

Predation, physical disturbance, and sublethal arm damage in ophiuroids: a Jurassic-Recent comparison

Richard B. Aronson

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA

ABSTRACT: The proportion of ophiuroids with sublethal arm damage (regenerating arms) was censused over 4 yr (1987 to 1990) in a lagoonal population of *Ophioderma brevispinum* (Say) (Ophiodermatidae) at Belize, and over 3 yr (1988 to 1990) in back-reef populations of *O. appressum* (Say) at Belize and Jamaica. The Jamaican population was sampled in sheltered and wave-exposed areas. Over the study period, the frequency of injuries within populations did not differ significantly, nor did the 2 *O. appressum* populations show consistent differences. Arm injuries were more common in the 3 living populations (30 to 74 % injured) than in a Lower Jurassic population composed of 2 ophiodermatid species (0 % injured) from a similar warm-water habitat. The incidence of sublethal disk damage was negligible in all cases. Hurricane-generated rubble movement did not cause any detectable damage to either the protected or exposed Jamaican *O. appressum* subpopulations. Predation is the primary source of arm injuries in living *Ophioderma* spp. This study supports the hypothesis that predation on ophiuroids increased when durophagous teleostean fishes and decapod crustaceans diversified in the late Mesozoic.

INTRODUCTION

The late Mesozoic diversification of skeleton-crushing fish and crustaceans increased predation pressure in shallow water, judging from the increased defensive architecture of prey and from changes in prey bathymetric distributions (Meyer & Macurda 1977, Vermeij 1977, 1983, 1987, Ward 1981, Aronson & Sues 1987, Aronson 1989a). Unfortunately, many of these late Mesozoic predators, including teleosts, neoselachian sharks and decapods, preserve poorly compared to their more heavily skeletonized prey. Therefore, while we can detect new functional grades of predators and their presumed evolutionary effects on prey, we will never know how abundant novel predators were in ancient communities.

How then can we detect historical changes in predation? One direct approach is to census sublethal damage in fossil prey. Vermeij et al. (1981) and Vermeij (1987) showed that the incidence of repaired shell breaks in gastropods increased beginning in the Late Jurassic, despite the evolution of architectural defenses (or because of the evolution of defenses, if fewer

attacks were lethal as a result). An obvious difficulty is determining whether particular classes of injury were caused by predators or by physical agents such as storms.

Furthermore, Schoener (1979) pointed out that, even when injuries are attributable to predators, sublethal damage data are not without their complications. There can actually be an inverse relationship between predator-prey encounter rates and the frequency of sublethal damage. Such a situation will arise when the preponderance of encounters in higher-predation communities are lethal for the prey (see also Vermeij 1982).

Previously, I (Aronson 1987) used sublethal damage data to test for increasing predation on ophiuroids since the Jurassic, a predicted outcome of the 'Mesozoic marine revolution' (Vermeij 1977). I compared the frequency of regenerating arms between *Ophioderma brevispinum* (Say) (Ophiodermatidae) living in a mangrove creek in Belize, and fossil confamilials from the Lower Jurassic of Great Britain. I argued that the observed higher frequency of regenerating arms in the Recent population reflected a higher encounter rate with predators. This interpretation was not confounded

by the problem of increasing predator efficiency during the Mesozoic, because increasing efficiency by itself should have decreased injury levels. Paleozoic and early Mesozoic predators of ophiuroids, which probably included other ophiuroids, asteroids, and polychaete worms, were less efficient than modern, durophagous teleosts and decapods, yet the frequency of sublethal damage increased (Aronson 1987, 1989b).

That comparison (Aronson 1987) was based only on one living *Ophioderma* population in one habitat. Here, I extend that study with time-series data on sublethal damage for 2 species of *Ophioderma* at several Caribbean back-reef sites. I also explore the importance of severe physical disturbances (hurricanes) as agents of sublethal arm injury.

STUDY AREAS AND SPECIES

Two species of ophiidermatid brittlestars occur in the Lower Jurassic (Pliensbachian) 'starfish bed' in Dorset, southwest England (51° 15' N, 3° 15' W): *Palaeocoma milleri* (Philippis) and ?*Ophioderma tenuibrachiata* Forbes (Hess 1960, 1964). These well-preserved ophiuroids are found singly or in groups of up to 5 individuals. They were buried in life position, or at most transported short distances (Goldring & Stephenson 1972, Ensom 1984). *P. milleri* and ?*O. tenuibrachiata* lived in a warm, shallow-water setting (Arkell 1956). Aronson (1987) quantified the occurrence of sublethal damage in 60 specimens from the British Museum of Natural History (London, UK), the Dorset County Museum (Dorchester, UK), and the Museum of Comparative Zoology (Cambridge, Massachusetts, USA). To this data set I add 4 specimens of *P. milleri* from the Springer Collection of the Smithsonian Institution's National Museum of Natural History (Washington, D.C., USA).

I collected *Ophioderma brevispinum* (Say) from Elbow Cay, a rhomboid shoal within the Belizean Barrier Reef lagoon (16° 42' N, 88° 10' W). Elbow Cay is an atoll-like island, with a central, sediment-covered, water-filled depression surrounded by a submerged rim of coral limestone. Most of the rim is topped by red mangrove *Rhizophora mangle* Linnaeus, but part of the western, leeward edge forms a shallow, subtidal, sandy shoal (< 1 m depth). *O. brevispinum* is abundant under coral rubble and rhodoliths on this shoal, occurring singly or in groups of up to 5 or 6.

Ophioderma appressum (Say) is the most common *Ophioderma* species living under coral rubble in Caribbean back-reef habitats (Kissling & Taylor 1977, Lewis & Bray 1983, Hendler & Peck 1988). It is found singly or in groups that sometimes exceed 10 individuals, depending on the size of the rock under which they are

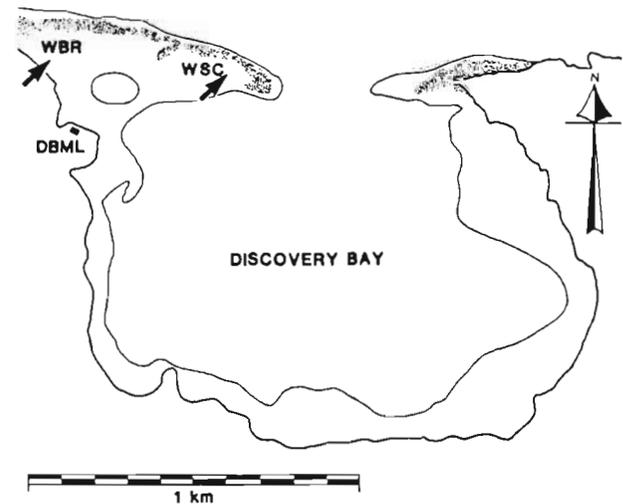


Fig. 1. Discovery Bay, Jamaica, showing locations of West Back Reef (WBR) and West of Ship Channel (WSC) sites and 5 m depth contour. DBML: Discovery Bay Marine Laboratory [adapted from Karlson (1988, Fig. 1)]

sheltering. In Belize this species was collected under plates of dead elkhorn coral *Acropora palmata* (Lamarck), behind the reef crest along Tobacco Reef, just north of South Water Cay (16° 50' N, 88° 06' W; 1 to 2 m depth). Collections were also made in *A. palmata* rubble at 2 sites in the back reef at Discovery Bay, Jamaica (18° 30' N, 77° 20' W; 1 to 2 m depth). These were designated West Back Reef (WBR) and West of Ship Channel (WSC; Fig. 1). WSC is more exposed to wave action than WBR (Wahle 1985).

Ophiuroids were sampled yearly from June 1987 to May 1990 at Elbow Cay; in December 1988, July 1989, and May 1990 at Tobacco Reef; and every few months from November 1988 to August 1990 at Discovery Bay. Sampling at Discovery Bay was initiated 2 mo after Hurricane Gilbert passed across Jamaica on 12 September 1988.

Recent *Ophioderma* species, including *O. brevispinum* and *O. appressum*, are benthic predators and/or detritivores (Reimer & Reimer, 1975, Hendler 1982). The short, appressed arm spines of the 2 fossil species suggest a similar feeding ecology (Goldring & Stephenson 1972).

MATERIALS AND METHODS

Living *Ophioderma brevispinum* and *O. appressum* were collected haphazardly by hand while snorkeling, and examined under a dissecting microscope. An arm was scored as regenerating if there was a discontinuous decline in its diameter, corresponding to a breakage point. Although few breakages occurred in collecting, arms that were broken but not yet regenerating

were not counted. Regenerating disk damage was also noted. Sample sizes varied from 50 to 100 individuals censused per visit (see Table 3). After examination, ophiuroids were released well away from the study sites.

The Jurassic ophiuroids were examined in a similar fashion. Many of the fossils lacked distal portions of their arms, probably an artifact of preservation. To eliminate the bias that post-mortem breakage would introduce, I noted where along the arm each repaired break was located in the living or fossil specimen. Each regeneration was scored as occurring on the proximal, middle, or distal ('tip') third of the arm, following Bowmer & Keegan (1983) and Aronson (1987).

The measure used to compare sublethal damage between times and populations was the proportion of individuals regenerating one or more arms. The proportion of arms regenerating was not calculated, because multiple arm injuries in an individual may not be statistically independent [see Aronson (1989b) for further statistical discussion]. The 95% confidence limits of each proportion, p , are calculated as $p \pm d$, where

$$d = t[p(1-p)/n]^{0.5};$$

t is the normal deviate (1.96 at the 95% level), and n is the sample size (Cochran 1963).

RESULTS

Between 46 and 57% of *Ophioderma brevispinum* at Elbow Cay (disk diameter range 3 to 13 mm), and between 30 and 74% of *O. appressum* at Tobacco Reef and Discovery Bay (4 to 18 mm) were regenerating one or more arms. The 95% confidence intervals for all arm injuries overlap among visits within sites. This is also true when injuries to the proximal two-thirds of the arm only are considered, and when injuries to the proximal one-third of the arm only are considered (Figs. 2 & 3). Although the proportions were generally greater at the WSC site than at WBR, this was not a consistent difference. Except for 2 sampling dates, the confidence intervals overlap (Fig. 3). With a few exceptions, the Tobacco Reef (Fig. 2B) and Discovery Bay (Fig. 3) results also overlap. The injury data revealed no consistent seasonal (Jamaica) or year-to-year (Belize) variations.

By contrast, among the fossil specimens, none of the 51 *Palaeocoma milleri* (4 to 19 mm), or 13 *Ophioderma tenuibrachiata* (7 to 9 mm) was regenerating arms. In no case does the 95% confidence interval for injuries in a living population include zero (Figs. 2 & 3). G -tests of independence with Williams' correction (Sokal & Rohlf 1981) revealed significant differences in frequency

between the 64 fossil specimens and each sample of the living populations for all arm injuries, for injuries to the proximal two-thirds of the arm only, and for injuries to the proximal one-third of the arm only ($df = 1$, $p < 0.005$ in all cases). Since many of the fossil specimens have broken arms, it is unlikely that the lack of regenerating arms represents a collecting bias.

On the other hand, comparisons of sublethal arm damage may be biased by differences in population age-structure. Within a population, younger (smaller) ophiuroids might have fewer regenerating arms simply because they have experienced fewer predatory attacks than older (larger) individuals. It is impossible to compare injuries between Jurassic and Recent ophiodermatids by age class because we cannot measure the growth rates of the 2 extinct species. The question of growth rates aside, one could argue that the ophiuroid size-frequency distributions are important in themselves because (1) confamilial brittlestars of similar size should be equally susceptible to particular modes of predation, or (2) attacks on smaller brittlestars are more

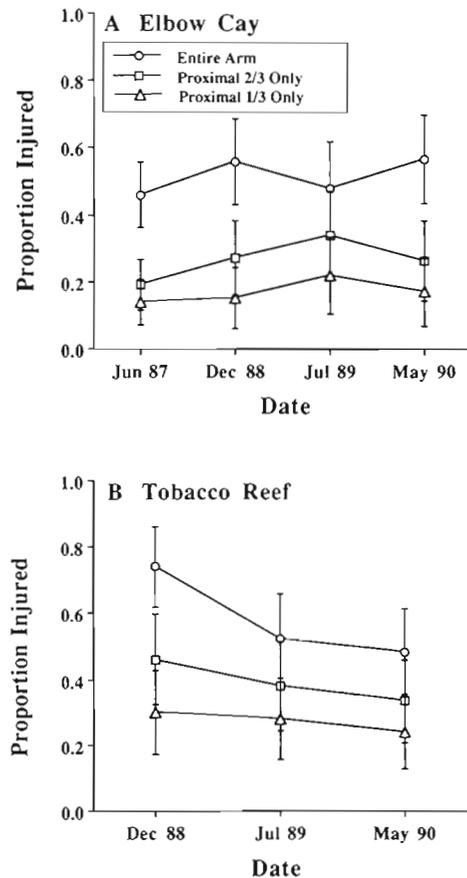


Fig. 2. *Ophioderma brevispinum*. Proportion of regenerating arms at (A) Elbow Cay and (B) Tobacco Reef through time. Three levels of arm injury are plotted. Error bars represent $\pm 95\%$ confidence intervals about proportions

often lethal, reducing the proportion of individuals sublethally injured compared to larger size classes.

Disk diameter explained essentially none of the variance observed in injury levels of Elbow Cay *Ophioderma brevispinum*, but it did explain between 50 and 83% of the variance in injury levels in the

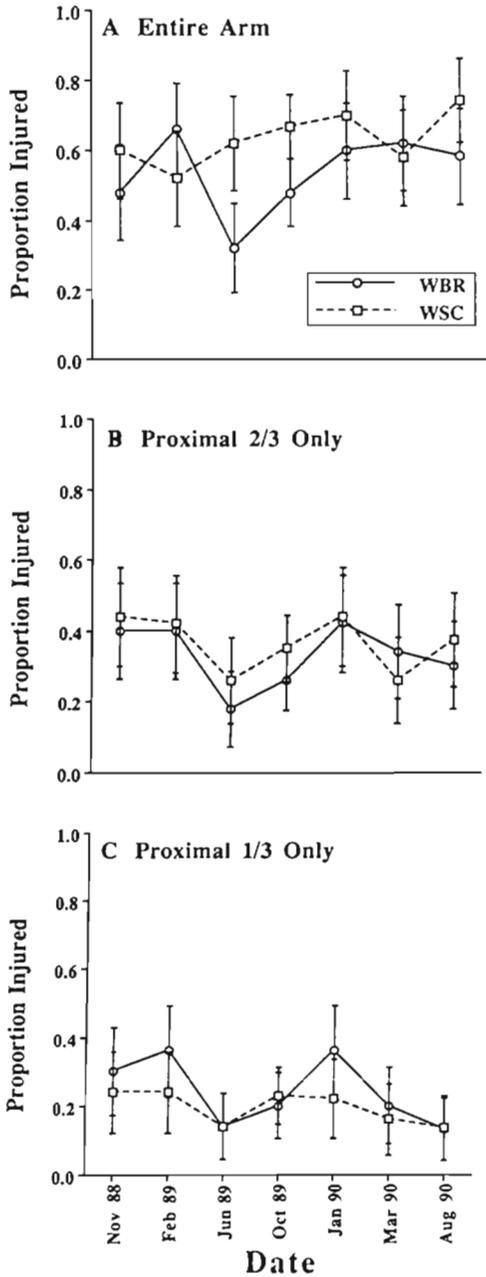


Fig. 3. *Ophioderma appressum*. Sublethal arm damage at 2 sites in Discovery Bay, Jamaica. (A) Proportion of individuals with one or more regenerating arms; (B) proportion with at least one injury to proximal two-thirds of an arm; (C) proportion with at least one injury to proximal third of an arm. Error bars as in Fig. 2

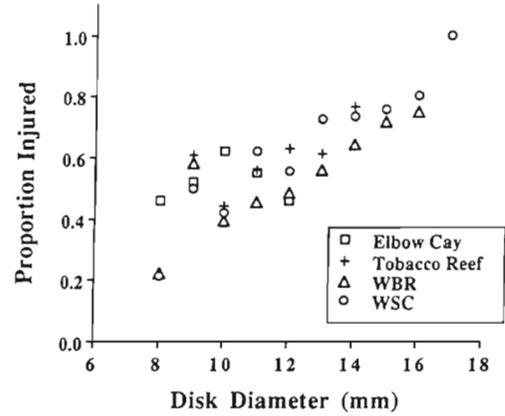


Fig. 4. *Ophioderma brevispinum* and *O. appressum*. Relationship between disk diameter and the proportion of ophiuroids with at least one sublethal arm injury at the 4 field sites. For each data point, n ≥ 10

Belizean and Jamaican *O. appressum* populations or subpopulations (Fig. 4, Table 1). The slope of the regression line was not significantly different from zero for the Tobacco Reef *O. appressum*, but it was nonzero for the ophiuroids at WBR and WSC. Although the distribution of disk diameters in the fossil sample (combining the 2 species) did not differ significantly from the size distribution of *O. brevispinum*, the fossil ophiuroids were significantly smaller than *O. appressum* (Table 2). Therefore, the higher injury levels observed in the Jamaican *O. appressum* samples, at least, may have been related to their larger size.

Sixty-one percent of the 62 fossils that were measured were 8 to 11 mm in disk diameter. In the living specimens, and considering only *Ophioderma appres-*

Table 1 *Ophioderma brevispinum* and *O. appressum*. Least-squares regressions of proportion of individuals injured (all injuries) on disk diameter for living populations. Data from all samples were combined for each population or subpopulation because of lack of seasonal or other temporal patterns. Proportions were arcsine-transformed (Sokal & Rohlf 1981), and only proportions based on ≥ 10 individuals were included in analysis. WBR: West Back Reef; WSC: West of Ship Channel. p: significance of slope

Population	Slope	Intercept	r ²	df	p
<i>O. brevispinum</i>					
Elbow Cay, Belize	0.004	0.770	0.008	3	> 0.50
<i>O. appressum</i>					
Tobacco Reef, Belize	0.042	0.414	0.499	4	> 0.10
WBR, Jamaica	0.054	0.168	0.738	7	< 0.01
WSC, Jamaica	0.087	-0.138	0.831	8	< 0.001

Table 2. Fossil and living ophiuroids. Disk diameters [means (SD)] of populations (or subpopulations) and results of Student's *t*-tests comparing each Recent population (all samples combined) to fossils. t_s : sample statistic of *t*-distribution

Population	Disk diameter (mm)	t_s	df	p
<i>Palaeocoma milleri</i> and ? <i>Ophioderma tenuibrachiata</i>				
Jurassic fossils	9.23 (2.76)			
<i>Ophioderma brevispinum</i>				
Elbow Cay, Belize	9.52 (1.58)	1.13	322	> 0.20
<i>Ophioderma appressum</i>				
Tobacco Reef, Belize	10.89 (2.29)	4.55	214	< 0.001
Jamaica: WBR	12.31 (1.99)	10.72	463	< 0.001
Jamaica: WSC	12.57 (2.39)	10.03	461	< 0.001

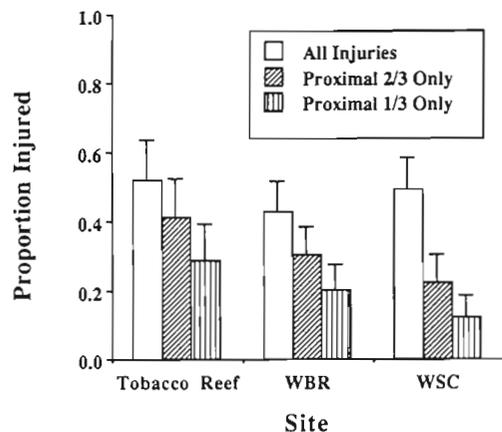


Fig. 5. *Ophioderma appressum*. Proportion of ophiuroids of 8 to 11 mm disk diameter with 3 classes of sublethal arm damage. Error bars represent upper limits of 95% confidence intervals about proportions. All samples were combined for each site. Sample sizes (number of individuals censused): Tobacco Reef, 73; WBR, 126; WSC, 106

Table 3. *Ophioderma* spp. Incidence of sublethal disk damage in living populations. Values are proportion injured, with the number of individuals censused (n) in parentheses. --: no data

Belize: <i>Ophioderma</i> spp.		
	<i>O. brevispinum</i>	<i>O. appressum</i>
Jun 1987	0.00 (100)	--
Dec 1988	0.00 (59)	0.00 (50)
Jul 1989	0.00 (50)	0.00 (50)
May 1990	0.00 (53)	0.02 (54)
Discovery Bay, Jamaica:		
	WBR	WSC
<i>Ophioderma appressum</i>		
Nov 1988	0.06 (50)	0.00 (50)
Feb 1989	0.00 (50)	0.04 (50)
Jun 1989	0.02 (50)	0.00 (50)
Oct 1989	0.02 (100)	0.01 (100)
Jan 1990	0.02 (50)	0.00 (50)
Mar 1990	0.04 (50)	0.00 (50)
Aug 1990	0.00 (53)	0.00 (51)

sum in the 8 to 11 mm range, the 95% confidence intervals about the injury levels still do not include zero (Fig. 5; Tobacco Reef data are included even though the regression equation had a slope not significantly different from zero). The zero injury level of the 62 measured fossil ophiuroids was still significantly lower than the frequency of *O. appressum* with any injury, the frequency with at least one injury to the proximal two-thirds of an arm, and the frequency with at least one injury to the proximal one-third of an arm at Tobacco Reef, WBR, and WSC (*G*-tests with Williams' correction; $df = 1$, $p < 0.005$ in all cases).

The living ophiuroid populations had a low incidence of damaged and regenerating disks (Table 3). The Jurassic specimens had no regenerating disk damage.

DISCUSSION

What are the relative contributions of predation and physical disturbance to sublethal arm injury in living *Ophioderma* populations? Like Hurricane Allen in 1980 (Woodley et al. 1981), Hurricane Gilbert had a severe destructive impact on the fore reef at Discovery Bay (Woodley 1989). However, although swells > 9 m high broke on the reef crest during Gilbert (J. D. Woodley pers. comm.), the storm had no discernible effect on ophiuroid species composition in the back reef (Aronson unpubl.). Arm injury data are not available for *O. appressum* from just before Hurricane Gilbert, yet 3 lines of evidence suggest that the 2 Discovery Bay subpopulations sustained no significant damage in the hurricane.

First, there was no monotonic decline in the frequency of regenerating arms within ophiuroid size classes at either WBR or WSC in the 23 mo following the storm. Such a decline would have been expected had Gilbert caused an immediate increase in arm injuries, which then gradually disappeared through

regeneration and was diluted by recruitment. In fact, injury frequency at WBR increased non-significantly from November 1988 to February 1989, declined in June 1989, increased monotonically until March 1990, and then declined slightly. Injury frequency at WSC fluctuated little during the same period. *Ophioderma appressum* can regenerate nearly 40% of the length of an arm within 3 mo in the laboratory (Sides 1981). Therefore, a steady decline in injuries would have been detectable during the course of sampling at Discovery Bay

Second, there was no significant change in the occurrence of regenerating arms in another ophiuroid, *Ophiothrix oerstedii* Lütken, at WBR from January 1987 to August 1990 (Aronson unpubl.). The latter species and *Ophioderma appressum* are equally unpalatable to predatory reef fish, relative to other Caribbean ophiuroid species (the high levels of sublethal damage indicate heavy predation pressure despite their relative unpalatability; Aronson 1988). The 2 species live under the same rubble, yet the arms of *Ophiothrix oerstedii* are considerably more fragile (Aronson 1988). If fragile *O. oerstedii* were not damaged significantly by Hurricane Gilbert, then it is doubtful that the sturdy *Ophioderma appressum* suffered damage.

Third, Sides (1981) found that 74% of *Ophioderma appressum* from WSC were regenerating arms in the late 1970s, before Hurricanes Allen and Gilbert. Prior to Allen, no hurricane had passed close to Jamaica for decades (Woodley 1989). The 95% confidence interval for the proportion recorded by Sides, 0.62 to 0.86 ($n = 54$, $d = 0.12$), overlaps the 1988 to 1990 confidence intervals for WSC, and overlaps or exceeds the confidence intervals for WBR in the present study.

If Hurricane Gilbert did not increase the proportion of sublethally damaged *Ophioderma appressum* at WBR or WSC, it is doubtful that these ophiuroids are damaged by normal, background levels of turbulence-induced rubble movement in back-reef environments. This conclusion is borne out by the lack of a consistent difference in injury occurrence between WBR and WSC, which differ in degree of wave exposure. However, generalizing to other ophiuroid species would be premature. Sides (1981, and in Woodley et al. 1981) observed increased arm damage to *Ophiocoma echinata* (Lamarck) following Hurricane Allen, although she reported her data as total arm length missing per individual and not as the proportion of injured individuals.

Vermeij's (1983) data suggest that storms do not increase the frequency of sublethal damage in tropical Pacific gastropods. Likewise, most arm injuries in back-reef *Ophioderma* are probably due to predation by fishes (primarily Labridae, Haemulidae, Tetraodontidae, and Diodontidae in the Caribbean) and crabs

(Portunidae) (Randall 1967, Sides 1981, Aronson & Harms 1985, Aronson 1988, 1989b, and unpubl.). The level of sublethal arm damage in *Ophiothrix oerstedii* correlated with predator activity when pristine back-reef sites were compared to a fish-free saltwater lake (Aronson 1987). The reef crest apparently protects *Ophioderma* (as well as *O. oerstedii*) from hurricane damage. Predation and physical disturbance caused negligible arm damage or none at all to the Lower Jurassic ophiodermatids.

While Aronson & Sues (1987) documented extremely low levels of arm damage in Paleozoic and early Mesozoic ophiuroid populations (<2% injured), the injury data presented here and those in Aronson (1987) are particularly important because they compare Jurassic and Recent confamilials of similar size from similar environments. The present study supports the conclusion that predation on ophiodermatid brittlestars increased after the Early Jurassic as part of the Mesozoic marine revolution (Aronson 1987). I have generalized that conclusion by censusing sublethal damage repeatedly over several years in 2 living species from a second habitat type [back-reef/lagoonal settings as opposed to Aronson's (1987) mangrove creek] at 3 Caribbean field sites.

Whether or not increased predation in the late Mesozoic and Cenozoic selected for defensive adaptations in ophiodermatids is unclear. The Jurassic and Recent species examined here have no obvious morphological difference that could be interpreted as an increase in antipredator architecture through time. The increase in the frequency of sublethal damage, despite a concomitant increase in predator efficiency, and without an increase in defensive architecture, suggests that both lethal and sublethal predation increased. Other possibilities, albeit untestable, are that the living species possess better developed chemical deterrents or refuging behaviors, or that they have a greater propensity to autotomize their arms, than did their Early Jurassic confamilials.

Acknowledgements. I am grateful to M. A. Buzas, L. A. J. Clements, G. Hendler, J. M. Lawrence, D. R. Levitan, R. J. Mooi, D. L. Pawson, W. F. Precht, G. J. Vermeij, J. D. Woodley and 2 anonymous reviewers for advice and/or comments on the manuscript. J. N. Havenhand assisted with field work in Belize, and R. Mooi drew Fig. 1. I thank J. D. Woodley and K. Ruetzler for access to the facilities of the Discovery Bay Marine Laboratory and the Smithsonian Institution's Belize field station, respectively. Research support was provided by the Smithsonian's Caribbean Coral Reef Ecosystems (CCRE) Program (partially funded by Exxon Corporation), the Smithsonian Scholarly Studies Program, and Northeastern University. This paper is Contribution No. 320 of the CCRE Program and Contribution No. 506 of the Discovery Bay Marine Laboratory.

LITERATURE CITED

- Arkell, W. J. (1956). Jurassic geology of the world. Oliver & Boyd, Edinburgh
- Aronson, R. B. (1987). Predation on fossil and Recent ophiuroids. *Paleobiology* 13: 187-192
- Aronson, R. B. (1988). Palatability of five Caribbean ophiuroids. *Bull. mar. Sci.* 43: 93-97
- Aronson, R. B. (1989a). A community-level test of the Mesozoic marine revolution theory. *Paleobiology* 15: 20-25
- Aronson, R. B. (1989b). Brittlestar beds: low-predation anachronisms in the British Isles. *Ecology* 70: 856-865
- Aronson, R. B., Harms, C. A. (1985). Ophiuroids in a Bahamian saltwater lake: the ecology of a Paleozoic-like community. *Ecology* 66: 1472-1483
- Aronson, R. B., Sues, H.-D. (1987). The paleoecological significance of an anachronistic ophiuroid community. In: Kerfoot, W. C., Sih, A. (eds.) *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, New Hampshire, p. 355-366
- Bowmer, T., Keegan, B. F. (1983). Field survey of the occurrence and significance of regeneration in *Amphiura filiformis* (Echinodermata: Ophiuroidea) from Galway Bay, west coast of Ireland. *Mar. Biol.* 74: 65-71
- Cochran, W. G. (1963). *Sampling techniques*, 2nd edn. Wiley, New York
- Ensom, P. C. (1984). Examples of the trace fossil *Asteriacites* sp. or tool marks from the Starfish Bed (Middle Lias) near Thorncombe Beacon. *Proc. Dorset nat. Hist. archaeol. Soc.* 105: 165-166
- Goldring, R., Stephenson, D. G. (1972). The depositional environment of three starfish beds. *Neues Jb. Geol. Paläont. Mh.* 1972: 611-624
- Hendler, G. (1982). The feeding biology of *Ophioderma brevispinum* (Ophiuroidea: Echinodermata). In: Lawrence, J. M. (ed.) *Echinoderms. Proceedings of the International Conference, Tampa Bay*. A. A. Balkema, Rotterdam, p. 21-27
- Hendler, G., Peck, R. W. (1988). Ophiuroids off the deep end: fauna of the Belizean fore reef slope. In: Burke, R. D., Mladenov, P. V., Lambert, P., Parsley, R. L. (eds.) *Echinoderm biology. Proceedings of the Sixth International Echinoderm Conference*. A. A. Balkema, Rotterdam, p. 411-419
- Hess, H. (1960). *Ophioderma escheri* Heer aus dem unteren Lias der Schambelen (Kt. Aargau) und verwandte Lias-Ophiuren aus England und Deutschland. *Eclog. geol. Helv.* 53: 757-793
- Hess, H. (1964). Die Ophiuren des englischen Jura. *Eclog. geol. Helv.* 57: 756-802
- Karlson, R. H. (1988). Size-dependent growth in two zoanthid species: a contrast in clonal strategies. *Ecology* 69: 1219-1232
- Kissling, D. L., Taylor, G. T. (1977). Habitat factors for reef-dwelling ophiuroids in the Florida Keys. *Proc. 3rd int. Coral Reef Symp., Miami* 1: 225-231
- Lewis, J. B., Bray, R. D. (1983). Community structure of ophiuroids (Echinodermata) from three different habitats on a coral reef in Barbados, West Indies. *Mar. Biol.* 73: 171-176
- Meyer, D. L., Macurda, D. B. Jr (1977). Adaptive radiation of the comatulid crinoids. *Paleobiology* 3: 74-82
- Randall, J. E. (1967). Food habits of reef fishes of the West Indies. *Stud. trop. Oceanogr., Miami* 5: 665-847
- Reimer, R. D., Reimer, A. A. (1975). Chemical control of feeding in four species of tropical ophiuroids of the genus *Ophioderma*. *Comp. Biochem. Physiol.* 51A: 915-927
- Schoener, T. W. (1979). Inferring the properties of predation and other injury-producing agents from injury frequencies. *Ecology* 60: 1110-1115
- Sides, E. M. (1981). Aspects of space utilization in shallow-water brittle-stars (Echinodermata, Ophiuroidea) of Discovery Bay, Jamaica. Ph.D. dissertation. University of the West Indies, Mona, Jamaica
- Sokal, R. R., Rohlf, F. J. (1981). *Biometry*, 2nd edn. W. H. Freeman & Co., San Francisco
- Vermeij, G. J. (1977). The Mesozoic marine revolution. evidence from snails, predators and grazers. *Paleobiology* 3: 245-258
- Vermeij, G. J. (1982). Unsuccessful predation and evolution. *Am. Nat.* 120: 701-720
- Vermeij, G. J. (1983). Shell-breaking predation through time. In: Tevesz, M. J. S., McCall, P. L. (eds.) *Biotic interactions in Recent and fossil benthic communities*. Plenum Press, New York, p. 649-669
- Vermeij, G. J. (1987). *Evolution and escalation: an ecological history of life*. Princeton University Press, Princeton
- Vermeij, G. J., Schindel, D. E., Zipser, E. (1981). Predation through geologic time: evidence from gastropod shell repair. *Science* 214: 1024-1026
- Wahle, C. M. (1985). Habitat-related patterns of injury and mortality among Jamaican gorgonians. *Bull. mar. Sci.* 37: 905-927
- Ward, P. (1981). Shell sculpture as a defensive adaptation in ammonoids. *Paleobiology* 7: 95-100
- Woodley, J. D. (1989). The effects of Hurricane Gilbert on coral reefs at Discovery Bay. In: *Assessment of the economic impacts of Hurricane Gilbert on coastal and marine resources in Jamaica*. UNEP Regional Seas Rep. Stud. 110, Nairobi, p. 71-73
- Woodley, J. D. and co-authors (1981). Hurricane Allen's impact on Jamaican coral reefs. *Science* 214: 749-755

This article was presented by J. M. Lawrence, Tampa, Florida, USA

Manuscript first received: October 16, 1990

Revised version accepted: April 15, 1991