

## Rapid Arm Movements in Stalked Crinoids

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**Abstract.** Stalked crinoids in the family Isocrinidae have been observed to wave individual arms actively. Using video cameras mounted on a manned submersible, we studied these movements and investigated the factors that elicit them. Crinoids wave their arms in response to sand or detritus dropped on their crowns, to entanglement in tentacles of adjacent sea anemones, and to contact by small crustaceans that might steal from the food grooves. There was no evidence that arm waving functions in food collection. In most cases, the movements could be attributed directly to mechanical stimulation by some natural stimulus. The rapid effective stroke of an arm flexure is caused by contraction of dorsal longitudinal arm muscles. The slower return stroke results from the elastic recoil of large ligaments near the aboral sides of the arms.

### Introduction

Stalked crinoids are passive suspension feeders with limited mobility but are nevertheless capable of several kinds of movements. The most characteristic behaviors are slow movements used to orient with respect to currents and to hold the arms and pinnules in a parabolic feeding-fan posture (Macurda and Meyer, 1974, 1976; Conan *et al.*, 1981). The mechanisms by which these postures are maintained and controlled are poorly understood. Orientation of the stalk, which contains no muscles, is dependent on mutable collagenous tissues (Wilkie *et al.*, 1993). The tonic posture of the parabolic feeding fan is probably maintained by a similar mechanism, but there is as yet no morphological or physiological evidence for mutable arm ligaments (I. Wilkie, pers. comm.).

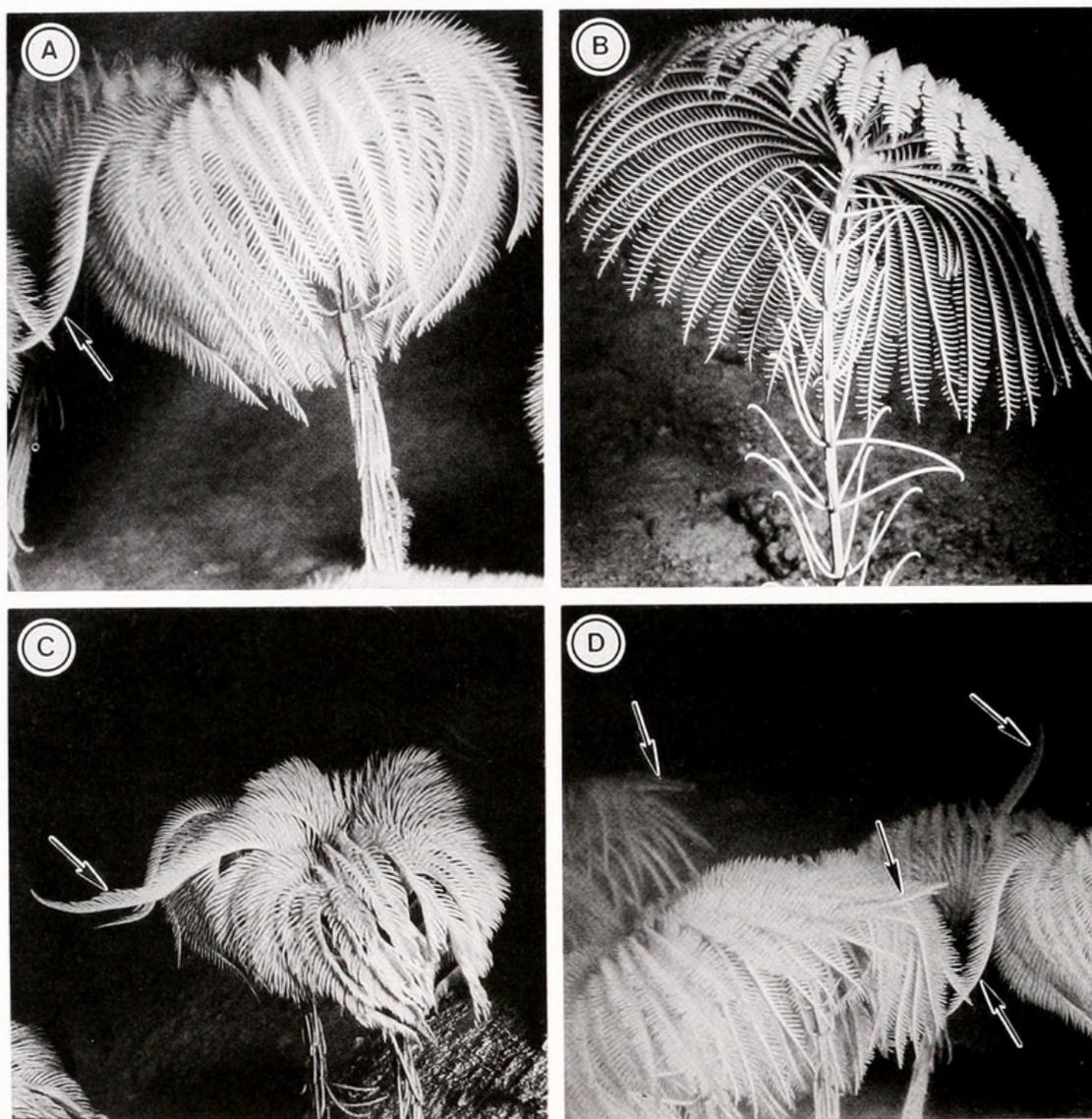
Stalked crinoids occasionally demonstrate fast muscular movements. Several species are thought to be capable of moving between attachment sites (Carpenter, 1884;

Conan *et al.*, 1981; Roux, 1976), and stalked crinoids have recently been observed crawling across the bottom (Messing, 1985; Messing *et al.*, 1988). When stimulated by the manipulator arm of a submersible or by very bright lights, this same species, *Endoxocrinus parrae*, rapidly flexes some or all of its arms in an adoral direction (Messing *et al.*, 1988; Young and Emson, unpub.). Except for an unpublished anecdotal observation suggesting that crinoids may respond to suspended sediment (W. I. Ausich, pers. comm.), all reports of rapid active arm movements have involved strong artificial stimuli. The natural roles of rapid arm movements remain undocumented. Here, we describe in detail rapid arm flexures of some bathyal isocrinids and present evidence that this behavior defends crinoids against various biotic and abiotic threats.

### Materials and Methods

Several species of stalked crinoid were observed from Johnson-Sea-Link (JSL) submersibles at depths ranging from 400 to 900 m in the northern Bahamas (see map in Young, 1992). Still photographs were taken with a Benthos 35-mm camera equipped with an 80-mm lens, mounted on the front of the submersible and focused with twin laser beams that converged on a fixed focal plane. Video footage was obtained with a Photosea Camera on a pan-and-tilt mechanism and was recorded on 1/2" or hi-8 videotape. Video still sequences were taken from the tape with a Seikosha VP-1500 video printer.

We obtained numerical data on arm-waving frequency and crustacean abundance directly from the videotape. We stopped the tape every 30 s and counted the number of arm movements, the number of crinoids involved in arm-waving behavior, and the total number of crinoids visible in the frame. We ran the tape forwards and backwards a few frames at each census point to be certain that arms counted as waving were really in motion and not



**Figure 1.** (A) *Endoxocrinus parrae* with arms drooping in slack current. Note the single arm waving in the water column (arrow). (B) *Cenocrinus asterius* in current, showing parabolic feeding fan characteristic of all Bahamian isocrinids. (C) *E. parrae* engaged in arm-waving behavior (arrow indicates moving arm). (D) A dense population of *E. parrae* with numerous individuals waving arms (indicated by arrow).

being held in a static posture. The number of small crustaceans in a frame was estimated by repeatedly passing the video forward and back, frame by frame, while scanning each part of the frame in succession for moving organisms.

The velocity of arm movement during effective and recovery strokes was documented by laying down a time code on the videotape with a hi-8 video editing machine (Sony EVO-9700), then, during frame-by-frame analysis, recording the time that movements were initiated and completed (resolution: 0.067 s).

To investigate the possibility that sediment particles might elicit arm waving, we used a suction tube on the manipulator arm of the submersible to pick up a small amount of sediment and release it about 1 m above an aggregation of crinoids. This experiment was repeated on

six different occasions, while recording the responses of crinoids on videotape. On some occasions, the sediment consisted of fine silt; at other times, it was dominated either by coarse sand or coarse, flocculent organic particles.

Crinoid arm pieces were fixed in 4% neutral buffered formalin, decalcified in 70% acid alcohol, then embedded in paraffin by standard histological procedures. Sections were cut at a thickness of 8  $\mu\text{m}$  and stained with Milligan's trichrome (Humason, 1972).

## Results

### *Description and mechanics of arm waving*

At times of slack current, three Bahamian isocrinids, *Endoxocrinus parrae*, *Cenocrinus asterius*, and *Diplocri-*

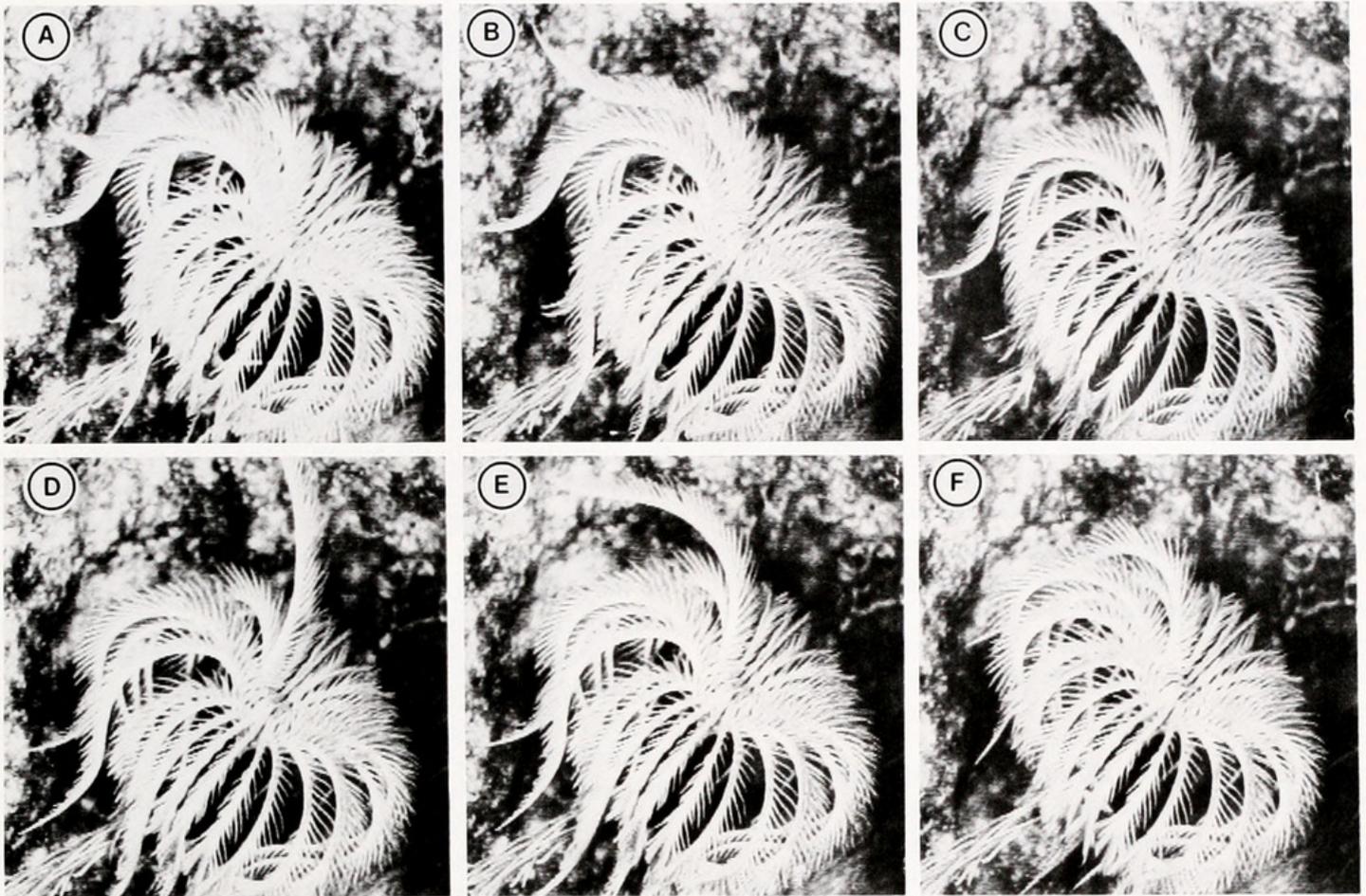


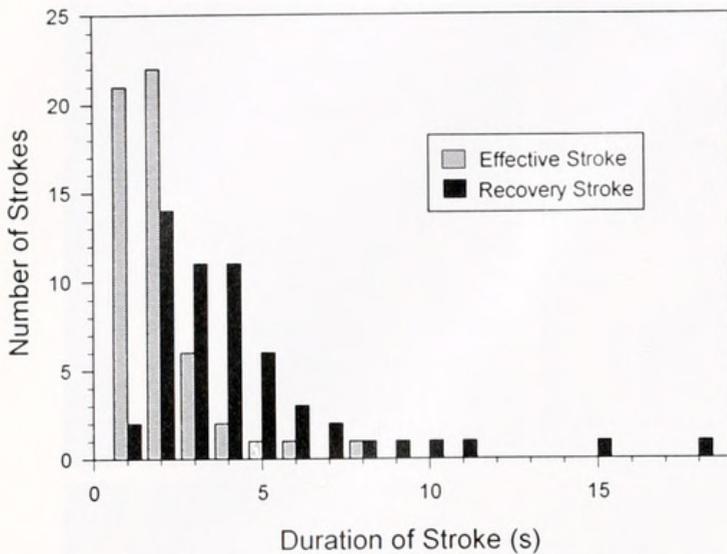
Figure 2. Video sequence of characteristic arm waving behavior in *Endoxocrinus parrae*. (A–C) Sequential steps of the effective stroke. (D) Maximum arm extension. (E–F) Recovery stroke.

*nus maclearanus*, stand erect with arms drooping down near the stalk (Fig. 1A). In a current, these same species form their arms into a parabolic fan for feeding (Fig. 1B; see also Macurda and Meyer, 1974, 1976), though the uppermost few arms of the fan may sometimes be extended straight up into the water column. All three species have been observed with individual arms waving up and down rapidly (Fig. 1A, 1C). In dense populations, large numbers of individuals have been observed to engage in arm-waving behavior simultaneously (Fig. 1D), particularly after several minutes of illumination by the submersible.

Although we have occasionally observed arm flicking or waving in animals with their arms extended in the feeding posture, arm-waving behavior has been observed more commonly in animals with drooping arms. The arm is moved rapidly away from the stalk, sweeping outward and upward until it is fully extended above or to the side of the calyx (Fig. 2). The arm pauses only briefly at the end of the stroke before reflexing downward more slowly to its initial position. This entire movement may take as little as 2 s or as much as 21 s. Frequency histograms of

the durations of effective and recovery strokes (Fig. 3) show that the recovery strokes were more variable and often longer than the effective strokes, but the two distributions overlapped substantially. For individual strokes, the ratio of the effective component to the recovery was nearly always greater than 1 (Fig. 4), and the difference between the durations of paired effective and recovery strokes was highly significant (paired Student's *t* test, 54 d.f.,  $t = 5.75$ ,  $P < 0.0000$ ). The arms were flexed through arcs ranging from a few degrees to more than 180 degrees. Most arms were flexed only once before another arm was brought into play. Often, one arm was flexed while another on the same animal was in its recovery stroke.

Examination of histological sections of the arm of *E. parrae* revealed the presence of large dorsal (oral) longitudinal muscles linking the arm segments (Fig. 5). These muscles, which are described elsewhere (Hyman, 1955) as flexor muscles, are clearly responsible for the flexure of the arms. There are no opposing longitudinal muscles, but large ligaments are found ventral (aboral) to the flexor muscles (Fig. 5). The recovery phase of arm waving must



**Figure 3.** Frequency histogram comparing the durations of the effective strokes (hatched) and recovery strokes (solid black) during arm flexure of *Endoxocrinus parrae*.

therefore be achieved by elastic recoil. Small dark-staining cell bodies at the insertions of the ligaments (Fig. 5B) appear to be juxtaligamental cells (Wilkie, 1984), which are known to regulate collagen viscosity in other echinoderms. The largest axons in arm cross sections measured  $3.75 \mu\text{m}$  in diameter, and most were between  $2.5$  and  $3.5 \mu\text{m}$  in diameter.

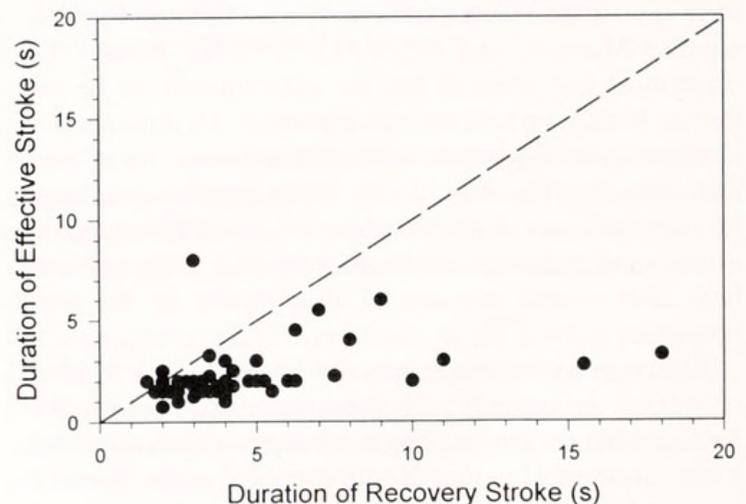
#### Functions of arm waving

With the use of a close-up video camera, we determined that flexures often occurred in response to mechanical stimuli caused by various organisms and particles. For example, when the arms of stalked crinoids become entrapped in the tentacles of adjacent sea anemones, arm flexures allow them to escape. Arms are also flexed in response to contacts by small crustaceans. Such crustaceans are always attracted to the lights of the submersible in large numbers, affording us increased opportunities for observing encounters between crinoids and crustaceans. On 17 February 1980, we came upon a rocky ridge supporting more than 200 *E. parrae* and *C. asterius* at a depth between 409 and 500 m off Booby Rocks, New Providence Channel, Bahamas. As we passed up the ridge without stopping, we filmed 49 crinoids in two aggregations, observing all the while only two instances of arm-waving behavior. We then rested the submersible near a third large aggregation and filmed it from a distance of 3 m for 7 min. The percentage of animals participating in arm waving and the number of arm waves per individual increased linearly with the number of crustaceans visible (Fig. 6). Although these regressions are consistent

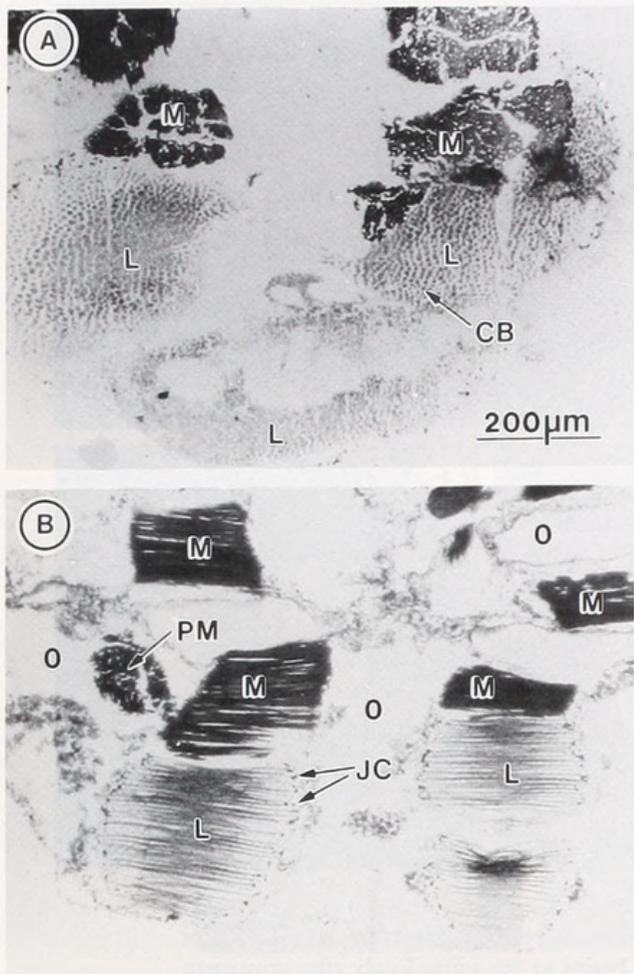
with the idea that crustaceans stimulate arm waving, we could not dismiss the possibility that density of crustaceans covaried with some other factor (e.g., illumination time) until video cameras with higher resolution were installed in 1991.

On 24 October 1991 at a depth of 642 m off Egg Island, we located a large aggregation of *E. parrae*. By focusing on inactive individuals, we recorded 10 instances of arm waving that were clearly stimulated by a single crustacean. A representative encounter is shown in Figure 7. The time required for initiation of a visible response to the impact of this crustacean was 0.47 s. In every case, the crustacean contacted the crinoid on the oral side of the arm between the pinnules and in the region of the food groove. In one observed encounter, the crustacean remained attached during three sequential flexures before becoming dislodged; in all other instances, the crustacean was dislodged by the initial arm movement and swam away. On subsequent dives, crustacean-induced arm movements were also recorded for *C. asterius*, one of which is shown in Figure 8. Here, the crustacean was swimming upstream in the turbulent downstream wake of a crinoid feeding passively in the current. When the crustacean contacted the oral side of the arm, a small flexure was elicited immediately (Fig. 8), and the crustacean moved downstream.

We dropped sediment from the manipulator on six separate occasions with two to four attempts on each experiment. Sediment containing a mixture of particles ranging in size from 1 to several millimeters elicited discrete flexures of individual arms when individual particles struck (Fig. 9). Small amounts of very fine silt did not



**Figure 4.** Durations of individual effective strokes plotted against durations of corresponding individual recovery strokes for individual arm flexures of *Endoxocrinus parrae*. If flexure and recovery were of the same duration, all points would fall on the dashed line. Most points lie below the line, indicating that recovery strokes are generally, but not always, longer than effective strokes.



**Figure 5.** Cross section (A) and longitudinal section (B) of an arm of *Endoxocrinus parrae* showing longitudinal flexor muscles (M), and extensor ligaments (L) connecting portions of ossicles (O). Individual bundles of collagen (CB) are visible in the ligaments. Cell bodies of juxtaligamental cells (JC) are visible at the points where collagen fiber bundles insert into the brachial ossicles. PM: longitudinal muscle of a pinnule cut in cross section.

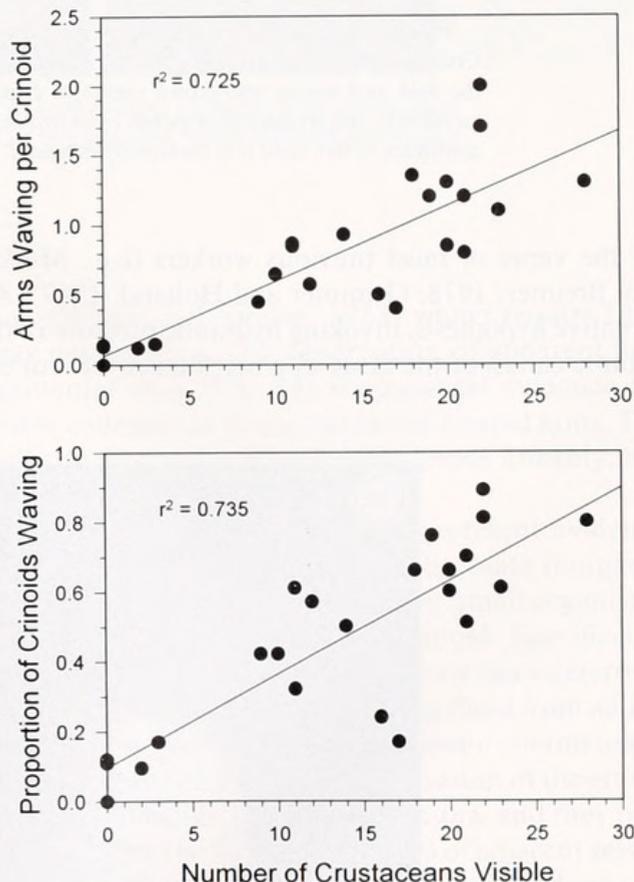
stimulate waving, but fine sediment in large quantities sometimes elicited a dramatic arm-waving response involving numerous arms. Figure 10 shows the response of one *E. parrae* individual to a large piece of flocculent organic matter that lodged firmly on an arm. The crinoid moved the affected arm as well as adjacent arms several times until the material was dislodged.

Various kinds of crabs and ophiuroids (e.g., euryalids) commonly perch on sessile organisms, including large sponges, gorgonians, and antipatharians, on the Bahamian slope. These same organisms live on the stalks of crinoids, but we have never seen a single individual occupying the crown region. We suppose that arm waving might deter occupation of the crown by ophiuroids and crabs, but cannot prove this with observations.

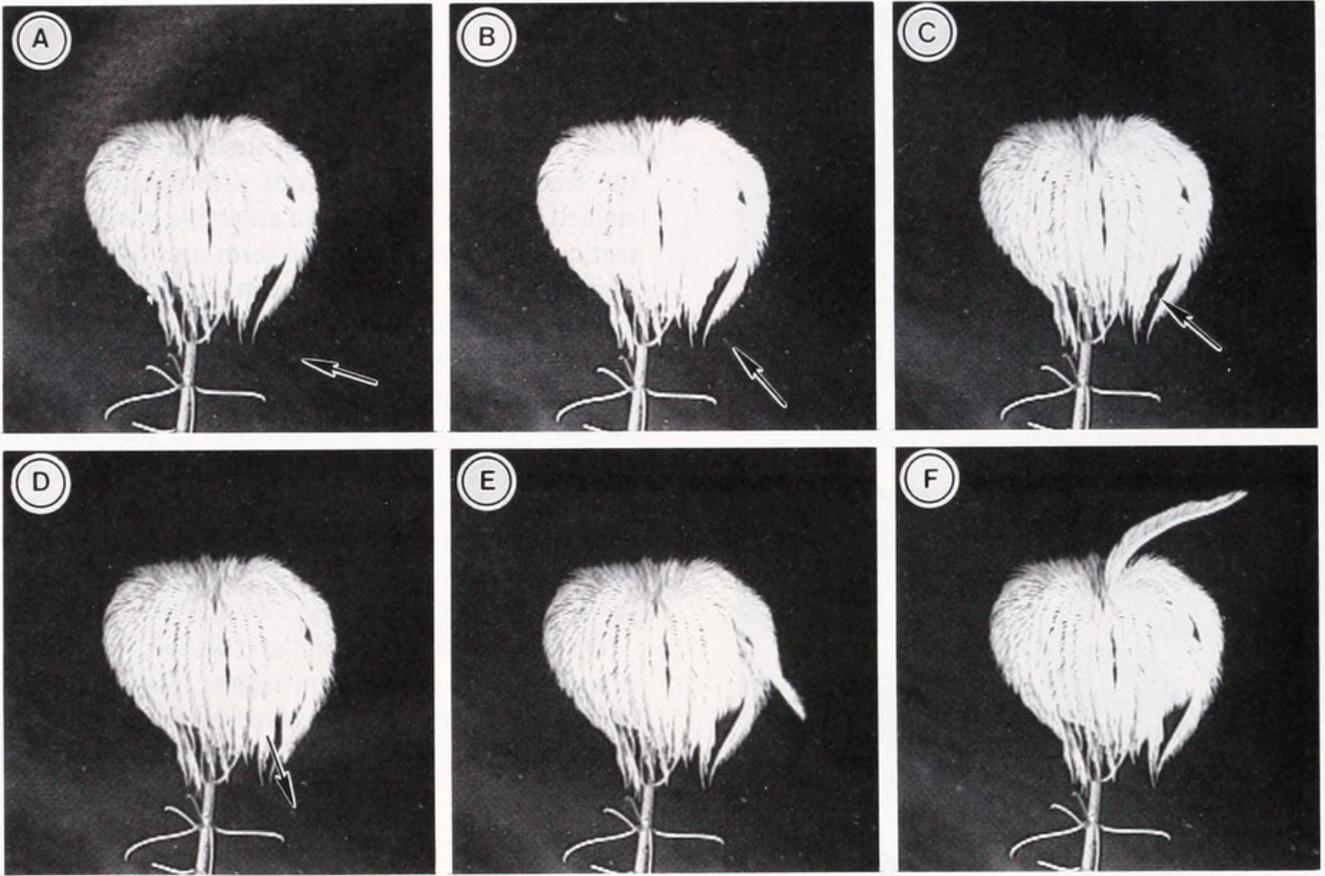
**Discussion**

Virtually all sessile animals have neuromuscular mechanisms for ridding themselves of impinging organisms or objects that threaten them or that interfere with the feeding process. It is not surprising, therefore, that stalked crinoids would have an active mechanism of protection appropriate to their form and life style. In echinoderms, some protective mechanisms involve the use of giant nerve fibers and very rapid (0.25 s) reaction times (Cobb, 1985; Cobb and Ghyyot, 1993). The nerve fibers of *E. parrae* measured between 2.5 and 3.75 μm in diameter, only about 30% as large as the giant fibers in *Ophiura ophiura* (Cobb, 1985). However, these are larger than the 1 μm diameter neurons found in most echinoderms (Cobb, 1985). Reaction times of stalked crinoids (about 0.5 s) were about twice as long as those reported for ophiuroids (Moore and Cobb, 1985).

On the basis of behavioral and histological observations, it appears that arm flexure results from the contraction of large flexor muscles, and that recovery results from the elastic recoil of ligaments. This interpretation is consistent



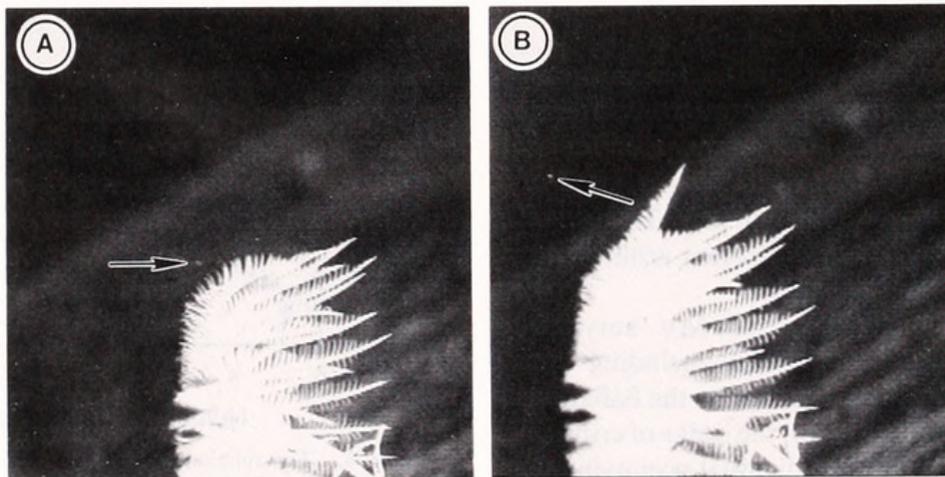
**Figure 6.** The relationships between crustacean density and the number of arms waving per crinoid (top panel) and proportion of crinoids waving arms (bottom panel) during a single 7-min taping session in a dense bed of *Endoxocrinus parrae* at 409 m depth at Booby Rocks, Bahamas.



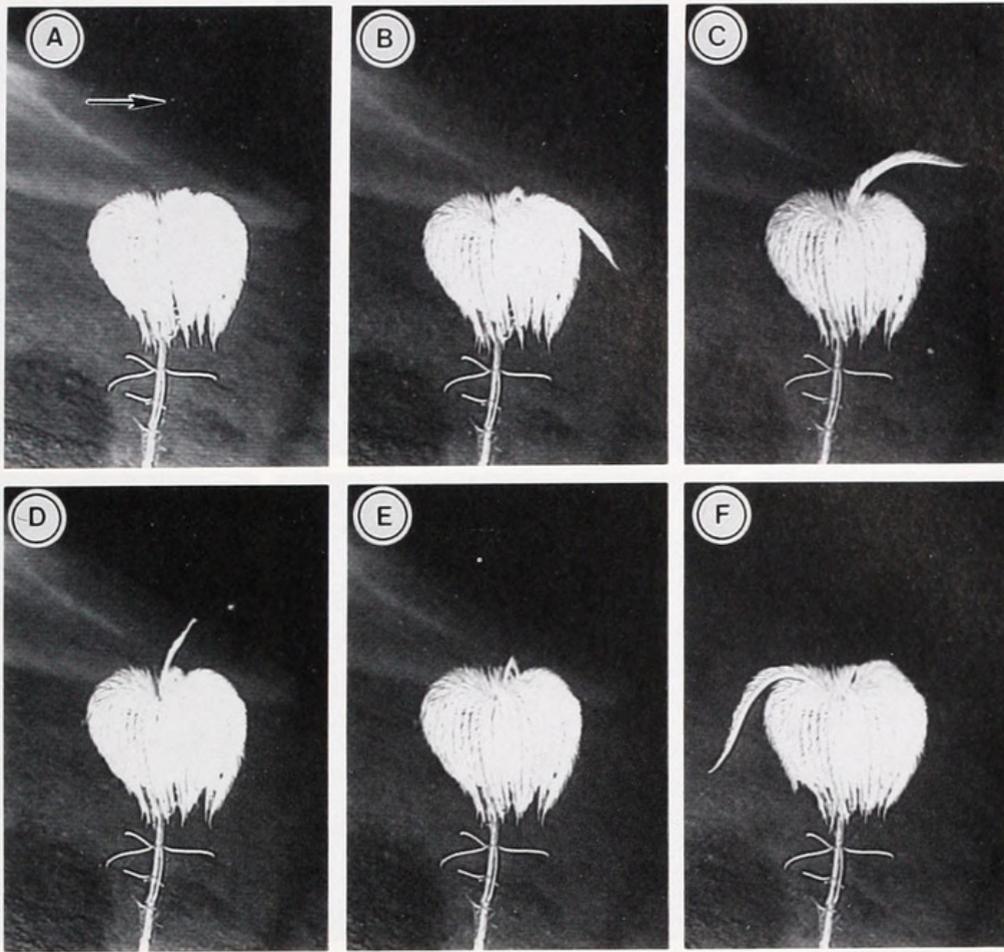
**Figure 7.** Response of *Endoxocrinus parrae* to an individual crustacean contacting the arm. (A-C) Crustacean (position and direction of swimming indicated by arrows) enters rapidly from the right side of the field and moves into crown region of crinoid. (D) Arm begins to flex immediately after crustacean contacts it, and crustacean responds by swimming rapidly away (arrow). (E-F) Arm contacted by crustacean continues to flex until it is maximally extended.

with the views of most previous workers (*e.g.*, Muller, 1843; Breimer, 1978; Grimmer and Holland, 1987). An alternative hypothesis, invoking hydraulic pressure in the coelomic canals of the arms as a mechanism of arm ex-

tension, has been put forward by Candia Carnevali and Saita (1985). Grimmer and Holland (1987), however, showed experimentally that destruction of these coelomic canals did not affect recovery from flexure in the coma-



**Figure 8.** (A) Small crustacean swimming upstream (in direction of arrow) within the turbulent wake of a feeding *Ctenocrinus asterius*. (B) Small arm flexure following contact by crustacean (arrow), which is thrown downstream.



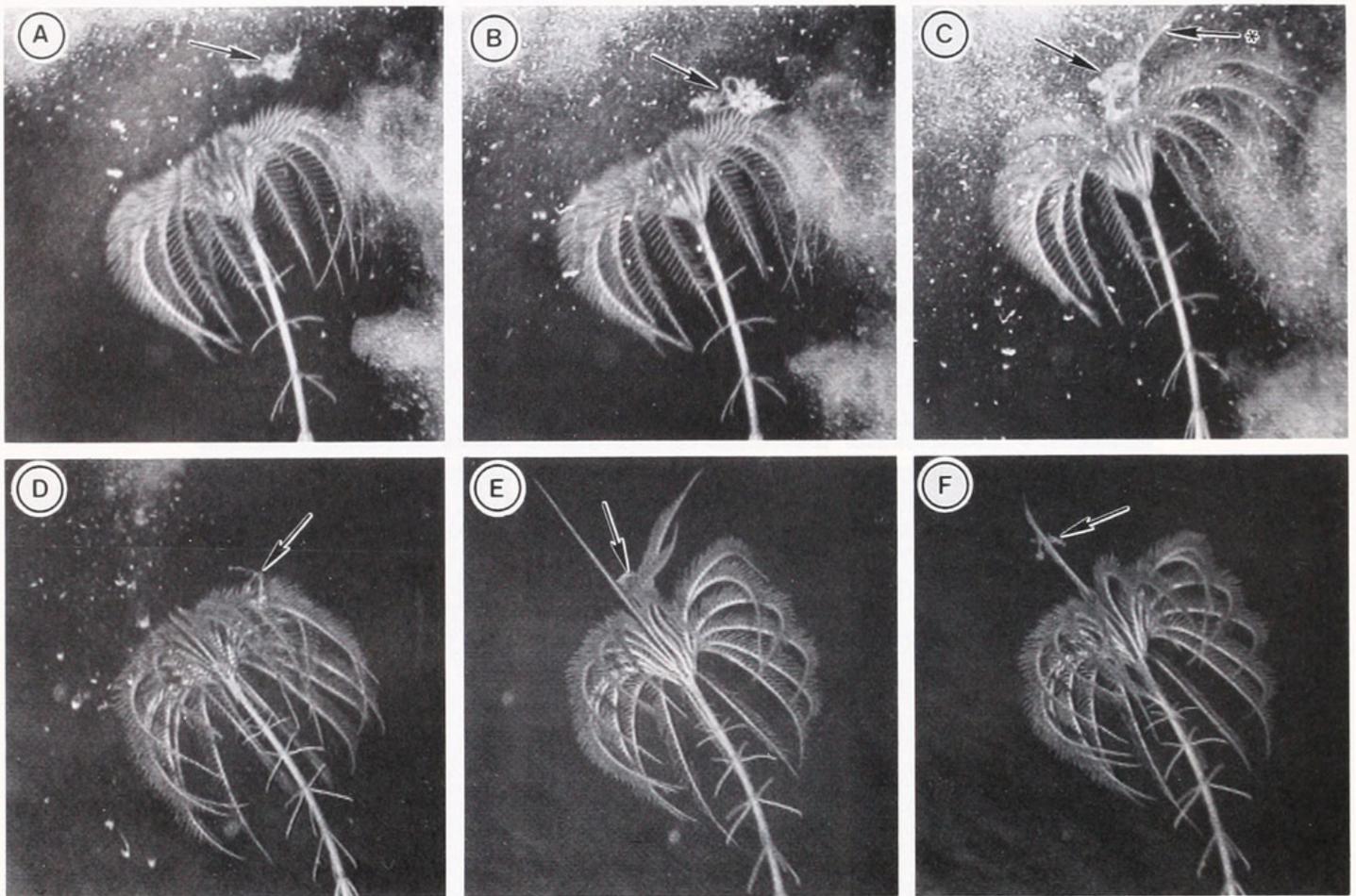
**Figure 9.** Arm flexures of *Cenocrinus asterius* in response to sand particles dropped on the crown. Sand particles (one is indicated by arrow in A) were falling throughout this sequence, which involved movements by arms on all sides of the crown.

tulid *Florometra serratissima*. In fact, their experimental results demonstrate that elastic forces in the aboral soft tissues of the arm of a comatulid were alone sufficient to drive a power stroke in active swimming. We suggest that a similar mechanism is involved in the recovery stroke of stalked crinoids such as *E. parrae*.

Existing evidence does not support the idea that arm waving is involved in food collection. Unlike some other sedentary filter-feeding echinoderms at bathyal depths (e.g., brisingid asteroids: Emson and Young, 1994), stalked crinoids are not known to capture large particles (Meyer, 1982; Lawrence, 1987). Indeed, our observations indicate that large particles contacting the crown are thrown away from the crown, not toward the mouth. Arm waving could enhance encounters with small particles, particularly in still water. However, such a feeding strategy would seem inefficient in the oligotrophic habitats where these animals live, since arm flexure requires considerable muscular involvement and might result in a net energy loss. By contrast, the maintenance of posture for passive feeding may involve catch connective

tissues (Wilkie and Emson, 1988) which require little energy expenditure. Our observation of apparent juxtagalagental cells (Fig. 5B) is equivocal evidence for mutable collagenous tissues in stalked crinoid arms. The use of arm flexing for filter feeding seems unlikely, but cannot be discounted completely.

Arm-waving behavior appears on present evidence to be principally a mechanism to eliminate inorganic particles from the crown and to deter small organisms from settling on the arms of the crinoid. Specifically, we have demonstrated that the behavior has a deterrent effect on small crustaceans, preventing them from acting as predators, food thieves, or opportunistic commensals. Arm movements may prevent colonization of the crown by crabs, ophiuroids, and other epifauna, and they permit escape from the feeding structures of adjacent sessile organisms such as sea anemones. Inorganic and organic particles that fall on the arms also elicit arm waving, so the behavior may have evolved as a general mechanism for ridding the crown of unwanted particles. As all stalked crinoids that have been examined histolog-



**Figure 10.** Response of *Cenocrinus asterius* to fine sediment and a large flocculent mass of detritus dropped on the crown. (A) Sediment contacts the crown, and a large particle of detritus (arrow) falls toward one arm. (B) Detrital mass lands on the arm. Note that the fine silt elicits no dramatic responses from the arms. (C) Arm (asterisk) with large detrital particle flexes, dislodging a portion of the mass. (D) Remainder of detrital mass (arrow) remains on the arm. (E, F) Various arms in the region of the detrital mass flex repeatedly, apparently attempting to dislodge the attached detritus.

ically have similar flexor muscles, we suspect that arm waving may be a behavior of great antiquity and common to many living and extinct crinoids.

### Acknowledgments

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