. The density for each species was the mean value calculated from all the dredgings over the whole area. To analyse community structure, the mean dominance of the main species (percentage of individuals compared to the total number of all species of asteroids) was calculated. To estimate prey numbers available to primary carnivores, macrofauna abundance was sampled using a Smith-McIntyre grab in 1982 and 1988.

To estimate the effects of particular predator groups on their prey (for example, the effect of primary carnivores on molluscs, or of secondary carnivores on primary carnivores), each trophic level production was examined and compared. Annual production $(gC . m^{-2} yr^{-1})$ was estimated on the basis of estimated values of productivity for the dominant species of each trophic group. These values were obtained directly through the study of the population dynamics of the species studied in the Bay of Douarnenez and from data obtained in similar biotopes (reviewed by Bodin *et al.*, 1985). To determine whether trophic relations were balanced (*i.e.* whether the food demand of primary and secondary carnivorous echinoderms was met by the lower levels), the food demand of the two carnivorous levels was compared to the production of their potential prey species. The food requirements were assessed using the production of the given trophic level and a mean efficiency rate of food utilization of 20 % (percentage production to consumption) corresponding to the mean value obtained by Chardy and Dauvin (1992) and Jean (1994) for the trophic level of carnivores in two nearby localities, Morlaix Bay and Brest Bay.

RESULTS

Temporal evolution of the asteroid and ophiuroid populations

A factorial analysis of correspondence was applied to data from October 1981 (dominances of the main asteroid and ophiuroid species on different bottom types in Bay of Douarnenez). This analysis separated the species according to their association with bottom sediment type (Guillou, 1990). For each bottom type, these echinoderms are grouped according to their trophic level and, at the same level, according to their feeding preferences. Five trophic groups were distinguished. On the first level was the filter-feeding ophiuroid, *Ophiothrix fragilis*. For primary carnivores, a distinction was made between *Ophiura ophiura / Astropecten irregularis*, species characteristic of fine sands, the ubi-

Figure 1

Distribution of sediment types in the Bay de Douarnenez and location of the area studied. The abbreviations correspond to the French terminology. SG (sables grossiers): coarse sands; SF (sables fins): fine sands; FV (sables fins vaseux): fine muddy sands; SHV (sables hétérogènes envasés): heterogeneous muddy sands. Dark areas represent rocks.
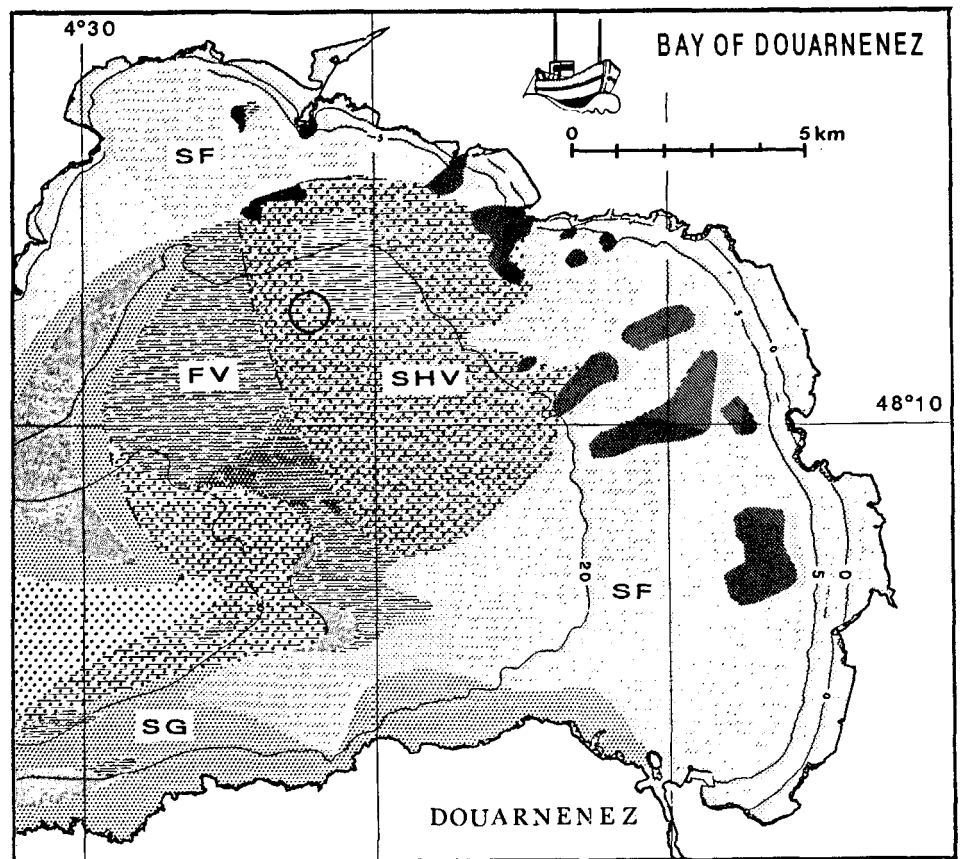
quitous species, *Asterias rubens,* and the asteroid *Marthasterias glacialis,* which was found on heterogeneous muddy sands. The top level was composed of the secondary carnivores, *Luidia ciliaris* and *Luidia sarsi.*

Between 1981 and 1988, temporal changes were observed in the dominance of these feeding groups (Tab. 1). *Ophiothrix fragilis,* which dominated the echinoderm community in 1981, had completely disappeared by 1983. It was progressively replaced firstly by small carnivores (*Ophiura ophiura* and *Astropecten irregularis*) and then by large carnivores (*Asterias rubens* and then *Marthasterias glacialis*). *Asterias rubens* and *Marthasterias glacialis* were the most abundant asteroids in 1984. After 1984, the density of the super predators, *Luidia sarsi* and *Luidia ciliaris,* began to increase (Tab. 1).

The increase in the largest primary asteroids led to an increase in the total biomass of the community, reaching a

Table 1

Temporal changes in the autumnal relative densities (%) of the main large echinoderm species in the Bay of Douarnenez from 1981 to 1988.

	1981	1983	1984	1985	1986	1987	1988
Ophiotrix fragilis	65	0	0	0	0	0	0
Ophiura Ophiura Astropecten irregularis	21	60	14	18	32	6	2
Asterias rubens	11	18	39	43	32	12	37
Marthasterias glacialis	3	20	46	36	27	61	40
Ludia ciliaris Luidia sarsi	1	2	1	3	9	21	21

peak in 1984. Then the primary asteroid biomass declined until 1988. An inverse relationship was observed between the biomass of the primary carnivorous echinoderms and that of their predators *Luidia sarsi* and *Luidia ciliaris* (Fig. 2).

Analysis of the trophic relationships

Examination of the production of the three trophic levels (bivalves, primary carnivorous echinoderms and *Luidia* spp.) respectively, and of the food demand of the upper levels, suggested trophic imbalances at various levels of the food web, depending on the year (Fig. 3). The annual production of primary carnivorous echinoderms began to decline when the production of *Luidia* peaked in 1986. Bivalve production was almost identical in the two years when samples were taken, 1981 and 1988, amounting to 3.6 and 3 gC m^{-2} respectively. It is probable that mean annual production was not greater in the intermediate years when predation pressure from the asteroids was high.

Our calculations suggest that from 1983 to 1985, an average of only 50 % of the food requirements of the asteroids could have been met by the production of their potential prey, the bivalves. Bivalves represented about 30 % of the production of the total macrofauna. Even if there had been other sources of food for these echinoderms, which can be opportunistic feeders (Jangoux, 1982), a trophic imbalance would be indicated between predators and their preys in 1983 and 1984. During these two years, the asteroid food demand could not have been met by the production of bivalves or of the total macrofauna. Since primary carnivorous asteroids were not the only predators of the benthic
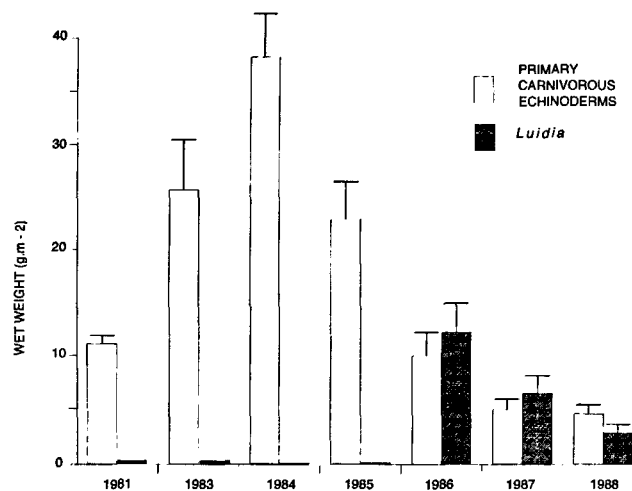
Figure 2

Temporal changes in the mean autumnal biomass (± SE) of Luidia spp. and of the primary carnivorous echinoderms.
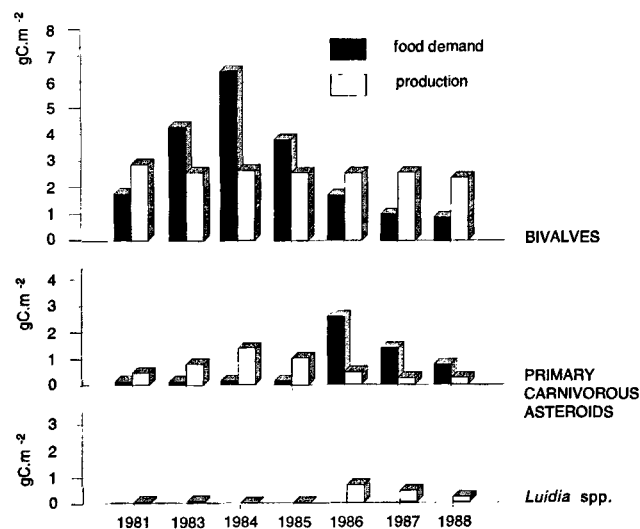

Figure 3

Temporal changes in the production in gC m^{-2} (white bars) of the three trophic levels (bivalves, primary and secondary carnivorous echinoderms). The annual food demand of the upper trophic level (black bars) is associated with each annual value of production (e.g. annual food demand of Luidia juxtaposes annual production of primary carnivorous asteroids). The bivalve production values for 1983-87 are the average of the 1981 and 1988 measures (see above explanation).

macrofauna, other carnivores could also have contributed to the decrease in bivalves.

After this period, during which echinoderm abundance exceeded the carrying capacity of the environment, a drop in primary carnivorous starfishes led to a reestablishment of the trophic equilibrium. Between 1986 and 1988, primary carnivore echinoderm abundance was not sufficient for the food requirements of *Luidia*. For example, in 1986 and 1987 the estimated energy requirement of *Luidia* was 6.5 times greater than the production of primary carnivorous echinoderms.

DISCUSSION

Although the large starfish aggregations in temperate waters are most often observed in the intertidal zone, our study documented an asteroid outbreak in the subtidal area. The subtidal starfish outbreaks had characteristics which differed from increases in the intertidal zone. In the intertidal zone the increases are sporadic, short-lived, occur during the warmer months, consist of a single year-class, and are monospecific. In contrast, the subtidal population increases can last for many years, are composed of several year-classes and comprise several asteroid species, both primary and secondary carnivores.

Potential biotic mechanisms regulating subtidal populations include: inter-and intraspecific competition, resource limitation and predation. Competitive interactions between *Asterias rubens* and *Marthasterias glacialis* are described by Guillou (1990). *Marthasterias glacialis* is the largest and best adapted species in the subtidal environment. It was the dominant primary carnivore when food abundance was low.

Bodin *et al.* (1984) suggested that a decrease due to the disappearance of prey (*i.e.* by resource limitation) was involved in the regulation of starfish proliferations in the Bay of Douarnenez in 1982. However, this was probably not the case, since molluscan production was almost identical at the beginning and end of our study. However, the types of the prey changed during our study, epifaunal bivalves being dominant in 1988 and infaunal molluscs in 1982.

Predation may be an important factor controlling subtidal asteroid populations. Our results, showing an inverse relationship between the biomass of the primary carnivorous starfish and that of the second order carnivore *Luidia* spp., are similar to the trophic relationships described by Menge (1982) between specialized secondary predators (*Luidia ciliaris* and *sarsi* in Europe and *L. magellicana* in South America) and their prey, which is composed of primary carnivorous echinoderms. The predatory impact of these specialized carnivores is greater than that of more generalized predatory asteroid such as *Stichaster australis* (Paine, 1971) and *Solaster dawsoni* (Mauzey *et al.*, 1968; Engstrom, 1974). Predation by these super predators may indirectly break up aggregations (Holme, 1984) as well as reducing the numbers of primary carnivorous echinoderms.

Luidia ciliaris and *L. sarsi* are known predators of ophiuroids and other species. Holme observed a negative association between the abundance of *Ophiothrix fragilis* and *Luidia ciliaris* and *L. sarsi* between 1895 and 1981 in the Western English Channel. The abundance data summarized by Aronson (1992) showed two phases of increase in *Luidia* spp. between 1898 and 1928 and between 1967 and 1981. Each increase coincided which a decrease in the abundance of *Ophiothrix*. The decrease in *Ophiothrix* numbers caused by *Luidia* spp. may be an indirect result of hydroclimatic factors. Holme related the variations in the abundance of the two stenothermal *Luidia* spp. to a change in plankton composition caused by a change in sea water temperature.

Directly or indirectly, the role of sea water temperature may be a factor causing the formation of starfish aggregations. Fluctuations in the numbers of *Asterias* juveniles in the Bay of Douarnenez during our study were correlated with water temperatures in Brittany (Guillou, 1990). From 1981 to 1984, a general increase in juveniles followed unusually mild winters (Fig. 4). The slight decrease in juveniles in 1985, which became more accentuated in 1986, may have occurred because of poor recruitment related to the cold winter of 1984-1985 and even colder winter of 1985-1986. In these years, an absence of recruitment of the burrowing ophiuroid *Acrocnida brachiata* was also recorded in the Bay (Bourgoin *et al.*, 1991). Although we did not examine the effect of water temperature on starfish recruitment, this factor is known to initiate invertebrate gonad maturation in many temperate waters (Giese and Pearse, 1974). This has been shown for the sea urchin *Sphaerechinus granularis* in West-Brittany (Guillou and Michel, 1993, 1994). However, prey and predator responses to temperature may differ. If temperature increase favours *Asterias rubens* recruitment, it should limit the numbers of *Luidia* spp. according to the Holme's observations. Thus biotic (predation) and abiotic (temperature) factors may act in synergy to control the starfish outbreaks.

We proposed the following model of interactive processes that could act on the regulation of starfish communities. Water temperature, through its direct effect on seastar spawning, induces fluctuations in asteroid abundance. Indirectly, temperature may alter circulatory patterns, nutrient levels and planktonic composition, and thus affect the densities of *Luidia* larvae (Holme, *op. cit.*). In the present study, temperature also promotes the development of thermal fronts at the entrance of the Bay. These fronts limit the dispersion of larvae during the summer. Current gyres retain the larvae in the centre of the bay. After population increases, biotic interactions take place. The high densities of asteroids are known to promote feeding (by feeding stimulus, Warner, 1979) and reproductive success (by spawning synchronization, Chaet, 1966) and thus eventually cause a further increase in the numbers of starfish. Later, intraspecific interactions control the population dynamics of asteroid outbreaks: competition regulates the number of
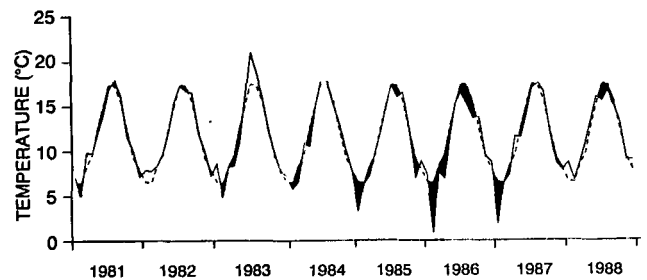

Figure 4

Mean daily air temperature in the Bay of Douarnenez compared to average annual cycle computed over the last 20 yr.

starfish within a given trophic level, and predation by higher order predators limits starfish numbers at the lower trophic levels. When secondary carnivorous starfish are abundant and food limited, migrations towards intertidal food sources may occur. There is little competition in these short-lived aggregations where the only asteroid species is *Asterias rubens*, and little predation (with except for a small loss due to predation by sea-gulls). Generally, such aggregations disperse during autumn storms (Sloan and Aldridge, 1981).

As for the tropical asteroid *Acanthaster planci*, the impressive aggregations of Asteridae thus result from a complex of external and internal factors. In both cases, abundance of localized food promotes the development of aggregations. The dynamics of the temperate and tropical asteroids, however, differ. The relatively opportunistic feeding behaviour of asteroids and the abundance of food in localized subtidal and intertidal temperate areas suggests that resources are not generally limited. Species exploit the resources with a maximum efficiency, then disappear due to biotic and physical factors. The aggregations are generally short-lived and confined to localized areas. For the highly specialized corallivore *A. planci*, food can be limited. The aggregations are maintained over time owing to the relative stability of physical factors and even enhanced by regular migrations of the individuals to new coral reefs.

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