Evidence for a sacrificial response to predation in the reproductive strategy of the comatulid crinoid *Antedon bifida* from the English Channel

Crinoidea
Antedon
Reproductive cycle
Predation
Crenilabrus

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Cycle reproductif
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Crenilabrus

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ABSTRACT

A population of the North-East Atlantic feather star *Antedon bifida* (Pennant) from a site in strong currents off South Devon, U.K., maintains a high level of maturity throughout its annual cycle, yet spawns only at a precise period of the year. Most individuals lose a proportion (mean: 17 %) of their pinnules from predation by the corkwing wrasse, *Crenilabrus melops*. An account of some aspects of predation of the crinoid by the fish is given. It is suggested that the crinoid maintains the maturity of its reproductive tissues at an unusually high level throughout the year so that the predator will take the pinnules, including the energy-rich gonads, in preference to the more vulnerable calyx. It is also suggested that a stress-response may be involved in the maintenance of continuous gametogenic activity by the crinoid, and, further, that attracting the predatory fish to itself may help rid the crinoid's exterior of epizoics.

RÉSUMÉ

Se sacrifier à la prédation, une stratégie de reproduction développée par la comatule *Antedon bifida* en Manche.

Une population de la comatule du nord-est Atlantique *Antedon bifida* (Pennant), située dans une zone de forts courants au large de la côte du sud du Devonshire (U.K.), maintient sa maturité à un haut niveau pendant tout son cycle annuel, alors qu'elle ne pond qu'à une période très précise de l'année. La plupart des individus perdent une partie (en moyenne 17 %) de leurs pinnules sous l'action prédatrice du labridé, *Crenilabrus melops*. Dans cette étude, qui décrit en partie cette action, il est suggéré que la comatule maintient la maturité de ses tissus reproducteurs à un niveau inhabituellement élevé durant toute l'année pour que le prédateur broute les pinnules, y compris les gonades riches en énergie, plutôt que les calices plus vulnérables. Il est d'autre part suggéré que le maintien de cette activité de gamétogénèse puisse aussi être une réponse engendrée par le stress et un moyen pour la comatule, en attirant le poisson prédateur, de se débarrasser de ses ectoparasites.

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INTRODUCTION

Antedon bifida (Pennant) spawns only in the late spring in the north-east Atlantic (Chadwick, 1907; Lahaye, 1987; Nichols, 1991). This aspect of seasonality is confirmed by the fact that *Antedon* broods its recently-shed fertilised eggs and subsequent early larvae in a mucous net attached to the outer surface of each genital pinnule (Miller, 1821). Brood-nets have been noted only in the month of July; later in the cycle, only the remains of the brood-net were seen, and there is no suggestion that eggs and sperm are shed at any other time of year. The shedding process does not necessarily eject all oocytes of sheddable size from the ovary: in all cases of ovaries with brooding-nets on their outer walls there were large oocytes and ova remaining in the ovarian lumen. Similarly in males, mature sperm are present in the testes of most individuals across the year (Nichols, 1994*a*).

Crinoids were formerly regarded as relatively immune from predation. H.L. Clark (1917) noted that crinoids allowed to free-fall in an aquarium were avoided by fish, and this observation was repeated by subsequent authors as evidence of non-predation (*e.g.* A.H. Clark, 1921; Mortensen, 1927; Fell, 1966; Breimer, 1978), until Brun (1972) reported finding crinoid ossicles from *A. bifida* in the stomach of the predatory starfish *Luidia ciliaris*.

More significantly, Vail (1987) reported that «the trigger-fish *Ballistoides conspicillum* (Bloch et Schneider) has been observed on three occasions to attack the arms of a...crinoid»; he does not state which parts of the arms were attacked, or whether the pinnules were removed from them. Fishelsen (1974), however, observed pinnular predation of the Red Sea *Lamprometra klunzingeri* (Hartlaub) and *Capillaster multiradiata* (L.) by the clingfish *Lepadichthys lineatus* Briggs. The fish was seen to lunge at and break off one pinnule at a time and swallow it; between eight and twelve pinnules a day were taken in this way. The fish also fed upon associated fauna, such as copepods, palaemonid shrimps and errant polychaetes present amongst the arms and pinnules, suggesting that the clingfish 'cleans' the crinoid of epizoic animals.

A random collection of individuals of *A. bifida* from an experimental site off the South Devon coast, U.K., showed that pinnule predation ranged from 1 % to 46 % loss of whole pinnules, with a mean of 17 % (Nichols, 1994*a*). In this paper, observations of the predation process are reported.

On the French side of the English Channel, there is a site at which *A. bifida* occurs in less-exposed water, where predation by *Crenilabrus* does not occur, and where there is substantial infestation by the proboscidean *Myzostoma*; at the French site, there is evidence that a sacrificial response does not seem to be a feature of the reproductive cycle of this population.

MATERIALS AND METHODS

The study site was at Berry Head, South Devon, U.K. (lat. 50° 24'N; long. 3° 29'W), at a depth of between 10 and 15 m below chart-datum.

Several dives were made on the site to establish the behaviour of the corkwing wrasse, *Crenilabrus melops* (L.), towards individual crinoids in the field. In addition, six specimens of the fish were carefully netted and transported to an aquarium tank at the laboratory, with rocks taken from the site complete with encrusting organisms. All specimens were less than 9.0 cm in length, and therefore immature (Wheeler, 1969). They were allowed to aclimatise for three weeks before observations on their feeding behaviour towards *A. bifida* were made. Attacks on the brittle-star *Ophiothrix fragilis* (Abildgaard) and the coralline alga *Corallina officinalis* L., both taken from the site, were also recorded.

RESULTS

Diver observations at the experimental site suggested that the corkwing wrasse, *Crenilabrus melops*, was the commonest fish in the area, and that, in addition to feeding upon organisms encrusting the reefs and rocks of the site, the fish also visited the clumps of *Antedon* periodically during forays, usually returning to the feather-star to the exclusion of other prey once the pattern of pinnule removal had been established, and continuing to attack the feather-star for up to 10 min. During this period, the fish would lunge at the arms and remove pinnules. The fish also appeared to be taking pelagic organisms, such as copepods, from amongst the arms of the crinoid.

Observations in the tank showed that, before the introduction of prey *Antedon* specimens, the fish established a dominance hierarchy, territoriality and a preference for certain areas of the tank. When *Antedon* specimens were introduced, the area-preference broke down as the fish explored the crinoids and began to attack them. More pinnules were removed from the arm-tips than from the central or basal regions of the arms. Table 1 shows the targets of strikes by the fish over six one-hour periods of observation on a single specimen of *A. bifida*. The fish also took other organisms sheltering among the arms and pinnules of the crinoid, such as planktonic crustaceans.

Table 1

Attacks during six periods of one-hour each by the corkwing wrasse, *Crenilabrus melops*, on three regions of the arms of the crinoid *Antedon bifida*.

Observation period	Total strikes	Region of Arm: Base No.	%	Middle No.	%	Tip No.	%
1	61	6	9.8	10	16.4	45	73.8
2	58	12	20.7	14	24.1	32	55.2
3	63	8	12.7	10	15.9	45	71.4
4	45	4	8.9	13	28.9	28	62.2
5	71	4	5.6	12	16.9	55	77.5
6	83	12	14.5	26	31.3	45	54.2
Means		7.7±3.3	12.0	14.2±5.5	22.3	41.7±9.0	65.7

The dominant fish made most frequent attacks on the crinoid, but, if it had a fragment of arm or a single pinnule protruding from its mouth after an attack, it would sometimes be pursued by fish lower in the hierarchy, and these sometimes succeeded in removing pinnules from the protruding arm-fragment and swallowing them.

Once removed, the pinnules were taken into the mouth, but often ejected again, sometimes repeatedly. On occasions, another fish, from any position in the hierarchy, would catch an ejected pinnule and ingest and eject it in a similar way. The robbed fish would sometimes chase the intruder until the stolen pinnule was dropped by the intruder and regained by the original fish, or finally ingested by the intruder. The response of the crinoid to pinnule removal was to curl its arms inwards momentarily. Sometimes the crinoid, after repeated attacks, would detach its cirri from the rock and swim to another area of the tank.

When the brittle-star *Ophiothrix fragilis* was introduced to the tank with *Antedon*, it would be investigated by the fish, but only initially would the fish lunge towards it as if to attack. The fish was never observed to make contact with the brittle-star's body, and subsequently the brittle-star would be ignored and further attacks directed to the *Antedon*. Introduced pieces of the coralline alga *Corallina officinalis*, which resembled the crinoid in size, posture and skeletal support, were investigated briefly but not attacked.

DISCUSSION

There can be little doubt that, despite unspawned oocytes being present over the entire annual cycle, *A. bifida* spawns only in July. Not only have the brood-nets, which hold the spawned eggs and subsequent early larvae to the outside of the genital pinnules, been seen at no other time of year, but also the fixed-stage *pentacrinule* larvae have been found only after July and up to the end of October (Clark and Clark, 1967). So the retention, in both sexes, of a high level of maturity at other times of year suggests that an extrinsic factor may be influencing the annual cycle (Nichols, 1994*b*). *A. bifida* is said to reach sexual maturity during its second year of life (Thomson, 1865), but the longevity of populations around Britain does not appear to have been recorded.

The maintenance of gonads at high levels of maturity was not revealed as a constant phenomenon, however: comparison of similar months in separate years throughout the study has shown marked differences in the relative occurrence of large oocytes (Nichols, 1994*a, b*), suggesting that some factor other than seasonality is influencing gametogenic development.

The observations described here show that the corkwing wrasse, *Crenilabrus melops*, takes pinnules from the entire length of the arm during feeding forays among the beds of *Antedon* at the study-site, and on individuals observed in aquaria. Two points of significance emerge: first, the fish takes only the pinnules or arm-tips and does not attempt to prey upon the calyx; and, secondly, the fish also takes encrusting epizoics and free associated fauna from the vicinity of the host *Antedon*.

After predation, the depleted *Antedon* will regenerate lost arm-tips and pinnules (Nichols, 1994*a*). While the rate of regeneration has not been studied, instances were observed of regenerated pinnules bearing gonads of smaller overall size than those of adjacent pinnules. Behaviour of the wrasse towards another echinoderm, the brittle-star *Ophiothrix*, which occurs sympatrically with *Antedon*, suggests that the brittle-star is distasteful, though it is not among brittle-stars reported to secrete acid mucus over their integument (Fontaine, 1955).

An interesting aspect of the behaviour of the predatory wrasse was that they did not investigate the introduced *Corallina officinalis* specimens, despite this being the preferred material for the entrance to the brood-nest in *C. melops* (Potts, 1985). It seems likely that taking up *C. officinalis* is confined to the breeding stage of the fish's life-cycle.

In addition to taking parts of arms and pinnules, the wrasse foraged among *A. bifida* for epizoics and other organisms sheltering amongst its arms, pinnules and cirri. An epizoic common among some populations of *A. bifida* is the proboscidean myzostomid *Myzostoma cirriferum* Leuckart, which when young wedges itself in the ambulacral grooves of the crinoid pinnules, then when older ranges more freely up and down the grooves; at all stages they take food-particles from the host's feeding system (Eeckhaut *et al.*, 1990). Despite intensive searches, no specimens of this ectoparasite were found on animals from the study-site on the northern coast of the English Channel off Devon, U.K. This contrasts markedly with a population of the same species from a less-exposed site on the southern coast of the Channel, at Morgat on the Brittany coast, some 320 km distant. Here, myzostomids are common, but the wrasse, *Crenilabrus*, is rare. Further, the Morgat population does not show pinnular predation or regeneration, and the reproductive cycle is typically seasonal and semelparous (I. Eeckhaut, M. Jangoux, pers. comm.).

Without further work, particularly synchronous comparative studies, such differences in reproductive strategy between crinoid populations cannot easily be explained. One possibility is that the presence of a voracious predator, as in the Devon coast (northern Channel) population of *A. bifida*, may induce unusually-prolonged gametogenic activity, thus providing a sacrificial food-source to deflect the predator from the vulnerable calyx to the easily-regenerated pinnules, some two-thirds of which bear gonads. Tolerating the fish's attentions in this way might also rid the crinoid of infestations of the ectoparasite *Myzostoma cirriferum*, along with other epifaunal associates that might compete with the filter-feeding host crinoid (Nichols, 1960) for food. That predation disturbs the crinoid is evidenced by their detachment and removal to another feeding-site, observed in crinoids suffering repeated attacks from the fish. Such behaviour is almost certainly stress-induced, but how the internal control-systems of the crinoid might induce a perturbation of the normal reproductive cycle and removal to another temporary site in the way revealed by this study cannot yet be suggested.

A strategy involving prolongation of the gametogenic process and continued production of semi-mature gametes is unlikely to be of benefit to the population unless the energy-equation is advantageous. Crinoid gonads are probably nourished by two sources of food: from the gut, *via* the coelomic and haemal systems (Holland 1992), and parenterically, through the absorption of dissolved organic material *via* the pinnular epithelium (West, 1978). Though the relative contribution of these two sources has not been investigated, West (1978) shows that crinoids exhibit preferential uptake of carbohydrates and proteins by the arms and pinnules compared with that across the tegmen to the calyx. Further study is clearly required to confirm whether the reproductive cycle of a population from the Devon coast of the English Channel is a response to fish predation, whether the fish also acts as a 'cleaner', and if so how the response is mediated.

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