

RELOCATION MOVEMENT IN A STALKED CRINOID (ECHINODERMATA)

Charles G. Messing, M. Christine RoseSmyth,
Stuart R. Mailer and John E. Miller

Of about 80 species¹ of extant stalked crinoids, or sea lilies, more than half attach permanently to hard substrates by cementation of a terminal stalk plate or to sediments by branching rootlets. The remainder compose the family Isocrinidae and anchor chiefly to hard substrates via segmented prehensile cirri that arise in whorls of five at intervals along the stalk. Several authors have inferred that cirral attachment is temporary; swimming with arms or cirri and passive drifting along the bottom have been suggested as means of relocation after detachment (Carpenter, 1884; Kirk, 1911; Conan et al., 1981). Roux (1976) suggested that increased sedimentation rates on a canyon-mouth population of *Diplocrinus (Annacrinus) wyvillethomsoni* (Jeffreys) could cause individuals to relocate. However, most isocrinids appear to favor relatively stable environmental conditions (indicated by sediment shadows, hydrographic records, and growth and orientation patterns of co-occurring sessile invertebrates). Significant mobility has not been demonstrated up to now.

Although isolated observations of the isocrinid *Endoxocrinus parrae* (Gervais), indicate that it can crawl with its arms, in situ observations from submersibles during the last 15 years (Macurda and Meyer, 1974; 1976; Neumann et al., 1977; Messing, 1985) have not included extended time-series data for individual specimens essential for understanding the details of detachment and locomotion. The establishment by Research Submersibles, Ltd. of daily, shore-based submersible dives to 250 m off Discovery Bay, Jamaica, and, more recently, Georgetown, Grand Cayman Island, has allowed us to make repeated observations of individuals of the isocrinid, *Cenocrinus asterius* (Linnaeus), over extended periods and document their movement, reported herein.

MATERIALS AND METHODS

Observations were recorded on audio tape, hand-held cameras, and externally mounted cameras during operations aboard the following research submersibles: DSRV ALVIN (Bahamas, March, 1984; A. C. Neumann, University of North Carolina at Chapel Hill, Principal Investigator), JOHNSON-SEA-LINK I and II (JSL) (Bahama Islands, 1983-1985; John E. Miller, Harbor Branch Oceanographic Institution, Inc., Principal Investigator), Research Submersibles, Ltd.'s PC-8B, PC-1203, PC-1802 (RSL) (Jamaica, Turks and Caicos Is., and Grand Cayman I., 1984-1986).

RESULTS AND DISCUSSION

Attempts to induce swimming in isocrinids have failed. When "nudged" with a submersible's manipulator arm, an isocrinid's parabolic filtration fan collapses; the arms flex further aborally, especially distally, and the pinnules (the short side branches) adduct toward the arms. When grasped by a manipulator during col-

¹ Taxonomic revision of several genera will undoubtedly reduce this number.

lection, the arms close together adorally. When a crown is cut off, it sinks to the bottom.

Observations made during a series of dives aboard JSL I in the Bahama Is. first suggested that isocrinids do move about, but by crawling rather than swimming (Miller et al., personal observations). On dive JSL-I-1361 (16 June 1983, off Grand Bahama I., 455 m), the crown of an unidentified isocrinid, inadvertently decapitated by a submersible propeller, was briefly observed crawling along the bottom with its arms. (Subsequent efforts to induce active locomotion by cutting off crowns have not been successful.) During dive JSL-I-1362 (17 June 1983, off Grand Bahama I., 403 m), a single isocrinid [probably *Endoxocrinus parrae* (Gervais)] was found detached and lying on its side on open sediment with an obvious drag mark over 1 m long behind its stalk (Messing, 1985). Confirmation of crawling in *E. parrae* came during dive JSL-I-1501 (23 October 1983, off Little San Salvador I., 539 m) when a single individual was observed crawling down a 35–40° lithified pavement slope veneered with sediment. The crinoid moved forward by using four to six arms in contact with the sea floor. The remaining arms were flexed aborally with pinnules adducted against the arms. Individual arm flexure consisted of moving an arm adorally until the distal tip encountered the substrate; subsequent aboral curling pulled the animal forward. This rowing movement of the "working arms," though coordinated, was not simultaneous. As some arms pulled, others flexed adorally. The stalk and cirri were pulled passively behind the crown and did not contribute to movement. [Sars (1868) observed dredged, uprooted *Rhizocrinus lofotensis* (Sars) (Bathycrinidae) to crawl with its arms, passively dragging its stalk.] It is likely that gravity coupled with slope angle contributed to the movement. From the observers' vantage point, however, the forward movement appeared much too controlled to be merely a downslope slide.

To further document stalked crinoid mobility, a prominent outcrop in 226 m north of Discovery Bay, Jamaica, bearing nine fully-grown *Cenocrinus asterius* was visited repeatedly over a 6-month period by two of us (MCR and SRM). *C. asterius* is the only large stalked crinoid commonly found on sediment-veneered pavements and outcrops on West Indian island slopes in 180–250 m. Like *E. parrae*, it is rheophilic, forming a parabolic filtration fan with arms recurved into the current and oral surface directed downcurrent (Macurda and Meyer, 1974). From about 20% to more than 50% of the stalk length may parallel the bottom. *Endoxocrinus parrae* has a denser filtration fan and a shorter stalk than *C. asterius* and ranges chiefly between 300 and 700 m (although the two species overlap bathymetrically).

The outcrop under study, "Nine-Lily Rock," is about 6 m long, 3 m wide, and 1.8–2.4 m high on its upslope side. It is a small example of the numerous limestone "haystacks" found below 200 m on the Jamaican island slope (Lang, 1974; Moore et al., 1976). In photographs taken on 2 October 1984, the nine specimens form three clusters of two, four, and three individuals along the southern, upslope crest of the block (Fig. 1A). By 19 February 1985, at least two specimens had relocated (Fig. 1B). Although some specimens did not move during this period (as indicated by identical orientations of stalk bases relative to adjacent solitary corals between photographs), it cannot be definitely stated that the specimens at C and D in Fig. 1B were the only ones to relocate (from positions A and B in Fig. 1A). Removal of the submersible to Grand Cayman precluded further observations on this site.

Cenocrinus asterius occurs under similar conditions off Grand Cayman where additional observations have been made. Of a group of five *C. asterius* on a promontory adjacent to the wreck of the freighter KIRK PRIDE in 230 m off Georgetown Harbor, submersible pilots Allen Wright and Dennis Denton report

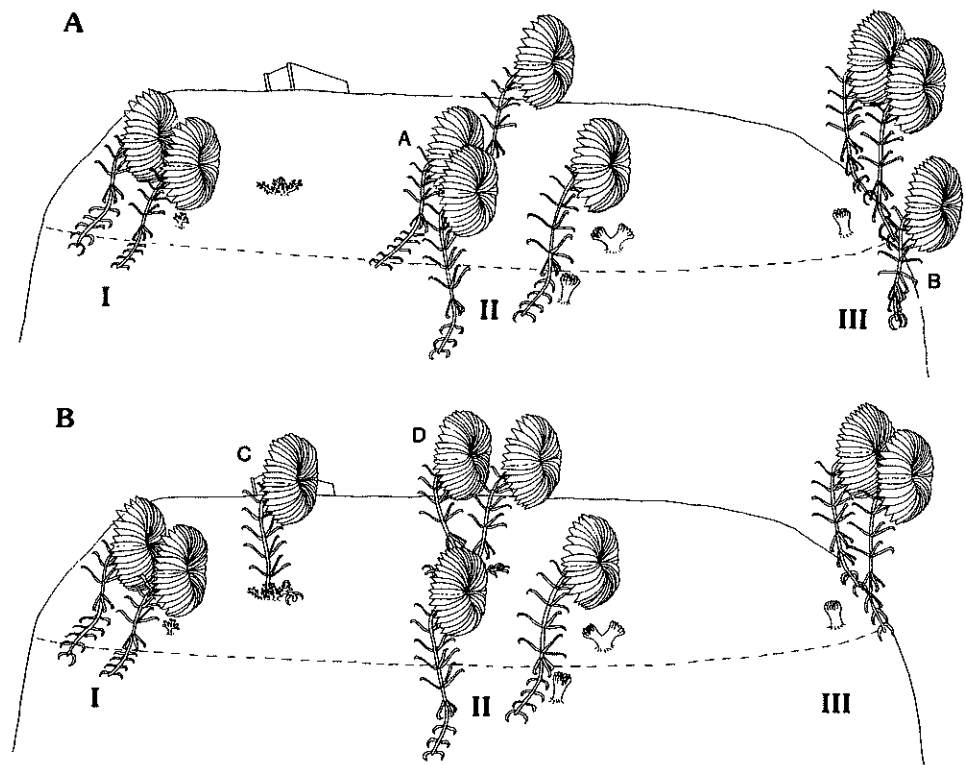


Figure 1. Distribution of *Cenocrinus asterius* (Linnaeus) on "Nine-Lily Rock," Discovery Bay, Jamaica, 226 m. A. 2 October 1984. B. 19 February 1985. Illustrations by C.G.M. from photographs taken by S.R.M. and M.C.R.

that one made several excursions over a period of several months. It maintained an upright feeding posture most of the time but was observed several times to move up to 1 m between dives on successive days. Actual locomotion was not observed due to short dive durations but the crinoid was occasionally seen in a crawling posture. Figure 2 (arrow) shows a different individual in this group of five that assumed the crawling posture as the submersible approached during a dive in May 1986. None of us has seen this reaction before; this instance appears to be coincidental with rather than elicited by the submersible's approach. The stalk lies along the sediment-veneered substrate but turns up apically so that the oral surface of the crown faces upward. The arms are splayed out with most tips touching the substrate, and the pinnules are adducted toward the arm axis. (Meyer et al., 1984, noted tightly adducted pinnules among actively arm-crawling comatulids.) The cirri are extended and do not appear to cling to any object although the terminal cirri curve toward each other.

In September 1986, one of us (CGM) observed a *C. asterius* in the crawling posture in 260 m, the sediment slope around its crown bearing short radiating scratch marks. An area of confused but similar marks scored the sediment surface behind the crinoid, between it and a boulder about 2 m away. Unfortunately, the short periods of observation during each dive prevent us from determining frequency, duration, or possible variations in means of progression.

Factors inducing relocation likewise remain unknown although several possi-

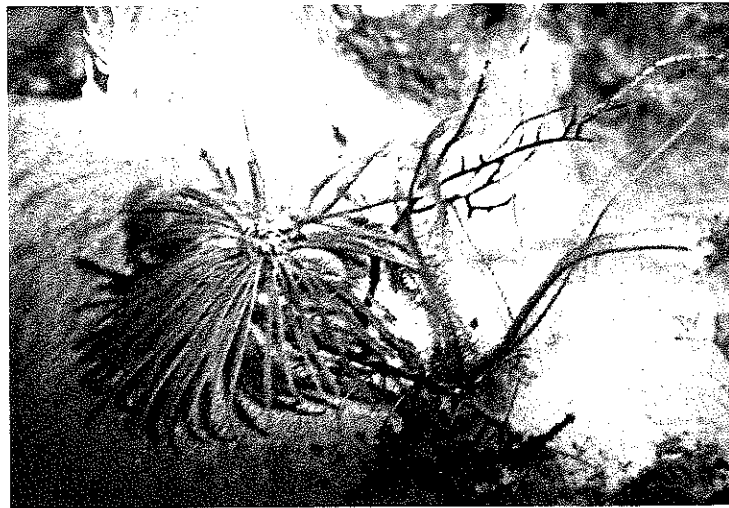
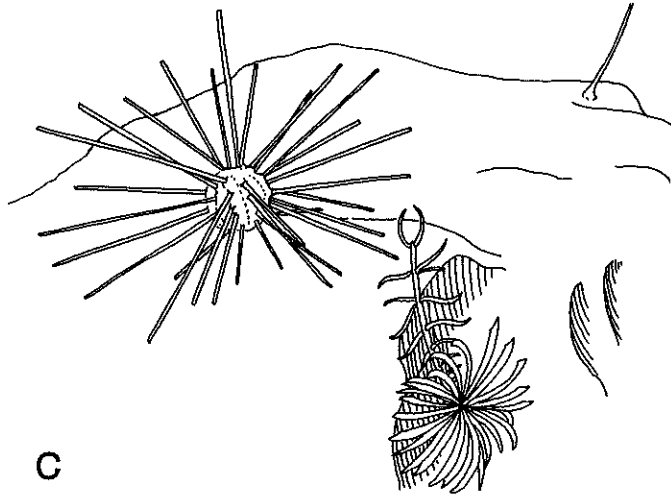
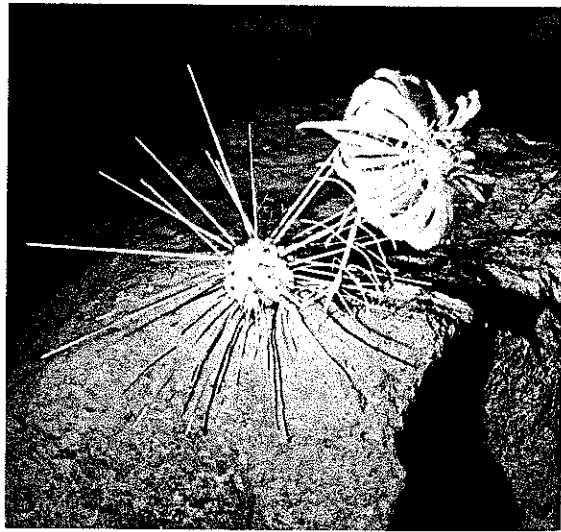
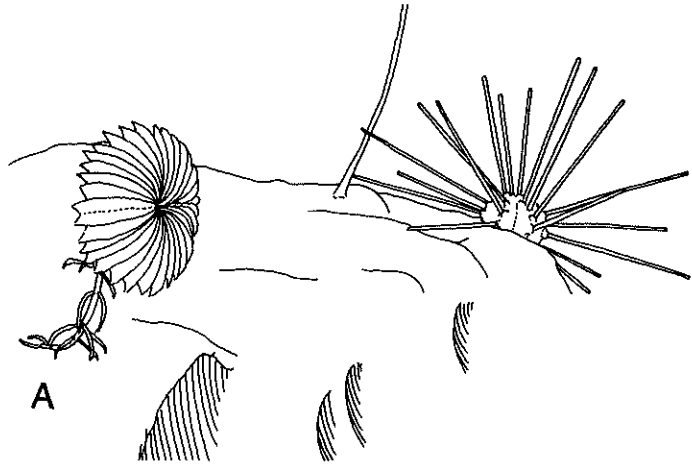


Figure 2. *Cenocrinus asterius* on a promontory adjacent to the wreck of the KIRK PRIDE off Georgetown, Grand Cayman, 230 m. A. A group of five individuals including four actively filtering and one (arrow) in the "crawling" posture. Two large comatulids (*Comactinia meridionalis hartlaubi*) are visible at lower right (c). B. Close-up of specimen in "crawling" posture with *C. m. hartlaubi* clinging to its cirri. Both photographs by Dennis Denton, Research Submersibles, Ltd.



bilities exist. Figure 3 illustrates an interaction between *C. asterius* and *Calocidaris micans* (Mortensen), a large, cidaroid echinoid occasionally observed among West Indian isocrinid assemblages. Schematic illustrations (Figs. 3A and 3C) are taken from photographs. The echinoid was first observed about 1.5 m from the crinoid on 21 October 1985 (Fig. 3A). By the next day (Fig. 3B), it had moved adjacent to the crinoid's stalk, its long primary spines penetrating and apparently disrupting the filtration fan formed by the crinoid's arms. The pinnules are adducted against the arms and the arms are aborally curled more strongly than in actively filtering individuals, particularly on the side away from the viewer. By 23 October (Fig. 3C), the crinoid had detached itself and was lying prostrate against the side of the rock below its former perch in the crawling posture described above. Subsequent dives found the echinoid departed and the crinoid in its original position.

Filtration-fan disruption by an echinoid is an obvious enough disturbance, but large, mobile, benthic organisms are surprisingly uncommon among isocrinid assemblages in the Atlantic. Of 561 external 35-mm photographs (automatically triggered by an intervalometer) taken during three DSRV ALVIN dives in 600–625 m in the northeastern Straits of Florida and showing hard bottom assemblages (Messing et al., in prep.), crinoids (chiefly isocrinids) appear in 83%. Vagile macrofaunal groups (e.g., echinoids, asteroids, fish, decapod crustaceans, and large gastropods) each appear in fewer than 7% of the frames. Large, benthopelagic fishes may be important disruptive agents, however. Solitary or paired wreckfish (*Polyprion americanus*), exceeding 1 m in length, were seen on almost every dive and appear to be resident on crinoid-festooned ridges here. We have also seen large members of the families Serranidae, Carangidae, Berycidae, and Odontaspidae over isocrinid assemblages. Similarly, Conan et al. (1981) report relatively few large, mobile animals in association with large numbers of *Diplocrinus* (*Annacrinus*) *wyvillethomsoni* in the Bay of Biscay but their records include a large gadid (*Physis*?). They also show a photograph of an oreosomatid supposedly feeding on a specimen of *D. (A.) wyvillethomsoni* that is missing some arms. It appears that the "missing" arms are merely foreshortened towards the viewer and that the fish is not feeding, however.

Crowding and predation may also stimulate relocation. Although clusters of two to five *C. asterius* occasionally appear, specimens are usually separated by more than a meter when more than one are visible at a time. Observations chiefly have been made on groups in which relative positions were easily observed. Such crowded individuals may be more likely to relocate; crowns that overlap relative to current flow will likely reduce feeding efficiency.

Recent studies have documented predation on crinoids by fishes (Meyer and Macurda, 1977; Meyer, 1985) and invertebrates (Mladenov, 1983). *Cenocrinus asterius* has been observed off Jamaica, Grand Cayman and Providenciales I., and Turks and Caicos Is., with regenerating arms. These arms are almost always few in number and at least one-third regrown. If they were removed by another organism and not simply autotomized, the "grazer" is apparently content to take only a portion of the resource available and then only at long intervals. However,

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Figure 3. *Cenocrinus asterius* with echinoid, *Calocidaris micans*, off Georgetown, Grand Cayman. A. About 1300 hr, 21 October 1985. B. About 1400 hr, 22 October 1985: echinoid apparently disrupting the crinoid's filtration fan. C. About 1030 hr, 23 October 1985: crinoid below original perch in crawling posture. Illustrations by C.G.M. from photographs courtesy of Research Submersibles, Ltd. and M.-J. Bodden.

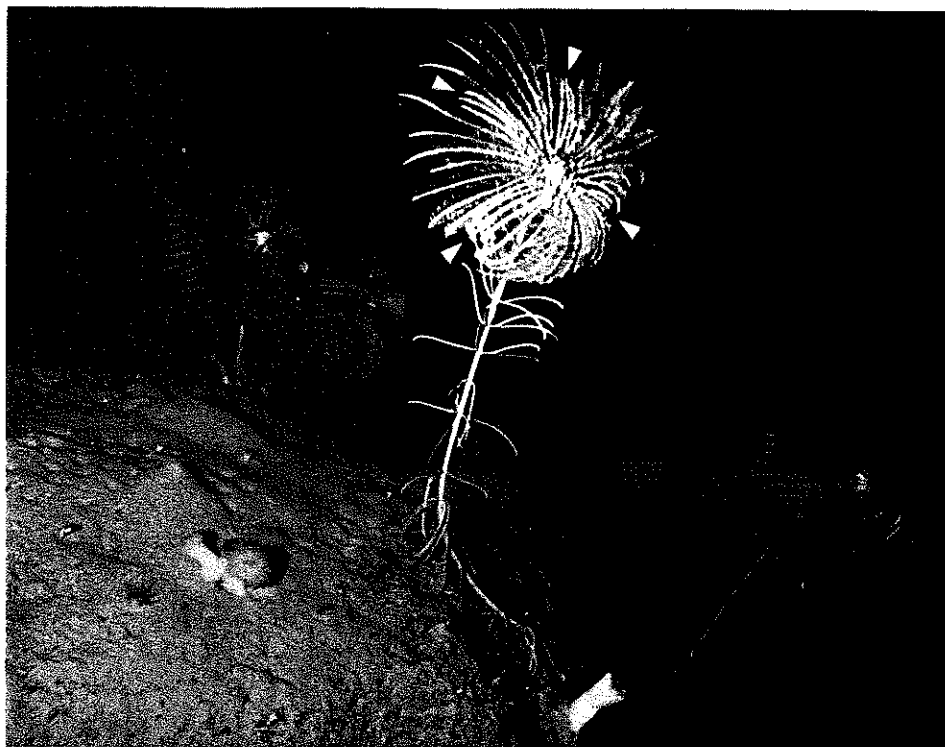


Figure 4. *Ctenocrinus asterius*. A member of group II on "Nine-Lily Rock," Discovery Bay, Jamaica, 19 February 1985: arrows show four groups of regenerating arms. Orientation of stalk base relative to adjacent solitary corals is the same as in October 1984. (Print reversed from original 35 mm slide.) Photograph by S.R.M.

even extensive arm loss may not be cause for relocation. Figure 4 shows a member of group II on "Nine-Lily Rock" (19 Feb 1985) with 15 regenerating arms in four groups. The same individual had no regenerating arms the preceding October. Uniformity of regeneration suggests that these arms were lost at about the same time. Together, they account for nearly 25% of the crinoid's filtration fan. Despite this loss, the animal remained in place.

The arrow crab, *Stenorhynchus seticornis*, often clings to the convex oral surface of the *C. asterius* crown but is an unlikely predator. Williams (1984) suggests that *S. seticornis* is a suspension feeder, ingesting planktonic particles that snag on its setae. The crab likely uses the crinoid as an advantageous perch; its small chelae appear unable to clip off arms although it may steal boluses of food from the crinoid's ambulacral grooves.

Planned investigations using time-lapse cinematography should provide more information on the crinoids' mode of locomotion, reasons for moving, and extent and nature of predation. They also may reveal postural or filtration-related activity cycles. Similar studies are planned for assemblages in the Straits of Florida in order to examine possible mobility and activity cycles in other isocrinid genera (i.e., *Endoxocrinus*, *Diplocrinus*, and *Neocrinus*) as part of a larger inquiry into the dynamics of deep shelf and slope, hard bottom assemblages.

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ADDRESSES: Nova University Oceanographic Center, 8000 N. Ocean Drive, Dania, (C.G.M.) Florida 33004 33173; (M.C.R. and S.R.M.) Research Submersibles, Ltd., P.O. Box 1014, Grand Cayman I., British West Indies; (J.E.M.) Harbor Branch Oceanographic Institution, Inc., 5600 Old Dixie Hwy, Fort Pierce, Florida 34946.