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Author(s): Tatsuo Oji

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Is predation intensity reduced with increasing depth? Evidence from the west Atlantic stalked crinoid *Endoxocrinus parrae* (Gervais) and implications for the Mesozoic marine revolution

Tatsuo Oji

Abstract.—The number of regenerated arms was counted on specimens of two distinct phenotypes of the stalked crinoid *Endoxocrinus parrae* (Gervais) from a wide bathymetric range in the Caribbean (178–723 m). In one phenotype, the sample was divided into two groups, one from shallower (< 500 m) depths, the other from deeper (\geq 500 m); in the other phenotype the group divided at 550 m. In both phenotypes, the frequency of regenerated arms is significantly higher in specimens from shallower water than in those from deeper water. If the regenerated arms in *Endoxocrinus parrae* were the result of sublethal predation, as previously suggested, then predation intensity is higher in shallow water than deep water. These results are consistent with the idea of the late Mesozoic marine revolution—that there has been stronger predation on various invertebrates in shallow-water environments since the late Mesozoic. The stalked crinoids may have been unable to cope with increased predation in shelf environments, and they migrated to offshore environments.

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

Present address: Geological Institute, University of Tokyo, Hongo, Tokyo 113, Japan

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Introduction

The Mesozoic marine revolution is believed to have caused dramatic changes in the habitats and lifestyles of many shallow-marine invertebrates since the late Mesozoic (e.g., Vermeij 1977, 1987). Stalked crinoids, for example, have undergone a striking decline in shallow-water environments and today they are almost restricted to deep-water environments (Meyer and Macurda 1977; Bottjer and Jablonski 1988 for isocrinines). These crinoids are now found mainly in bathyal depths; the shallowest records of living stalked crinoids are from approximately 100 m in the western Pacific (Oji 1989), and approximately 170 m in the western Atlantic (Messing 1984). As an explanation for the disappearance of the stalked crinoids from shallow shelf environments, a hypothesis was proposed that they have been subjected to increased predation by fishes, which have diversified since the late Mesozoic (Meyer and Macurda 1977; Meyer 1985). Meyer (1985) demonstrated that shallow-water comatulid (stalkless) crinoids in the Great Barrier Reef are subjected to predation by bony fishes of several families. Although there are

no direct observations of predation on stalked crinoids they, like comatulid crinoids, are considered to be prey of certain predators.

Brittlestars, another anachronistic echinoderm group, show similar trends. Examining the frequency of regenerated arms of Jurassic and Recent brittlestars, Aronson (1987, 1989) pointed out that predation pressure on ancient ophiuroid populations was low, and it has increased since the Jurassic. In addition, dense brittlestar beds have become rare since the Early Cretaceous.

Stalked crinoids live in relatively deep water, usually 100–1000 m, and in situ observations of predation have yet to be made. They are believed to be preyed upon by bony fishes and decapod crustaceans (Meyer 1985; Oji and Okamoto 1994; Donovan and Pawson in press). Sublethal predation in stalked crinoids is indicated by the existence of many regenerated arms in isocrinines (Oji 1986), and also by radice-like extensions above the stalk in bathyrcrinids (Donovan and Pawson in press).

There have been almost no studies on how the intensity of predation on stalked crinoids varies at different times or in different environments. In order to argue for a historical

change in predation intensity, a study of predation intensity at a particular time (for example, Recent) in different environments should first be undertaken before we can estimate differences in predation pressure along a long time axis (see Hansen and Kelley 1995). Meyer (1985) examined predation and regeneration of the Recent comatulids of the Great Barrier Reef and demonstrated that comatulid crinoids in different habitats (exposed vs. cryptic), and with different life habits (diurnal vs. nocturnal), can differ in frequencies of missing or regenerating arms and visceral masses. He considered such lifestyles (nocturnal or cryptic) as adaptations to reduce predation and concluded that the comatulids have been able to cope with increased predation by teleost fishes since the late Mesozoic onward (see also Schneider 1988). Oji (1986) studied frequencies of regenerated arms in two superficially similar species of common Japanese stalked crinoids, *Metacrinus rotundus* from 130–150 m, and *Saracrinus nobilis* from deeper water (182–400 m). *M. rotundus* had lower frequencies of regenerated arms than *S. nobilis*, and this difference may reflect differences in sublethal predation on these species. However, these differences in the Japanese species cannot be interpreted at face value. The data, based on two different species, may not represent an actual difference in predation intensity, because the two species have different numbers of arms and they may have different rates of growth in regenerating arms.

If bony fishes are the main predators of crinoids and the decline of the stalked crinoids in shallow environments is attributable to the diversification of fishes, the extant stalked crinoids, especially those living at relatively shallow depths, must be subjected to high predation by fishes. Also, there should be less predation on stalked crinoids living in deeper environments. The purpose of the present study is to demonstrate how predation pressure on a stalked crinoid species changes according to water depth, using specimens of *Endoxocrinus parrae* (Gervais), an isocrinine species most commonly found in the Caribbean (Fig. 1). Such documentation is an important test of the hypothesis that the present-day deep sea environment is a "refuge" for

many invertebrates that had been common and diverse in shallow water until the late Mesozoic marine revolution (Vermeij 1987).

Material and Methods

A total of 203 specimens of *Endoxocrinus parrae* (Gervais), in the collections of the Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. were examined (see Appendix for information about the examined specimens). *E. parrae* is the most common of the five isocrinine species in the western Atlantic. It is distributed in the Caribbean from the Yucatan Channel to the Lesser Antilles, and it has been collected in abundance from the Straits of Florida and the Bahamas. The species also extends to San Luis, Brazil (Meyer et al. 1978) and probably occurs off Rio Grande, Brazil (described/identified as *Diplocrinus maclearanus* in Tommasi 1969).

There are many old samples of *E. parrae* in the National Museum of Natural History, collected since 1879. However, only specimens collected after the 1960s were selected for this study, because their station data, especially their depth records, are considered as more reliable. All the specimens were collected within the Caribbean: off the Yucatan Peninsula, Cuba, the Strait of Florida, the Bahamas, and the West Indies. They were collected mostly by R/V Gerda and R/V Pillsbury of the University of Miami, and by submersibles Johnson-Sea-Link I and II of the Harbor Branch Oceanographic Institution.

Previously, *Endoxocrinus* from the west Atlantic was divided into two species, *E. parrae* (Gervais) with a smooth dorsal surface on the arms and *E. prionodes* (H. L. Clark) with a serrate dorsal surface on the arms (Clark 1941). These two species were believed by Meyer et al. (1978) to be synonymous. They probably represent two phenotypes of a single species (Oji 1990). There are also a few intermediate forms between the two.

For the sake of convenience, the smooth form is herein called PA and the serrate form, PR. Of the 203 specimens examined, PA = 131 and PR = 62; ten specimens were intermediate. The phenotype PR is found predominantly in the northern part of the distribution (Oji

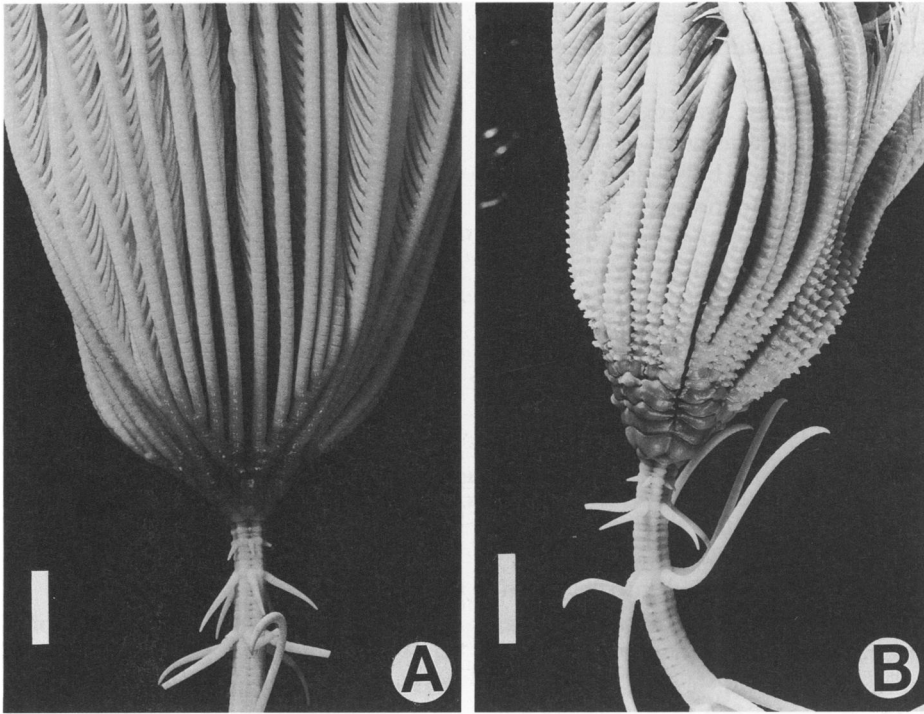


FIGURE 1. *Endoxocrinus parrae* (Gervais). A, Smooth form (PA). No. E-33406, collected at south of Rock Port, Great Abaco, Bahama Islands. B, Serrate form (PR). No. E-32644, collected at west of Wood Cay, Great Abaco, Bahama Islands. Scale bars are 1 cm.

1990), and its bathymetric range is usually deeper than that of PA (Fig. 2). Although the two forms are considered to be the same species, they were treated separately when counting and comparing the number of regenerated arms, because the regenerated arms of the serrate form (PR) are usually less conspicuous

and more difficult to detect, due to their rough surface, than those of PA, and also because PR usually has a deeper range than PA.

Frequency of Regeneration in Different Depths.—To determine intensity of predation on the basis of frequency of arm regeneration, all arms of the 203 specimens were examined, and all regenerated arms per individual were counted. Regenerated arms usually exhibit clear and sudden change in arm diameter at their bases. The diameter change is sometimes difficult to discern owing to growth of the regenerating part. Sometimes a color change is associated with the diameter change. However, regeneration was counted only when diameter change was apparent; cases with no clear change in arm diameter, or with color difference alone, were not treated as proof of regeneration. Regeneration of pinnules (small branchlets of arms) is extremely rare and is not considered herein.

Many specimens were collected by trawling within some bathymetric ranges. In such cases the maximum and the minimum depth rec-

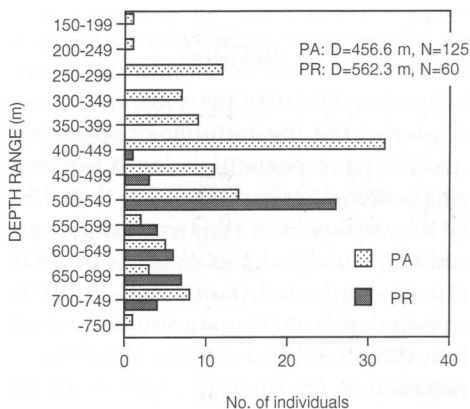


FIGURE 2. Depth ranges of *Endoxocrinus parrae*. PA: smooth form. PR: serrate form. Mean depth of PR is significantly deeper than that of PA ($p < 0.001$).

ords were averaged and the mean depths used. Specimens with vertical ranges exceeding 100 m were excluded.

Size of the specimen was determined by measuring the stalk diameter at the point where the radial pores between columnals disappear. Small specimens with stalk diameter of less than 2.5 mm were excluded. Also many specimens do not retain their original number of arms, because some arms were damaged or autotomized during or after sampling. Specimens with less than half of the original number of arms were also excluded. The number of arms here refers to the number of the most distal arm-branching series.

Of the total 203 specimens, the total number of available specimens for the regeneration frequency study was 154 (PA = 103 and PR = 51). PA and PR were classified into seven and four groups, respectively, according to their bathymetric range, each group corresponding to a 100-m depth interval.

Two methods were used to determine predation intensity at different depths. First, the number of regenerated arms per individual was counted. The average number of regenerated arms per individual is shown for specimens from particular depth ranges. Second, presence or absence only of regenerated arms was determined. In many cases, more than one arm may be regenerating in a specimen; adjacent arms regenerating suggest a single attack by a predator. To avoid overcounting, the percentages of specimens with regeneration present and those without were counted.

Total Number of Arms versus Depth.—The total number of arms per individual varies, ranging from fewer than 20 to almost 40. The total arm number may influence the frequency of arm regeneration per individual, because individuals with more arms might have a greater chance of attack by a predator than those with fewer arms. Total arm numbers are plotted at different depths for both PA and PR. Not all the specimens retain their original number of arms, and the total number of the arms was estimated for some specimens by the width of the space left between the adjacent arms, or by the typical endotomous branching pattern of this species, if possible. As in the previous analysis, specimens with

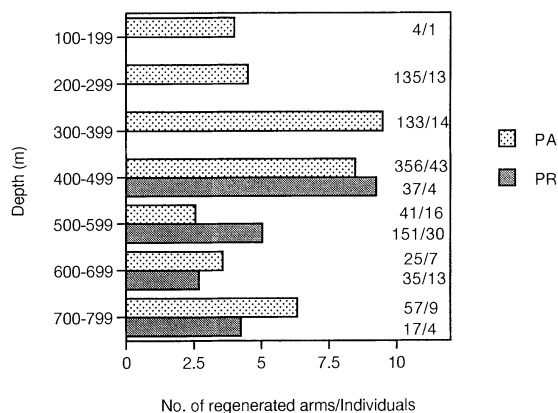


FIGURE 3. Frequency of regeneration versus depth. A, PA. B, PR. The frequency is shown as the number of regenerated arms per individual from a particular depth range. Fractions beside each bar represent the number of all the regenerated arms (numerator) divided by the number of specimens from that depth range (denominator).

stalk diameter of less than 2.5 mm were excluded. The number of specimens used for this count is 85 in PA and 45 in PR.

Number of Regenerations versus Size.—Generally, older specimens must have more sublethal predation incidents than young specimens. If the repair process is slow, aged specimens should have a greater number of regenerated arms. The number of arm regenerations was plotted against stalk diameter to determine if there is indeed a relationship between size of the specimens and number of regenerations. Specimens with more than half of the total arms preserved were selected for this count. The number of specimens used for this count is 111 for PA and 50 for PR.

Results

Bathymetric Distribution of PA and PR.—Figure 2 shows the the number of specimens of PA and PR from particular depth ranges, and the shallower distribution of PA than PR. Because the variances of the two samples are assumed to be unequal, the Welch's approximate *t*-test was conducted (Sokal and Rohlf 1995). The mean depth of PA is significantly shallower than that of PR ($t = 6.42$, $p < 0.001$).

Frequency of Predation in Different Depths.—Figure 3 shows the frequency of regeneration in the arms of the two forms of *Endoxocrinus parrae* from different depth ranges. In PA,

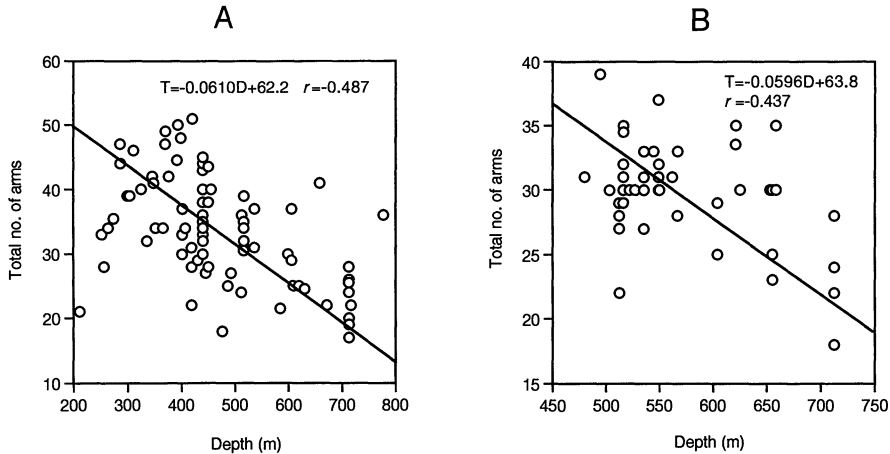


FIGURE 4. Relationship between depth and total number of arms. A, PA. B, PR. Regression (reduced major axis) in both cases represent the tendency toward decrease in arm number as depth increases. T: total number of arms; D: depth.

there is a clear decline in the frequency of arm regeneration at approximately 500 m depth. If PA individuals are separated into two groups at 500 m, one from shallower (150–499 m) and the other from deeper (500–699 m) water, the shallower group has a significantly higher frequency of regenerated arms than the deeper group (G -test; $G = 85.14$, $p < 0.001$). In PR, which has relatively deeper habitats than PA, there is also significantly higher frequency of regenerated arms in the shallower group (439.5–549 m) than in the deeper group (550–712.5 m), if PR specimens were divided at 550 m ($G = 13.85$, $p < 0.001$).

The total number of arms per individual may have an influence on the above data concerning frequency of regeneration. There is a weak negative correlation between the depth and the total number of arms in both PA (Fig 4A) and PR (Fig 4B); i.e., specimens from deeper water have relatively fewer total arms than those from shallower water. Thus, the general decrease in the number of regenerations per specimen may not be explained solely by the frequency of predation. In order to exclude the effect of variation in the total arm number on the frequency of regenerated arms, the number of regenerated arms (R) of each specimen, for both PA and PR, should be calibrated against the total number of the remaining (observable) arms of each specimen and against the average number of the total

arms remaining, by means of the following equation:

$$R = R_0 \times (T_a/T)$$

where R_0 is the original number of regenerated arms, T_a is the average number of the total remaining arms of the specimen, and T is the total number of remaining arms of the specimen.

Even after such a calibration, the revised frequencies of regeneration in PA showed that the shallower (< 500 m) specimens have significantly greater frequency of regenerated arms than the deeper (≥ 500 m) specimens ($G = 35.07$, $p < 0.001$). In PR, there is also significantly higher frequency of regenerated arms in the shallower (< 550 m) specimens than the deeper (≥ 550 m) specimens ($G = 9.95$, $p < 0.05$).

As for the analysis of change of predation versus depths, based solely on the presence/absence of regeneration, there is a slightly higher percentage of regeneration in the shallower environment for PA (Fig. 5A), but the pattern is reversed for PR (Fig. 5B). When considering the frequency of the PA specimens with regenerated arms, the frequency of shallower (< 500 m) specimens does not significantly differ from that of deeper (≥ 500 m) specimens ($G = 1.03$, $p > 0.1$). This is probably due to the fact that most specimens have some regenerated arms even in the specimens from

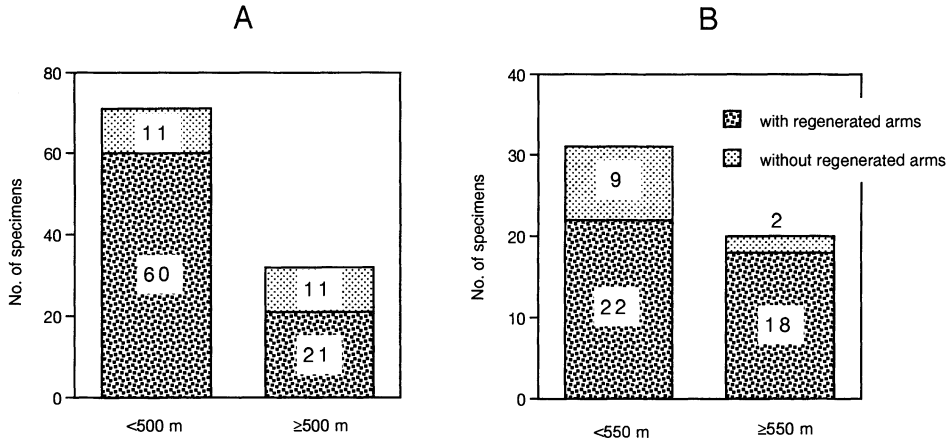


FIGURE 5. Frequency of individuals with/without regenerated arms, from shallower and deeper waters. A, PA; B, PR. In both cases, the difference in the frequency of specimens from shallower/deeper waters does not show significant difference ($p > 0.1$).

deeper water, and regeneration-free specimens occupy only a small percentage of the total. In addition, as Schoener (1979) pointed out, frequency of animals with regeneration may be related to efficiency of predation, not intensity of predation.

Number of Regenerated Arms as a Function of Size.—There was no clear correlation between stalk diameter and the number of regenerated arms (Fig. 6). In other words, older individuals do not always show more regenerated arms than younger individuals. The number of regenerated arms must be more than the number detected, because traces of regeneration seem to disappear rapidly.

Discussion

The results of PA show a significant decrease in the frequency of arm regeneration in specimens collected from depths greater than 500 m and suggest that predation on an isocrinid species in the Caribbean is stronger for shallower populations (< 500 m) than for deeper ones. In PR, there is also a decrease in the number of regenerated arms toward greater depths.

If regenerated arms are the result of sublethal predation, the decrease in the number of regenerated arms toward deeper waters is consistent with the hypothesis that predation

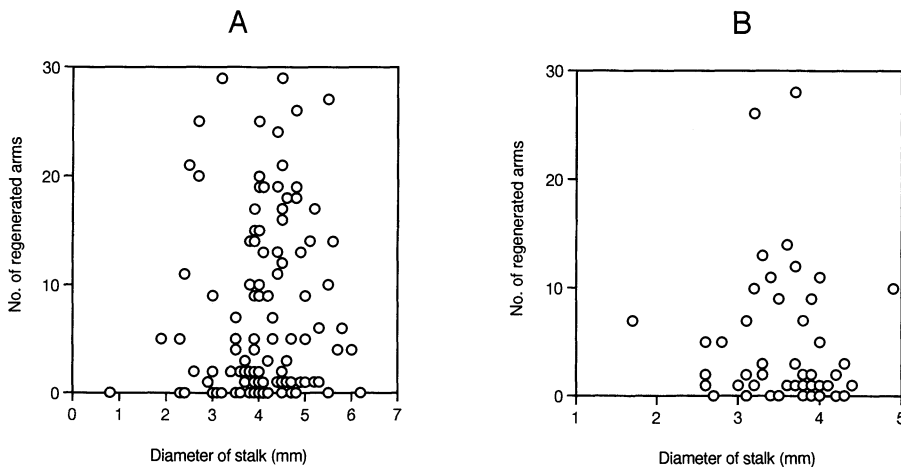


FIGURE 6. Relationship between size (stalk diameter) and number of regenerated arms. A, PA; B, PR. There is no clear increase in number of regenerated arms in larger individuals.

pressure is generally stronger in shallow water than in deeper water. Presumably, in the Caribbean at least, predation pressure in depths of less than 150 m is strong enough to eliminate any species of stalked crinoids. The present data suggest that stalked crinoids have undergone considerable predation in Recent marine environments, especially in shallow depths, and they have been eliminated from shallow water. The data on predation and regeneration in comatulid crinoids (Meyer 1985; Schneider 1988) also support the idea of strong predation pressure in shallow water.

Bottjer and Jablonski (1988) demonstrated in their time-environment diagram that Isocrinida except Pentacrinitidae and Comatulina (these must be revised to Holocrinidae and Isocrinina according to a new classification scheme of Simms 1988) lived in shallow water until the middle Cretaceous, but in the Cenozoic they were almost confined to the "outer shelf" to "slope-deep water basin." These data were based exclusively on European and North American occurrences, but they contain the majority of previous global records.

There are at least four records of shallow-water crinoids since the middle Cretaceous, and these records were not used in the diagram by Bottjer and Jablonski (1988). They are from the Southern Hemisphere, the former Gondwana Realm. *Metacrinus* sp. was described from the Paleocene from a very shallow-water, conglomeratic deposit on South Island, New Zealand (Stillwell et al. 1994). They suggested that the supposed shift of some isocrinines from a shallower to a deeper environment occurred much later in the Paleogene, and not during the Late Cretaceous as previously supposed. From the late Paleocene of western Australia, ?*Nielsenicrinus* sp. was described from a calcarenite deposited in an open-shelf sea at 50 to 100 m depth (Milner 1989). Also, *Metacrinus fossilis* occurs from the Eocene shallow-water deposit of Seymour Island, Antarctic Peninsula (Rasmussen 1979; Meyer and Oji 1993). Eagle (1993) described an isocrinine from a late Oligocene limestone on the North Island of New Zealand. This last fossil occurred in a deposit of a shallow inner-shelf environment. The affinity of this fossil to

the genus *Nielsenicrinus* is questionable (Oji in press).

These new discoveries may lead to the notion that the disappearance of stalked crinoids may not be synchronous on a global scale, and that at least in the former Gondwana Realm they remained in shallow water for some time after the initiation of the Mesozoic marine revolution. However, the majority of the data still seem to suggest crinoid decline from shallow water since the middle Cretaceous (Bottjer and Jablonski 1988). There is also negative evidence that there have been no isocrinines in the Upper Cretaceous shallow marine environments: in Japan, despite the common occurrence of Cretaceous deposits with wide environmental variation, isocrinine fossils are found only in the deep offshore deposits (Oji unpublished data).

Smith (1994) proposed that the time-environmental data during the Mesozoic through Recent are biased by eustatic sea-level changes. There is an onshore bias from the base of the Triassic through about 150 Ma, and an offshore bias from 100 Ma through about 35 Ma, due to sea-level curve (Smith 1994). Overall patterns of offshore migration of stalked crinoids must be reviewed in light of additional data. However, absence of stalked crinoids from the inner to middle shelf environments in Recent waters and abundant occurrence of shallow-water stalked crinoids from the Jurassic to the middle Cretaceous are good evidence that the stalked crinoids have disappeared from shallow water.

Autotomy or loss of crinoid arms might be induced not only by nonlethal predation but also by nonbiological factors such as physical stress and thermal change. Specimens of *Metacrinus rotundus* transferred from their habitats to flow tanks often shed their arms without any apparent physical damage to the crinoids (Amemiya and Oji 1994), and *Cenocrinus asterius* and *Endoxocrinus parrae* autotomized their arms when they experienced great thermal change during the ascent of a submersible (Baumiller et al. 1991). The question is whether physical/thermal factors in the natural environment are the possible cause of arm autotomy of crinoids. If such stresses are the main cause of arm autotomy, the pattern of

frequency of regeneration along a bathymetric transect would be the same as shown in Figure 3, because shallower waters have more fluctuations in physical/thermal factors.

If there are physical stresses, temperature changes, and strong currents affecting the stalked crinoids in the present-day marine environment, there must also have been such stresses on ancient crinoids. If such physical stresses are the main cause of arm autotomy and regeneration of today's stalked crinoids, we would also expect fossil isocrinines to show many examples of regenerated arms. However, the available data show that fossil isocrinines had an extremely low frequency of regenerated arms, in contrast to the usually high frequency of regenerated arms in Recent isocrinines.

Data on the regenerated arms of fossil crinoids are few, and no quantitative data are available at present. Hess and Holenweg (1985) noted that there are "a rather high number of regenerated arms" in the Middle Jurassic *Chariocrinus andreae* from one locality of Switzerland. He did not give any quantitative data on the frequency of regeneration. This is the only information available on the existence of regenerated arms from Mesozoic isocrinines. From the Aptian of Japan, more than 20 specimens of well-preserved *Isocrinus* (*Chladocrinus*) *hanaii* were described (Oji 1985), but no regenerated arms were detected. On the basis of sedimentary characteristics and associated organisms, this species is considered to be a shallow-water inhabitant. Many specimens of Mesozoic isocrinines in the Natural History Museum, London also show very rare cases of regenerated arms (Oji unpublished data). A total of 64 specimens of *Metacrinus fossilis* from the Eocene of Seymour Island, Antarctic Peninsula showed a lower incidence of regenerated arms than do extant *Metacrinus rotundus* from Japanese waters (Meyer and Oji 1993). The fossil specimens usually have well-preserved crowns. *Metacrinus fossilis* is also considered to be a shallow-water inhabitant, as previously mentioned. It is difficult to evaluate the frequency of regenerated arms quantitatively because the sample size of fossil crinoids is usually limited. However, there are

extremely few examples of regenerated arms in fossil isocrinines as a whole.

Stalkless crinoids (comatulids) can also autotomize their arms, and they have many regenerated arms. According to Meyer (1985), comatulid species living in a cryptic environment in the Great Barrier Reef have a lower frequency of regenerated arms than do species that live exposed on rocks in the same area and in similar depths. Thus it is difficult to attribute the causes of arm regeneration of these comatulids to temperature change.

Observations from submersibles confirm that crinoids do not autotomize their arms, even when considerably disturbed during sampling. For example, they are often collected by a suction tube, and individuals are severely disturbed when sucked into the tube (video shows all of the arms forced up inside of the tube as suction begins), but almost all of the arms remain intact during the sampling (Oji unpublished data). On the contrary, it was observed that *Metacrinus rotundus* will autotomize their arms when the distal parts of arms are damaged by scissors while the proximal arm is being held (Oji and Okamoto 1994). These lines of evidence suggest that the crinoids in their natural environment can autotomize their arms only when their arms are bitten or picked up by predators.

Stalked crinoids stand on the sea floor with no obvious protection from predators. Even though some isocrinines can move on the sea floor by crawling with their arm movements, the speed is very slow (Messing et al. 1988; Baumiller et al. 1991), and it is probably not possible for them to escape from predatory attacks. Rather, the well-developed ability to regenerate lost body parts (Amemiya and Oji 1993) probably enables these crinoids to survive, even after the most severe predatory attack. This regenerative power is surely a key element in the survival of stalked crinoids during their long evolutionary history.

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Appendix

Shown below are registered number of specimens, phenotype (PA: with smooth dorsal arm surface; PR: with serrate dorsal arm surface; INT: intermediate between PA and PR), depth of occurrence (in meters, maximum and minimum depth records averaged), number of regenerated arms, presence or absence of regeneration (0 = absent, 1 = present), total number of arms preserved, total arm number (averaged if there is some range in estimation), and stalk diameter (in mm).

No.	Phenotype	Depth (m)	No. of regenerated arms	Presence/absence of regeneration	Total arm no. preserved	Total arm no.	Stalk diameter
E-17052	PA	777	6	1	34	36	5.3
E-17514-1	PA	512	5	1	12		4.3
E-17514-2	PA	512	0	0	24	24	3.0
E-17514-3	PA	512	0	0	16		2.4
E-17515-1	PA	275	12	1	34		4.5
E-17515-2	PA	275	19	1	22		4.0
E-17515-3	PA	275	4	1	29		3.9
E-17515-4	PA	275	21	1	28		4.5
E-17515-5	PA	275	13	1	18		4.1
E-17515-6	PA	275	3	1	10		4.5
E-17515-7	PA	275	10	1	14		3.5
E-17516-1	PR	512	2	1	29	29	2.6
E-17516-2	PR	512	5	1	29	29	2.8
E-17517-1	PR	604	1	1	25	25	3.8
E-17517-2	PR	604	11	1	31		4.0
E-17517-3	PR	604	2	1	26		3.9
E-17517-4	PR	604	0	0	29	29	4.2
E-17520	PR	544.5	0	0	20	33	3.9
E-17920	PR	516	5	1	32	32	4.0
E-17950	PR	503	1	1	30	30	3.2
E-17980	PA	303.5	0	0	0		4.8
E-17981	PR	550	2	1	30	30	3.8
E-17989-1	PR	535.5	5	1	31	31	2.8
E-17989-2	INT	535.5	1	1	29	29	3.0
E-17989-3	PR	535.5	0	0	26	27	2.7
E-17989-4	PR	535.5	1	1	33	33	2.6
E-17989-5	PR	535.5	0	0	30	30	3.5
E-17989-6	PR	535.5	7	1	18	18	1.7
E-17990-1	PR	658.5	1	1	35	35	4.4
E-17990-2	PR	658.5	2	1	24		4.2
E-17990-3	PR	658.5	1	1	30	30	4.1
E-17991-1	PR	567	2	1	33	33	3.1
E-17991-2	PR	567	5	1	28	28	2.6
E-17994-1	PA	401.5	7	1	30	30	4.3
E-17994-2	PA	401.5	26	1	33	33	4.8
E-17996-1	PA	535.5	1	1	26		4.0
E-17996-2	PA	535.5	10	1	30	31	3.8
E-18006	PA	393.5	0	0	17	50	6.4
E-18008	PA	366	0	0	33	34	4.1
E-18009	PA	512.4	3	1	36	36	3.7
E-18020-1	PA	430	25	1	30		4.0
E-18020-2	PA	430	17	1	29	29	3.9
E-18023	PA	252	1	1	33	33	5.0
E-18030-1	PR	512.4	1	1	28	28	4.0
E-18030-2	PR	512.4	0	0	22	22	3.8
E-18030-3	INT	512.4	0	0	31	31	3.8
E-18032-1	PR	494.5	9	1	39	39	3.9
E-18032-2	PR	494.5	10	1	27		4.9
E-18033	PA	198.5	4	1	58		6.0
E-18035-1	PA	439.5	2	1	21		4.0
E-18035-2	PA	439.5	5	1	31		3.9
E-18035-3	INT	439.5	4	1	38	38	4.7
E-18035-4	PA	439.5	24	1	36	36	4.4
E-18035-5	PA	439.5	9	1	43	43	4.0
E-18035-6	PA	439.5	16	1	35	35	4.5
E-18035-7	PA	439.5	1	1	38	38	4.4
E-18035-8	PA	439.5	17	1	44	44	4.5
E-18035-9	INT	439.5	16	1	36	36	4.0
E-18035-10	PA	439.5	1	1	32	32	4.6

Appendix. Continued.

No.	Phenotype	Depth (m)	No. of regenerated arms	Presence/absence of regeneration	Total arm no. preserved	Total arm no.	Stalk diameter
E-18035-11	PA	439.5	1	1	33	33	4.1
E-18035-12	PA	439.5	19	1	32	32	4.4
E-18035-13	PA	439.5	18	1	35	35	4.8
E-18035-14	PA	439.5	20	1	30	30	4.0
E-18035-15	PA	439.5	5	1	42		4.7
E-18035-16	PA	439.5	9	1	40	40	4.2
E-18035-17	INT	439.5	34	1	58	58	4.2
E-18035-18	PR	439.5	18	1	32		
E-18035-19	PA	439.5	1	1	45	45	5.2
E-18035-20	PA	439.5	9	1	27		5.0
E-18035-21	PA	439.5	19	1	40		4.1
E-18035-22	PA	439.5	1	1	35	35	4.1
E-18035-23	PA	439.5	15	1	34	34	4.0
E-18052	PA		17	1	37		5.2
E-18047	PA	403	5	1	37		5.0
E-18050-1	PA		6		46		5.8
E-18050-2	PA		27	1	50		5.5
E-18058	PA	251.5	10	1	33	33	5.5
E-19967	PA	256	0	0	10	10	0.8
E-19968	PA	402	1	1	36	37	3.9
E-19969	PA	256	2	1	28	28	3.4
E-21004	PA	455	14	1	40	40	5.6
E-21005-1	PR	300	2	1	13		4.2
E-21005-2	PR	300	1	1	10		3.8
E-21012	PA	420	0	0	30	51	6.2
E-21014	PR	625	1	1	8	30	4.7
E-21018-1	PA	476	1	1	18	18	2.9
E-21018-2	PA	476	2	1	18		3.8
E-21018-3	PA	476	0	0	28		3.8
E-21018-4	PA	476	0	0	19		4.1
E-21020-1	PR	549	13	1	36		3.3
E-21020-2	PR	549	0	0	17	30	3.4
E-21020-3	PR	549	28	1	33		3.7
E-21020-4	PR	549	0	0	30	32	3.8
E-21020-5	PR	549	2	1	36	37	3.8
E-21020-6	PR	549	0	0	31		4.0
E-21020-7	PR	549	0	0	31	31	4.3
E-21020-8	PR	549	1	1	6		4.3
E-21020-9	PR	549	0	0	10		
E-21022	PA	384	0	0	22		3.9
E-21024	PA	411	0	0	0		5.9
E-21037-1	PA	370	18	1	55		4.6
E-21037-2	PA	370	14	1	34	47	5.1
E-21037-3	PA	370	0	0	7		5.7
E-21037-4	PA	370	1	1	1		4.9
E-21037-5	PA	370	3	1	18	49	5.5
E-21042	PA	325	0	0	14	40	
E-21052	PA	450	2	1	26	28	4.5
E-21063	PR		2	1	29		
E-21071	PA	399	4	1	24	48	5.7
E-21072-1	PA						3.3
E-21072-2	PR						3.8
E-21076-1	PA	304	3	1	39	39	4.2
E-21076-2	PA	304	0	0	2		4.0
E-21083	PR	512	11	1	15	27	3.4
E-21084	PA	1033	0	0	10		4.0
E-25908-1	PA	516	5	1	33	39	3.5
E-25908-2	PA	516	0	0	21	34	3.6
E-25908-3	PA	516	0	0	25	31	3.8
E-26001	PA		1	1	44	45	4.7
E-26002-1	INT	516	17	1	26	29	3.6

Appendix. Continued.

No.	Phenotype	Depth (m)	No. of regenerated arms	Presence/absence of regeneration	Total arm no. preserved	Total arm no.	Stalk diameter
E-26002-2	PR	516	14	1	30	32	3.6
E-26002-3	PR	516	26	1	30	31	3.2
E-26002-4	PA	516	2	1	31	31	3.6
E-26002-5	PR	516	1	1	30	35	3.9
E-26002-6	PA	516	2	1	3	35	5.6
E-26002-7	PR	516	7	1	11	30	4.0
E-26002-8	PA	516	2	1	26	34	3.9
E-26002-9	PR	516	3	1	30	34.5	3.7
E-26002-10	PR	516	12	1	20	29	3.7
E-26002-11	PA	516	1	1	31	34	3.7
E-26002-12	PA	516	0	0	29	30.5	4.2
E-26002-13	PA	516	2	1	31	32	4.0
E-32636	PA	348.5	13	1	41	41	4.4
E-32637	PR	717	1	1	7		4.3
E-32638	PA	352	19	1	34	34	4.8
E-32639	PA	630	14	1	18	24.5	3.8
E-32640-1	PR	655	1	1	22	23	4.0
E-32640-2	PR	655	9	1	25	25	3.5
E-32640-3	PR	655	12	1	4		3.8
E-32640-4	PR	655	0	0	21	30	
E-32641	PA	346	11	1	42	42	4.4
E-32642	PA	336	0	0	27	32	3.6
E-32643	INT	608	6	1	26	28	3.4
E-32644-1	PR	621	3	1	22	33.5	4.3
E-32644-2	PR	621	1	1	35	35	3.6
E-32655	PA	377	13	1	39	42	4.9
E-32656	PA	392	0	0	39	44.5	5.5
E-32653	PA	599	9	1	21	30	3.9
E-32654	PA	584	0	0	17	21.5	3.5
E-32657-1	PA	450	0	0	32	43.5	4.0
E-32657-2	PA	450	3	1	38	38	4.6
E-32658	PA	311	29	1	46	46	3.2
E-32659	PA	584	0	0	4		3.4
E-32660	PA	492	0	0	26	27	4.8
E-32661	PA	482	0	0	2		4.6
E-32662	PA	211	7	1	21	21	3.5
E-32663	PA	609	0	0	13	25	3.1
E-32664-1	PA	671	0	0	21	22	4.5
E-32664-2	PA	671	2	1	0		4.7
E-32664-3	PA	671	0	0	0		4.2
E-32666	PR	522	1	1	29	30	3.7
E-32671	PA	658	1	1	35	41	4.9
E-32674	PA	321	5	1	20	20	1.9
E-33403-1	PA	605	10	1	36	37	4.0
E-33403-2	PA	605	11	1	9	29	3.7
E-33404	PR	527	1	1	26	30	3.2
E-33405	PA	300	9	1	39	39	3.0
E-33406-1	PA	287	29	1	44	44	4.5
E-33406-2	PA	287	14	1	47	47	3.9
E-42615	INT	473	0	0	26	26	3.0
E-42616	PA	536	1	1	36	37	5.3
E-42618	INT	676	1	1	31	32	4.1
E-42619	PA	665					3.9
E-42620	PR	653	3	1	30	30	3.3
E-42621	PA	619	0	0	24	25	3.9
E-42622	PA	445	20	1	26	27	2.7
E-42623	PR	562	10	1	31	31	3.2
E-42624	PA	627	0	0	6	10	2.3
E-42617	PA	407	2	1	34	34	3.4
E-42636	PA	264	2	1	34	34	3.0
E-42637	PA	439					4.1
E-42638-1	PA	486	11	1	25	28	2.4
E-42638-2	PA	486	21	1	25	25	2.5

Appendix. Continued.

No.	Phenotype	Depth (m)	No. of regenerated arms	Presence/ absence of regeneration	Total arm no. preserved	Total arm no.	Stalk diameter
E-42639	INT	449	0	0	27	27	2.3
E-42640	PR	480	0	0	30	31	3.1
E-42641	PA	434	5	1	19	29	2.3
E-42642	PA		0	0	24	24	3.1
E-42698-1	PA	419	0	0	22	22	4.7
E-42698-2	PA	419	0	0	26	31	4.5
E-42698-3	PA	419	2	1	24	28	3.8
E-43042-1	PA	274	1	1	28	35.5	4.5
E-45840	PR	712.5	1	1	22	22	3.0
E-45841	PR	712.5	7	1	18	18	3.8
E-45842	PA	712.5	2	1	17	17	2.6
E-45843	PA	712.5	2	1	26	26	3.7
E-45844	PA	712.5	3	1	20	20	3.7
E-45845	PA	712.5	4	1	28	28	3.5
E-45846	PR	712.5	7	1	23	24	3.1
E-45847	PR	712.5	2	1	28	28	3.3
E-45848	PA	712.5	0	0	19	19	3.2
E-45849	PA	712.5	0	0	22	25.5	3.5
E-45850	PA	712.5	15	1	21	24	3.9
E-45851	PA	716	25	1	22	22	2.7