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ARM REGENERATION FREQUENCY IN EIGHT SPECIES OF OPHIUROIDEA (ECHINODERMATA) FROM EUROPEAN SEA AREAS

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ABSTRACT

Eight ophiuroid species, six from the northern Kattegat-eastern Skagerrak and three from the northern Adriatic Sea, were examined for regeneration of arms. The species were separated into groups based upon mode of feeding and habitat. Comparison between groups collected in the northern Kattegat-eastern Skagerrak showed that infaunal suspension- and deposit-feeding species (*Amphiura filiformis* and *A. chiajei*) had significantly more scars per arm (mean number 0.78) than epibenthic suspension feeders (*Ophiothrix fragilis* and *Ophiocomina nigra*, 0.29) or epibenthic carnivores and deposit feeders (*Ophiura ophiura* and *O. albida*, 0.13). Spatial variation in arm regeneration incidence was found between sampling sites in the northern Kattegat-eastern Skagerrak for *Amphiura filiformis* and in the northern Adriatic Sea for *Ophiothrix quinquemaculata*. The ash-free dry weight (AFDW) and nitrogen (N) contents were measured in arms of six species of brittle-stars from the northern Kattegat-eastern Skagerrak. Differences between species were found, with highest concentrations of AFDW and N in *Amphiura filiformis*, intermediate in *A. chiajei*, *Ophiocomina nigra* and *Ophiothrix fragilis*, and lowest in *Ophiura ophiura* and *O. albida*. As the infaunal suspension- and deposit-feeding brittle-stars (*Amphiura* spp.) had the highest proportions of damaged arms and highest AFDW and N contents in their arms in this comparison, it is suggested that selective cropping of arms by demersal fish is the main cause of arm damage on *Amphiura* spp. in this area.

Key words: *Ophioderma longicaudum*, *Ophiura ophiura*, *O. albida*, *Ophiocomina nigra*, *Amphiura chiajei*, *A. filiformis*, *Ophiothrix quinquemaculata*, *Ophiothrix fragilis*, predation, Adriatic Sea, Kattegat, Skagerrak

1. INTRODUCTION

Recent studies have emphasized the frequency of arm loss and subsequent regeneration in burrowing ophiuroid populations (Bowmer & Keegan, 1983; Munday, 1993; Clements *et al.*, 1994; Stancyk *et al.*, 1994). Arm regeneration contributes significantly to secondary production of the infaunal ophiuroids *Acrocnida brachiata* and *Amphiura filiformis* (O'Connor *et al.*, 1986; Bourgoin & Guillou, 1994; Sköld *et al.*, 1994) and the energetic value of *Amphiura* spp. arms cropped by demersal fish and the Norway lobster *Nephrops norvegicus,* may also be important (Mattson, 1992; Pihl, 1994; Duineveld & Van Noort, 1986; Baden *et al.*, 1990). The significance of sublethal predation has also been demonstrated in tidal flats where flatfish crop on tails of the lugworm *Arenicola marina*. The secondary production due to regeneration of tails was estimated at 33% of the total production (De Vlas, 1979). Peterson & Quammen (1982) showed that habitat-specific cropping of siphons by small fish can explain differences in growth of the bivalve *Protothaca staminea*. Regeneration of cropped body parts thus seems to be a significant part of secondary production and body parts are probably an important food source in some marine areas.

Epifaunal ophiuroids are known to form dense populations (Broom, 1975; Fedra *et al.*, 1976; Davoult *et al.*, 1990; Dahm, 1993), but only few studies have dealt with the frequency of arm regeneration. Emson & Wilkie (1980) presented data on arm regeneration of ophiuroid species from Scotland, and Aronson (1989) compared sublethal predation on *Ophiothrix fragilis* and *Ophiocomina nigra* between dense brittle-star beds and subtidal rocky reef communities in

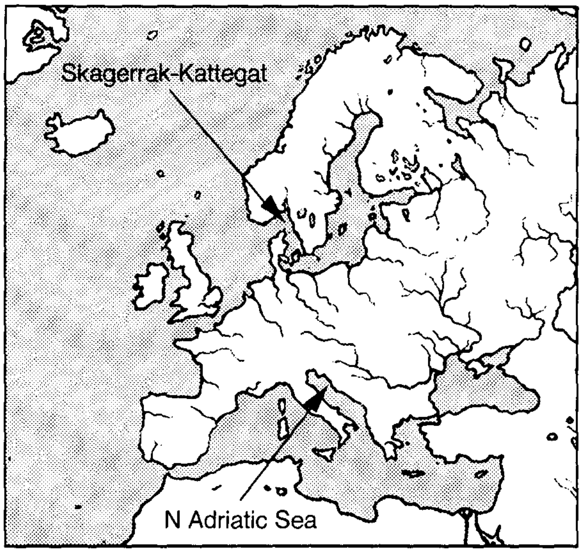

Fig. 1. Map of sampling areas.

the British Isles. Recently, in reviewing data on arm regeneration on fossil and recent ophiuroids, Aronson (1992) concluded that predation pressure on ancient ophiuroid populations were low before the Triassic but increased between the Triassic and the Cretaceous, parallel to the diversification of skeleton breaking predators.

This investigation compares the occurrence of sublethal arm injuries in brittle-star species to test the hypothesis that injury frequencies are related to different habitats and feeding strategies. The study was performed in 1994 in the Gulf of Trieste in the northern Adriatic Sea, and the coastal Kattegat-Skagerrak at the Swedish west coast (Fig. 1).

2. MATERIAL AND METHODS

2.1. SITE DESCRIPTIONS AND SAMPLING

Positions, depths and substrates of the sampling sites are shown in Table 1. Epibenthic species (*Ophioderma longicaudum*, *Ophiura ophiura* (synonym *O. texturata*), *Ophiura albida*, *Ophiocomina nigra*, *Ophiothrix quinquemaculata* and *O. fragilis*) were carefully picked with forceps using SCUBA and transported live, separated by species, in isolated tanks to the laboratory. Infaunal species (*Amphiura chiajei* and *A. filiformis*), collected in the northern Kattegat-eastern Skagerrak were sampled by box-corer (0.1 m^2). Each sample was gently rinsed and the respective individuals picked out directly from the sediment with forceps to avoid autotomy and breakage of arms, and transported as above. No autotomy or breakage of arms was observed during sampling.

2.2. MEASUREMENTS AND OBSERVATIONS

An ocular micrometer was used to measure oral width to the nearest 0.1 mm according to O'Connor *et al.* (1983). Specimens were closely examined under a binocular microscope and visible regeneration points on the arms were registered. Regeneration points were identified as changes in arm thickness and lighter colour of the regenerating portion of the arm (Bowmer & Keegan, 1983; Munday, 1993; Stancyk *et al.*, 1994; see also Fig. 2). All brittle-stars were examined alive since colours may change and arms may break off at preservation. The position of a scar was ascribed to the proximal (0-33%), middle (34-67%) or distal (68-100%) parts of the arm relative to disk periphery, using an intact arm of the same individual or an individual of similar size and species as reference. The mean number of scars per arm was

TABLE 1
Positions, depth and substrate of the sites sampled for brittle-stars in 1994.

site	*date*	*position*	*depth*	*substrate*
northern Adriatic Sea				
A	July	45°39'83"N, 13°35'77"E	20 m	clay with some silt
B	July	45°33'51"N, 13°21'10"E	20 m	rock, sand and gravel
C	July	45°32'95"N, 13°19'19"E	21 m	rock, sand and gravel
D	July	45°45'60"N, 13°35'35"E	10 m	mud-clay
northern Kattegat-eastern Skagerrak				
E	Sept.	57°17'95"N, 11°22'61"E	43 m	clay with some silt
F	Sept.	57°16'53"N, 11°25'59"E	87 m	clay with some silt
G	Sept.	57°16'84"N, 11°27'88"E	76 m	clay with some silt
H	August	58°18'00"N, 11°32'00"E	26 m	rock
I	August	58°15'95"N, 11°25'30"E	27 m	rock
J	October	58°17'68"N, 11°23'70"E	27 m	clay with little silt
K	October	58°14'72"N, 11°25'80"E	40 m	clay with silt

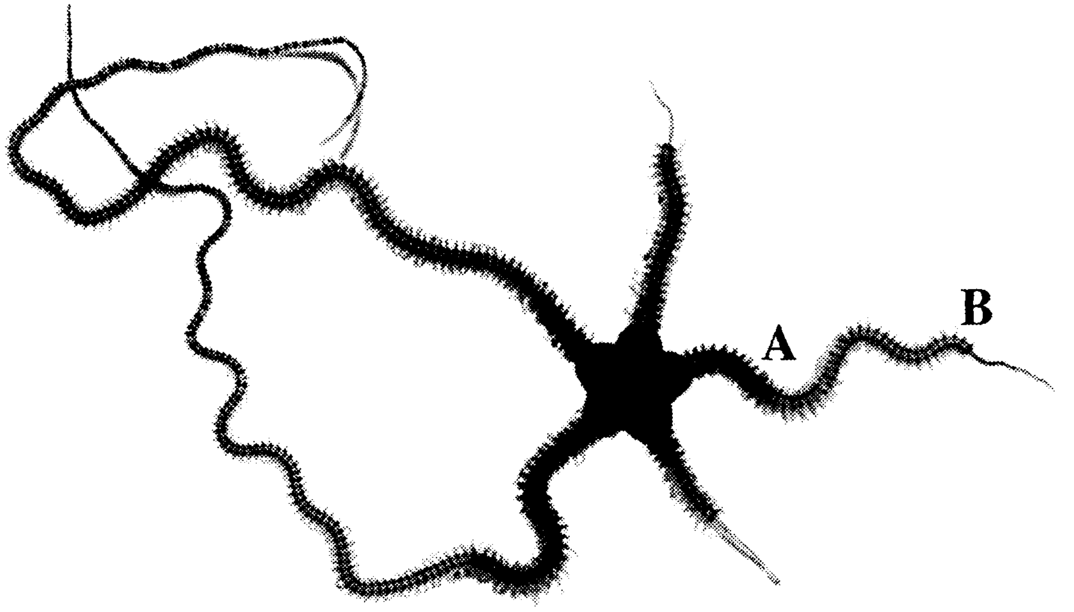

Fig. 2. *Amphiura filiformis* with arms regenerating. The scars are visible as colour change (A) and as a thinner portion of the arm (B).

defined as the total number of scars per individual brittle-star divided by its number of intact arms, *i.e.*, not recently broken. As a comparison with other literature data, regenerating arms as percentage of whole arms was also calculated for each population. The collected ophiuroid species were classified into three groups based on habitat and feeding strategy according to Warner (1982). The groups were as follows (Table 2): epibenthic carnivores and deposit-feeders, epibenthic suspension-feeders, and infaunal suspension and deposit-feeders. It should be pointed out that overlaps in feeding strategies occur, for example *Ophiocomina nigra* was here classified as a suspension feeder but may also be carnivorous and deposit feeding (Fell, 1966) and *Amphiura filiformis* is both a suspension and deposit feeder, while *A. chiajei* is only a deposit feeder (Woodley, 1975).

Ash-free dry weight (AFDW) and nitrogen (N) contents were analysed on homogenated whole arms from six individuals of each species. After freeze drying, parts of the homogenate was either burnt at 450°C for AFDW, or analysed with a Carlo Erba NA 1500 C/N analyser for N.

2.3. STATISTICS

Species for examination of regeneration frequency were randomly collected with respect to number of scars. Comparison of regeneration frequencies between groups (based on habitat and feeding strategy) of brittle-stars in the northern Kattegat-eastern Skagerrak was performed by using a factorial ANOVA. Group was considered as fixed factor and species as nested factor; factor group was tested over the nested factor mean square and the dependent variable was scar per arm. Since these variances were approximately equal to the mean, and zero values (individuals without scars) were included, data were transformed by $(x+1)^{1/2}$ (Sokal & Rohlf, 1995). One-way ANOVA was used in comparing data on mean number of scars per arm between brittle-star species in the northern Adriatic, and for comparisons between sites within the northern Adriatic (*Ophiothrix quinquemaculata*) and those in the northern Kattegat-eastern Skagerrak (*Amphiura filiformis* and *A. chiajei*). One-way ANOVA was used in comparing AFDW and N contents of arms of different species. The dependent variables, AFDW and N, were arcsine transformed as recommended for proportions (Sokal & Rohlf, 1995). Post-hoc comparisons were performed using Student-Newman Keul's test (SNK-test) (Sokal & Rohlf, 1995). All data were tested for presence of gross heterogeneity of variances with Cochran's C test (α=0.05) (Snedecor & Cochran, 1989) and balanced in order to get equal cell sizes.

Correlations between oral widths and mean number of scars per arm were performed for the separate populations of all species. Trends were considered significant with α=0.05 for the product-moment correlation coefficient, r (Sokal & Rohlf, 1995).

TABLE 2
Means of oral width, mean number of scars per arm (standard deviation in brackets) and mean number of scars in each position; n=number of individuals.

site	species	n	oral width (mm)		scars per arm		proximal part scars	middle part scars	distal part scars
northern Adriatic Sea									
	Epibenthic carnivores and deposit feeders								
A	*Ophiura ophiura*	16	11.3	(1.6)	0.30	(0.34)	0.00	0.00	0.53
B	*Ophioderma longicaudum*	6	8.4	(1.5)	0.13	(0.24)	0.00	0.00	0.33
C	*O. longicaudum*	131	9.9	(1.1)	0.40	(0.31)	0.04	0.05	0.72
	Epibenthic suspension feeders								
A	*Ophiothrix quinquemaculata*	33	4.5	(1.0)	0.39	(0.33)	0.05	0.23	0.48
B	*O. quinquemaculata*	37	3.0	(0.9)	0.22	(0.31)	0.00	0.05	0.41
D	*O. quinquemaculata*	37	4.3	(0.8)	0.47	(0.31)	0.09	0.28	0.47
northern Kattegat-eastern Skagerrak									
	Epibenthic carnivores and deposit feeders								
H	*Ophiura albida*	20	5.4	(1.1)	0.13	(0.21)	0.00	0.13	0.18
H	*O. ophiura*	8	8.3	(1.7)	0.24	(0.31)	0.00	0.18	0.32
	Epibenthic suspension feeders								
H	*Ophiothrix fragilis*	35	7.4	(1.4)	0.46	(0.35)	0.13	0.07	0.58
I	*Ophiocomina nigra*	36	5.4	(0.8)	0.19	(0.26)	0.06	0.07	0.32
	Infaunal suspension and deposit feeders								
G	*Amphiura chiajei*	41	3.0	(0.4)	0.57	(0.41)	0.15	0.16	0.52
E	*A. chiajei*	40	2.8	(0.2)	0.68	(0.36)	0.16	0.28	0.46
K	*A. chiajei*	40	2.6	(0.4)	0.53	(0.44)	0.12	0.26	0.39
E	*A. filiformis*	7	2.0	(0.2)	0.71	(0.37)	0.36	0.31	0.33
F	*A. filiformis*	39	2.3	(0.2)	0.57	(0.31)	0.07	0.27	0.56
K	*A. filiformis*	38	2.4	(0.3)	0.75	(0.32)	0.13	0.35	0.51
J	*A. filiformis*	38	2.5	(0.2)	1.06	(0.30)	0.19	0.53	0.32

3. RESULTS

Number of scars per arm, their position and oral width for the ophiuroids examined are presented in Table 2. Differences in mean number of scars per arm were observed among the ophiuroid groups within the northern Kattegat-eastern Skagerrak (Table 3). Post-hoc comparisons showed infaunal suspension and deposit feeding ophiuroids to have significantly more scars per arm than the epibenthic carnivorous and deposit feeding and the epibenthic suspension feeding groups (SNK-test $P<0.05$). No difference was found between the epibenthic carnivorous and deposit feeding group and the epibenthic suspension feeding group (SNK-test $P>0.05$). In the northern Adriatic only three species of ophiuroids, all epibenthic, were found in significant numbers and no statistical comparison could be made between ophiuroid groups. No difference was found in regeneration frequencies between *Ophiothrix quinquemaculata*, *Ophiura ophiura* and *Ophioderma longicaudum* (Table 4). Comparison between the epibenthic ophiuroids in the northern Adriatic Sea and those in the northern Kattegat-eastern Skagerrak showed rather similar regeneration frequencies, 0.1 to 0.5 (Table 2).

Proportionally more scars on the arms of the infaunal suspension and deposit feeding group from the northern Kattegat-eastern Skagerrak occurred on the proximal and middle parts of the arms relative to the

TABLE 3
Factorial ANOVA with group (species groups, depending on habitat and feeding strategy) of northern Kattegat-eastern Skagerrak as main effect, species (within groups) as nested factor and mean number of scar per arm as dependent variable (*: $P<0.05$).

source	df	sum of squares	mean square	F-value	P-value	error term
group	2	0.595	0.298	11.283	0.040*	species (group)
species (group)	3	0.079	0.026	1.392	0.258	residual
residual	42	0.796	0.019			

TABLE 4

One-factor ANOVA with species of northern Adriatic Sea as main factor and mean number of scar per arm as dependent variable (n.s: not significant).

source	*df*	*sum of squares*	*mean square*	*F-value*	*P-value*
species	2	0.054	0.027	0.304	0.739 n.s
residual	45	4.008	0.089		

other groups, which mainly had scars on the distal parts of the arms (Table 2).

Ophiothrix quinquemaculata in the northern Adriatic and *A. filiformis* and *Amphiura chiajei* in the northern Kattegat-eastern Skagerrak were each found at three sites, allowing statistical comparisons for each of these species between sites. ANOVA showed a difference in scars per arm between sites for *Ophiothrix quinquemaculata* (Table 5a, site b differed from d, SNK-test P<0.05). *Amphiura filiformis* also showed significant differences between sites (Table 5b, all sites differ from each other, P<0.05). No difference between sites was found for *Amphiura chiajei* (Table 5c).

Trend analyses showed positive correlations between oral width and scar per arm for 2 out of 6 populations in the northern Adriatic and 4 out of 11 populations in the northern Kattegat-eastern Skagerrak (Table 6).

Ash-free dry weight and nitrogen contents measured in arms of six species from the northern Kattegat-eastern Skagerrak showed a difference between

TABLE 6

Correlations between oral width and mean number of scars per arm; n: number of individuals; r: product-moment correlation coefficient; n.s=not significant; *=p<0.05.

site	*species*	*n*	*r*	*Sign.*
northern Adriatic Sea				
A	*Ophiura ophiura*	16	0.38	n.s
B	*Ophioderma longicaudum*	6	0.58	n.s
C	*O. longicaudum*	131	0.37	*
A	*Ophiothrix quinquemaculata*	33	0.16	n.s
B	*O. quinquemaculata*	37	0.18	n.s
D	*O. quinquemaculata*	37	0.51	*
northern Kattegat-eastern Skagerrak				
H	*Ophiura ophiura*	20	0.19	n.s
H	*O. albida*	8	0.12	n.s
H	*Ophiothrix fragilis*	35	0.35	*
I	*Ophiocomina nigra*	36	0.15	n.s
E	*A. filiformis*	7	0.26	n.s
F	*A. filiformis*	39	0.18	n.s
K	*A. filiformis*	38	0.36	*
J	*A. filiformis*	38	0.08	n.s
G	*A. chiajei*	41	0.53	*
E	*A. chiajei*	40	0.03	n.s
K	*A. chiajei*	40	0.56	*

TABLE 5

One-factor ANOVA with site as main factor (*: P<0.05, ***: P<0.001, n.s: not significant).

source	*df*	*sum of squares*	*mean square*	*F-Value*	*P-Value*
a. Dependent: scar/arm of *Ophiothrix quinquemaculata*					
site	2	0.628	0.314	3.224	0.0441 *
residual	96	9.348	0.097		
b. Dependent: scar/arm of *Amphiura filiformis*					
site	2	3.745	1.873	19.547	0.0001 ***
residual	96	9.197	0.096		
c. Dependent: scar/arm of *Amphiura chiajei*					
site	2	0.409	0.204	1.253	0.2902 n.s
residual	96	15.645	0.163		

species (Fig. 3; Table 7). Highest concentrations of AFDW and N were found in *Amphiura filiformis* (23 and 2.5%, respectively), intermediate in *A. chiajei, Ophiocomina nigra* and *Ophiothrix fragilis* (20, 2.1%), lower in *Ophiura ophiura* (14, 1.6%) and lowest in *O. albida* (9 and 0.8%). Significant differences were found between these species or groups for both AFDW and N as indicated above (SNK-test P<0.05).

4. DISCUSSION

Different life habits of ophiuroid species help them to cope with their exposure to predators. By burrowing into the soft-bottom sediment brittle-stars (Amphiuridae) expose only parts of their arms to predators (Woodley, 1975). *Ophiura ophiura* and *O. albida* live on the sediment surface or may burrow a few millimetres into the sediment, whereas species such as *Ophiothrix fragilis, O. quinquemaculata* and *Ophiocomina nigra* live in crevices and hollows, but also in the open on hard substrates such as boulders, rocks, gravel, and shell (Fell, 1966; Broom, 1975; Wilson *et al.*, 1977; Aronson, 1989). Aggregation, large size,

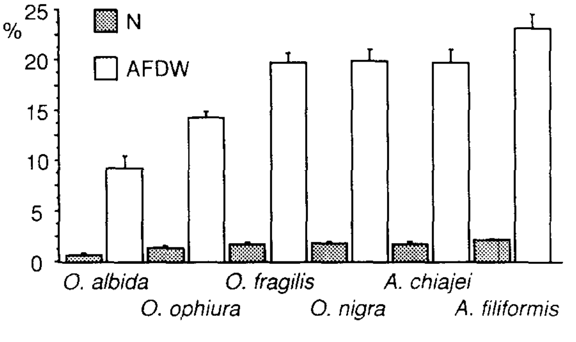

Fig. 3. Mean ash-free dry weight (AFDW), open bars, and nitrogen (N), filled bars, in percentage of dry-weight in arms of six brittle-star species from the eastern Skagerrak. Error bars are standard deviation.

TABLE 7

One-factor ANOVA with species of brittle-stars in the eastern Skagerrak as main factor (***: P<0.001).

source	*df*	*sum of squares*	*mean square*	*F-value*	*P-value*
a. Dependent: arcsine AFDW content of arms					
Species	5	0.077	0.015	110.2	0.0001 ***
Residual	28	0.0044	0.00014		
b. Dependent: arcsine N content of arms					
Species	5	0.001	0.00021	48.5	0.0001 ***
Residual	28	0.00012	0.00000043		

palatability, armour, spines and escaping behaviour are also features that may reduce lethal as well as sublethal predation. Below, we discuss the findings of frequently found arm scars in ophiuroids in relation to what is known about their biology and ecology. The wide-spread occurrence of ophiuroid arm regeneration both in European and South American waters is summarized in Table 8.

4.1. ARM REGENERATION IN DIFFERENT SPECIES

Age may explain differences in injury frequency since the possibility of receiving a scar increase with time. Populations of adult brittle-stars are often composed of one large, inseparable size group and a few small ones. Recent studies suggest long life spans (>5 years) for *Ophiothrix fragilis* (Gage, 1990), *Amphiura filiformis* (O'Connor *et al.*, 1983; Duineveld & Van Noort, 1986), *A. chiajei* (Munday & Keegan, 1992), *Ophiura ophiura* and *O. albida* (Dahm, 1993). brittle-star size measured as oral width or disk diameter is positively correlated with age during the first years (Gage, 1990). A positive correlation between oral width and number of scars per arm was found for 2 out of 6 populations in the northern Adriatic Sea and 4 out of 11 populations in the northern Kattegat-eastern Skagerrak. Age differences may therefore not be the only explanation for differences in arm scars between species.

As arm regeneration rate varies between species, arm deficiencies do not correspond directly to injury rates (Sides, 1987). Regeneration is also likely to be food and temperature dependent. Available data on arm regeneration rates are for *Ophiura ophiura*: 25 $mm \cdot y^{-1}$ (Hyman, 1955), *Ophiothrix fragilis*: 17 $mm \cdot y^{-1}$ (Hyman, 1955), *Amphiura filiformis*: 65 to 104 $mm \cdot y^{-1}$ (Salzwedel, 1974; Nilsson & Sköld, in press) *A. chiajei*: 9.4 $mm \cdot y^{-1}$ (M. Sköld & J. Gunnarson, in prep.). However, since the infaunal suspension and deposit feeding group (*Amphiura filiformis* and *A. chiajei*) in this study consisted of both the fastest and slowest arm-regenerating species in the above comparison, differences in arm-scar frequency between brittle-star groups do not seem to be explained by differences in regeneration rates only.

As Aronson (1989) points out for *Ophiothrix fragilis* and *Ophiocomina nigra* beds around the British Isles, the virtual absence of predators may explain a low predation intensity and a low occurrence of sublethal damage to brittle-star arms. Ophiuroids are generally attacked at the distal part of the arms and inwards, suggesting that regenerating arms in brittle-star populations indicate the frequency of predator-prey encounters (Aronson, 1989). Aronson's investigation compares monospecific brittle-star beds on pebble-sandy or silt-substratum (600-2000 $ind \cdot m^{-2}$) to rocky reefs with lower densities (~13 $ind \cdot m^{-2}$). Epibenthic brittle-star beds of those higher densities were not observed in this study; *Ophiothrix fragilis* and *Ophiocomina nigra* were found together on rocky reefs in the eastern Skagerrak in densities visually estimated to be <100 $ind \cdot m^{-2}$. Proportions of *Ophiothrix fragilis* regenerating one arm or more in the present study compared with Aronson's (1989) rocky-reef study in the British Isles give similar high values, 81 and 92%, respectively. For *Ophiocomina nigra*, the proportion of individuals regenerating one arm or more was 50% in the present study, which is similar to Aronson's low-predation *Ophiocomina* beds of 30-54%.

The lower injury frequency found in the epibenthic brittle-stars in the northern Kattegat-eastern Skagerrak than in the infaunal brittle-stars could be due to differences in predation intensity. This, however, is not likely since all three groups of brittle-stars existed within meters of each other in some places. Ophiuroid predators such as crustaceans (*Pagurus bernhardus*, *Liocarcinus depurator* and *Cancer pagurus*) and fish (labrids *Labrus bergylta*, *Labrus mixtus*, plaice *Pleuronectes platessa*, dab *Limanda limanda* and dragonet *Callionymus lyra*) (Warner, 1971; Duineveld & Van Noort, 1986; Aronson, 1989) were observed in the area (pers. obs.) and had the potential to exploit all three groups of brittle-stars in the eastern Skagerrak. Other explanations for the observed differences may be avoidance by predators of certain ophiuroid species, or preference by the predators for some ophiuroid species. In some invertebrates, production or accumulation of toxic substances acts as a defence mechanism. Within the Asteroidea, Echinoidea and Holothuroidea toxic species are common, but such toxicity in Ophiuroidea is suggested to be uncommon (Alender & Russel, 1966; McClintock, 1989). Yet, *Ophiocomina nigra* secretes a sulphated-acid mucopolysacharide which, coupled with active escape movements, is suggested to serve as an efficient predatory defence mechanism (Fontaine, 1964). Thus, the toxicity of *Ophiocomina nigra* may explain why that species had one of the lowest arm-scar frequencies in this study (Table 2). In addition, *Ophiothrix fragilis*, *O. quinquemaculata* and *Ophiocomina nigra* may be protected from some predators by the presence of long glassy (hyaline calcite) arm spines, as suggested by Aronson (1988) for *Ophiothrix oerstedi*. Spine development and degree

TABLE 8
Percentages of regenerating arms not recently broken; from different investigations, n=number of individuals examined.

species	*n*	*percentage of arms regenerating*	*site*	*reference*
Epibenthic carnivores and deposit feeders				
Ophiura albida	70	14	W Scotland	Emson & Wilkie, 1980
O. albida	20	13	Skagerrak[H]	This study
O. ophiura	65	62	W Scotland	Emson & Wilkie, 1980
O. ophiura	16	27	N Adriatic Sea[A]	This study
O. ophiura	8	24	E Skagerrak[H]	This study
Ophioderma longicaudum	140	40	N Adriatic Sea[C]	This study
Epibenthic suspension feeders				
Amphipholis squamata	2380	24	N France	Alva & Jangoux, 1990
A. squamata	60	44	W Scotland	Emson & Wilkie, 1980
Ophiocomina nigra	68	93	W Scotland	Emson & Wilkie, 1980
O. nigra	70	66	W Scotland	Emson & Wilkie, 1980
O. nigra	60	44	W Scotland	Emson & Wilkie, 1980
O. nigra	60	91	W Scotland	Emson & Wilkie, 1980
O. nigra	36	19	E Skagerrak[I]	This study
Ophiothrix fragilis	70	91	W Scotland	Emson & Wilkie, 1980
O. fragilis	37	46	E Skagerrak[H]	This study
O. quinquemaculata	32	39	N Adriatic Sea[A]	This study
O. quinquemaculata	37	22	N Adriatic Sea[B]	This study
O. quinquemaculata	37	47	N Adriatic Sea[D]	This study
Ophiopholis aculeata	65	46	W Scotland	Emson & Wilkie, 1980
Infaunal suspension and deposit feeders				
Amphiura filiformis	60	94	W Scotland	Emson & Wilkie, 1980
A. filiformis	100	93	E Scotland	Buchanan, 1964
A. filiformis	130	92	W Ireland	Bowmer & Keegan, 1983
A. filiformis	46	57	N Kattegat[F]	This study
A. filiformis	39	106[a]	E Skagerrak[J]	This study
A. filiformis	38	75	E Skagerrak[K]	This study
A. chiajei	60	99	W Scotland	Emson & Wilkie, 1980
A. chiajei	100	93	E Scotland	Buchanan, 1964
A. chiajei	107	84	W Ireland	Munday, 1993
A. chiajei	40	68	N Kattegat[E]	This study
A. chiajei	40	57	N Kattegat[G]	This study
A. chiajei	41	53	E Skagerrak[K]	This study
Other Ophiuroids				
Ophiactis asperula	23	80	Beagle Channel	Rosenberg, unpublished
Ophiuroglypha lymani	26	37	Beagle Channel	Rosenberg, unpublished
O. lymani	47	45	Beagle Channel	Rosenberg, unpublished
O. lymani	25	52	Beagle Channel	Rosenberg, unpublished
Ophioscolex nutrix	33	54	Beagle Channel	Rosenberg, unpublished

[a] More than 1 scar per arm visible makes values above 100 % possible.
[A, B, C, D, E, F, G, H, I, J] and [K] refer to sampling sites from Table 1.

of calcification vary between congeneric species of *Ophiocoma*. This has consequences for their behaviour in that the spinier species are comparatively more exposed in the open at night than those with shorter spines (Sides & Woodley, 1985).

AFDW and N in the arms of six species from the northern Kattegat-eastern Skagerrak were highest in *Amphiura filiformis* followed by *A. chiajei*, *Ophiocomina nigra* and *Ophiothrix fragilis* (Fig. 3). In comparison with AFDW contents in polychaetes (about 70% AFDW, Rumohr *et al.*, 1987), the ophiuroids in this study had low nutritious values. However, it was evident that glassy arm spines or a high degree of arm calcification influence the organic content of the arms in different species and possibly the palatability of the brittle-stars. The comparatively higher AFDW and N in *Amphiura filiformis* and *A. chiajei* suggest that these species may be preferred as food by demersal predators. This suggestion agrees with the findings of more arm scars on *Amphiura filiformis* and *A. chiajei* than in other species, and that arms of these brittle-stars are a significant food source for some demersal fish species and crustaceans, *e.g.*, haddock *Melanogrammus aeglefinus*, dab *Limanda limanda*, American plaice *Hippoglossoides platessoides* and Norway lobster *Nephrops norvegicus* (Duineveld & Van Noort, 1986; Baden *et al.*, 1990; Mattson, 1992; Pihl, 1994).

The breakage plane at autotomy of arms in ophiuroids takes place at an intersegmental joint proximal to the stimulus (Wilkie, 1978). The observed difference of more scars per arm on the proximal parts of *Amphiura* spp. as compared to other brittle-stars may be due to the process of autotomy of these species. Breakage occurs up to eight arm joints away from a stimulated 'attacked' joint of *Amphiura filiformis* and *A. chiajei*, whereas in *Ophiothrix fragilis* and *Ophiocomina nigra* breakage occurs one to three arm joints away from the stimulus (Wilkie, 1978). Consequently, findings of more proximal scars may lead to underestimates of arm scars in *Amphiura* spp., since previous distal scars may not be visible. Actual scars per arm of the infaunal amphiurid group were thus likely to be even higher than shown in the present study.

For visual predators it may be easier to spot epibenthic ophiuroids, which are motile and push themselves forward by means of their arms, than infaunal amphiurids (Fell, 1966). For example, efficient escape by *Ophiocomina nigra* can explain the reduced predation success on this species by the sea-star *Luidia ciliaris* (Brun, 1972). The size of epibenthic brittle-stars may also alter predatory efficiency or preference, *e.g.*, American plaice *Hippoglossoides platessoides* eat small (4-10 mm disk size) *Ophiura sarsi*, but rarely larger specimens (Packer *et al.*, 1994). Thus juveniles and smaller specimens of some species may be more prone to lethal predation, while larger brittle-stars may suffer sublethal damage. In the Kattegat, disks of the relatively small *Ophiura albida* are often found in the stomachs of *Hippoglossoides platessoides* and dab *Limanda limanda* in contrast to only arm fragments of other ophiuroids (Pihl, 1994; Pihl, pers. comm.). In addition to the low nutritious value of *Ophiura albida* arms, this lethal predation may explain the low frequency of arm-scars found on this species (Table 8).

Mean numbers of scars per arm in epibenthic ophiuroids in the northern Adriatic Sea were comparable to those of the northern Kattegat-eastern Skagerrak. These areas show some similarities such as low tidal amplitude, seasonal stratification with oceanic bottom-water salinities and co-occurring benthic species. The main differences seem to be the wide-spread presence, and in many areas high density of epibenthic suspension-feeding communities, and low abundance of major demersal fish predators on these communities in the northern Adriatic Sea (Fedra *et al.*, 1976). In the Kattegat-Skagerrak the infauna predominates and the epifaunal and nektonic predator communities are probably comparatively richer in the coastal areas (Pearson & Rosenberg, 1992; Pihl, 1994). Quantitative information on predatory fish and feeding behaviour is scarce for the northern Adriatic, but small benthic fish (Gobiidae and Blenniidae) are present (Fedra, 1977; pers. obs.). Whether those small fish nip the arms of *Ophiothrix quinquemaculata* is unknown. Known predators of *O. quinquemaculata* are crabs (Wurzian, 1977) and hermit crabs (Stachowitsch, 1979). Low abundance of predators might be an important factor explaining the overall high density and comparatively low sublethal predation of *O. quinquemaculata* found in this investigation (see Table 8).

4.2. SPATIAL VARIATION IN REGENERATION PATTERNS

Significant spatial variation in mean number of scars per arm was shown for *Amphiura filiformis* in the northern Kattegat-eastern Skagerrak and for *Ophiothrix quinquemaculata* in the northern Adriatic. On a larger scale, comparing the regeneration frequencies in these species with studies of Buchanan (1964) and Emson & Wilkie (1980) from Scottish waters, it appears that epibenthic suspension feeding species there generally have more arms regenerating than species from the northern Adriatic Sea and the northern Kattegat-eastern Skagerrak (Table 8). In Scotland, infaunal amphiurids, especially *Amphiura chiajei*, also seem to be more frequently injured than amphiurids from the northern Kattegat-eastern Skagerrak. It is difficult to draw any conclusion from these comparisons as methods of collection, densities and ages of populations may differ (*e.g.*, long-time predator-prey encounter rates should be reflected in higher percentages of regenerating arms). Spatial patterns on small scales, as shown in the present study, and temporal variation in predation may be important as well. Nevertheless, it seems that epifaunal suspension feeders may be more frequently injured around the British Isles than in the northern Kattegat-eastern Skagerrak and the northern Adriatic Sea (Table 8).

Mechanical damage of ophiuroid arms by trawling or storms was not investigated in the present study. However, storms do not appear to cause arm damage in brittle-star populations on tropical reefs, and predation is considered to be the prime source of arm injuries (Aronson, 1991). In areas sampled in the present study, demersal trawling occurs at the offshore sites of the Kattegat and beam trawling in the northern Adriatic, but trawling is not allowed in the coastal areas of the Skagerrak. A comparison of the sites in the northern Kattegat that may be trawled occasionally (sites E, F and G) with those not trawled in the eastern Skagerrak (K and J) showed no significant difference in mean arm-scar numbers for *Amphiura chiajei*, and more scars per arm were found in *A. filiformis* at the non-trawled site. This suggests that trawling is not a major cause of arm scars, but it may reduce the number of predators and their possible effects on the brittle-stars.

4.3. CONCLUSION

The frequent nipping of brittle-star arms, visible as arm scars, suggests that this has an energetic significance. Sublethal predation were found to be more frequent in infaunal than in epibenthic species. Further, infaunal species, especially *Amphiura filiformis*, was found to have the most nutritious arms in terms of organic matter and nitrogen content compared to epibenthic species. This suggest that this sublethal predation is selective. *Amphiura filiformis* and *A. chiajei* are often found together and are among the dominant infauna at most depths between 15 and 100 m in the Kattegat, the Skagerrak, the North Sea and Galway Bay (Ireland) (Petersen, 1915; O'Connor *et al.*, 1983; Pearson *et al.*, 1985; Duineveld *et al.*, 1987; Rosenberg *et al.*, 1987). As remains of *Amphiura filiformis* and *A. chiajei* make up as much as 60% of the stomach AFDW contents in dab *Limanda limanda* and 10-60% of the stomach wet-weight contents in Norway lobster *Nephrops norvegicus*, American plaice *Hippoglossoides platessoides* and haddock *Melanogrammus aeglefinus* (Duineveld & Van Noort, 1986; Baden *et al.*, 1990; Mattson, 1992; Pihl, 1994), these energy pathways must be of significant importance for these predators where they co-occur with these brittle-stars.

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