Coral Reefs (2006) 25: 213–222
DOI 10.1007/s00338-006-0089-6

REPORT

Tara Oak · Robert E. Scheibling

Tidal activity pattern and feeding behaviour of the ophiuroid *Ophiocoma scolopendrina* on a Kenyan reef flat

Received: 19 June 2004 / Accepted: 16 December 2005 / Published online: 15 March 2006

Abstract *Ophiocoma scolopendrina* exhibits a distinctive pattern of feeding activity on intertidal reef platforms off Kenya. With the first wave of the flooding tide, dense aggregations of these ophiuroids (up to 320 m^{-2}) engage in a 1–2 min burst of surface-film feeding, vigorously sweeping the air-water interface and associated sea foam with the ventral surface of 2–4 arms. Suspension feeding (with arms extended in the water column) is the primary feeding mode throughout the rest of the tidal cycle (involving 25–65% of the population at a time), while bottom feeding (with arms extended along the substratum) is infrequent ($<10\%$). Field experiments showed that surface-film feeding is regulated by water depth and can be triggered by suspended particles. This feeding mode appears to be an adaptation to the intertidal habitat, enabling the ophiuroids to exploit a nutrient-rich surface film during a temporal refuge (low tide) from fish predation. Dense populations of *O. scolopendrina* may represent an important trophic link between producers of particulate organic material and higher-level consumers in coral reef environments.

Keywords · Feeding behaviour · Intertidal zone · *Ophiocoma scolopendrina* · Ophiuroid

Introduction

Ophiuroids exhibit a variety of feeding mechanisms but generally separate into two main feeding types based on prey size: (1) species which consume large prey (carnivores and scavengers), and (2) microphagous feeders which extract plant animal and detrital particles from the water column or substratum (suspension and deposit feeders) (Warner 1982; Lawrence 1987). Different behavioural and morphological adaptations characterize the primary feeding modes, although some species are generalists using alternative prey capture mechanisms. The success of ophiuroids in the benthic marine environment has been attributed to this diversity of feeding habits (Fontaine 1965). Ophiuroids are highly vulnerable to predators and most shallow-water species are cryptic and expose only their arms to capture food (Aronson 1991; Munday 1993; Bourgoin and Guillou 1994). Where the threat of predation is low, some species emerge from refuges to feed although increased conspicuousness may have severe costs in terms of survival (Aronson and Harms 1985).

The genus *Ophiocoma* has a circumglobal distribution in the tropics and subtropics with the greatest number of species in the Indo-Pacific (Devaney 1974). Species of this genus are among the most abundant ophiuroids in intertidal and shallow subtidal reef habitats around atolls, islands and continental margins. They are primarily microphagous feeders and employ a variety of suspension and deposit feeding mechanisms (Chartock 1983). One species, *Ophiocoma scolopendrina* (Lamarck), which inhabits intertidal reef flats, has evolved a specialized method of capturing neuston and detrital particles and films suspended at the air-water interface (Ely 1942; Magnus 1962; Chartock 1983).

On the flooding tide, *O. scolopendrina* emerges from crevices and concealing vegetation to extend the ventral side of its arms along the air-water interface and vigorously sweep this surface. Suspended particles and scum are trapped on small mucous-covered spines that are cleaned by the tube feet and transported as a bolus to the mouth (Magnus 1962; Chartock 1983). At other stages of the tidal cycle, *O. scolopendrina* engages in microphagous suspension- and deposit-feeding typical of other members of the genus (Chartock 1983) and ophiuroids generally (e.g. Pentreath 1970; Warner and

Communicated by Environment Editor B.G. Hatcher

Tara Oak and Robert E. Scheibling contributed equally to this paper. The order of authorship is alphabetical

T. Oak · R. E. Scheibling (✉)
Dalhousie University, B3J 4H1, Halifax, NS, Canada
E-mail: rescheib@dal.ca
Tel.: +1-902-4942296
Fax: +1-902-4943736

Woodley 1975; Loo et al. 1996). The disc remains hidden in crevices or under vegetation and the arms are projected into the water column or along the substratum to accumulate particles on mucous nets or mucous-covered spines (Chartock 1983).

Our study, on an intertidal reef flat in Kenya, is the first to quantify patterns of feeding activity and behaviour of *O. scolopendrina* in relation to the tidal cycle, and to experimentally investigate factors associated with the flooding tide (including depth, water flow, and suspended particulate material) that may trigger or regulate surface-film feeding. We relate this unusual feeding behaviour to tidal patterns in the availability of different particulate food resources and the risk of predation. We also examine the potential role of these ophiuiroids as a trophic link between producers of particulate organic material in coral reef environments and higher-level consumers such as fish.

Materials and methods

Study site

Our study was conducted in March and April 2000 on an intertidal reef flat at Tiwi Beach, Kenya (4°14'S, 39°34'E). The reef flat (Fig 1a) extends ~300 m across a shallow gradient (< 1% slope) from the high tide mark to the seaward margin, where depth increases abruptly to 3–4 m (below chart datum). *Ophiocoma scolopendrina* was abundant on the reef flat between about 50 and 250 m offshore.

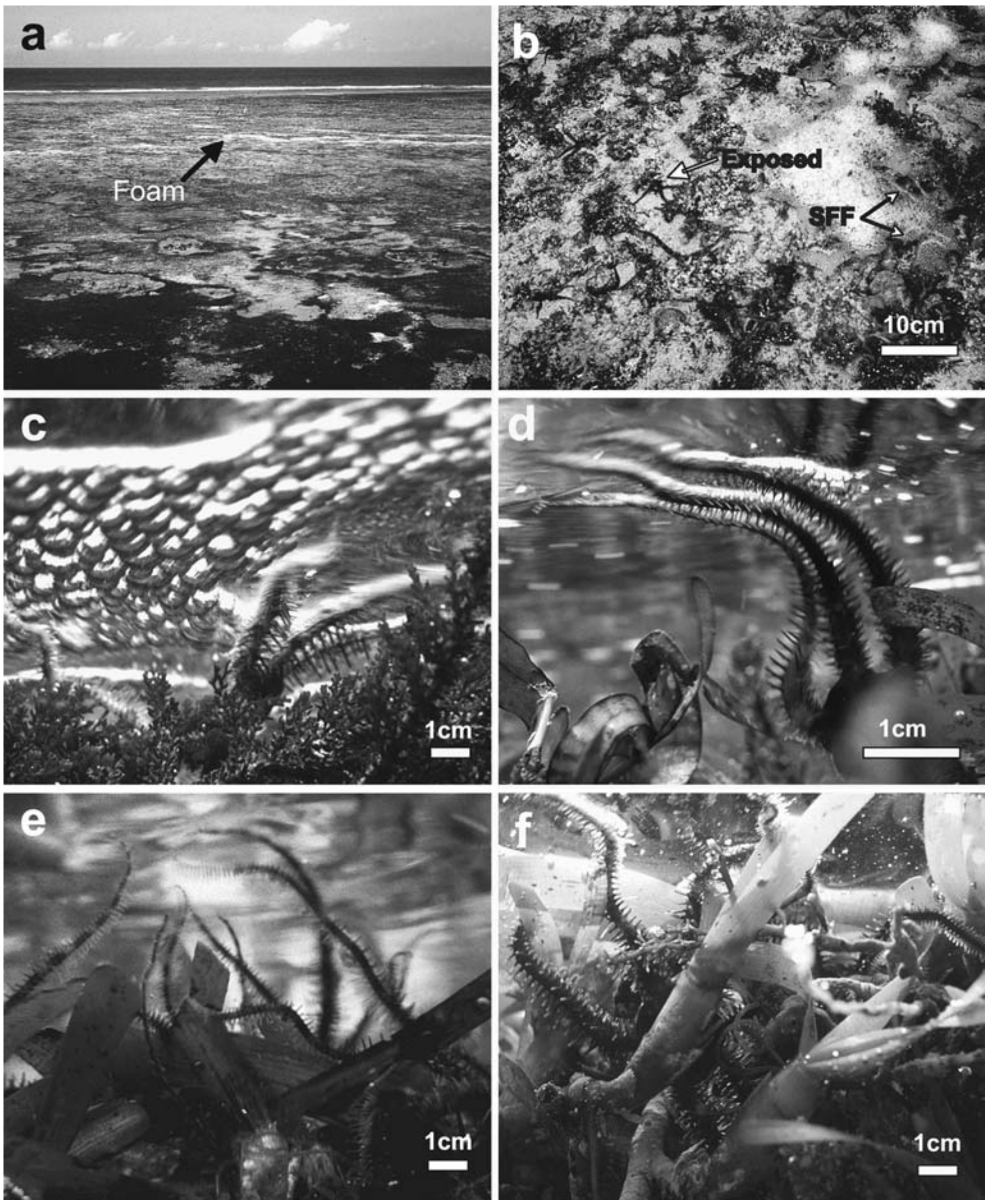


Fig. 1 **a** The intertidal reef flat at Tiwi Beach, Kenya, spanning ~300 m from the shore (lower right) to the seaward edge where waves are breaking. The arrow indicates a band of sea foam delivered with the flooding tide. Distant figures of the researchers (in Stratum 5, Table 2) are evident between the band of foam (above the *arrow*) and the edge of the reef platform. Dark patches in the foreground are seagrass. **b** *Ophiocoma scolopendrina* engaged in surface-film feeding (SFF) with arms upturned and sweeping the surface foam (two individuals are indicated with *paired arrows* on right). Also shown is an individual that has just completed surface-film feeding and remains largely exposed on the bottom (*single arrow* on left); other individuals have retreated to crevices with just their arms exposed. The band of foam is progressing from left to right. **c** An individual sweeping sea foam with 3 arms during first contact with the flooding tidal front. **d** As water level rises the arms are extended further to maintain contact with the surface. **e** Individuals with only the arm tips in contact with the surface during the last instant of surface-film feeding. **f** Individuals ascending seagrass to retain contact with the surface for feeding

The substratum of the reef platform is porous limestone of Pleistocene origin (Ngusaru 1997) with overlying patches of sand, and turfs of seagrass (*Cymodocea rotundata*) and macroalgae (mainly *Cystoseira myrica*, *Turbinaria decurrens*, *Padina boryana*, and *Laurencia papillosa*). Live corals are generally restricted to large rifts in the platform along the outer edge and to the deeper water beyond. Water depth, measured with a graduated pole at fixed locations in each sampling stratum (see below), ranged from 0 to 1.4 m at spring tides, and from 0.1 to 0.5 m at neap tides. Shallow tide pools (usually <20 cm deep) of varying dimensions occur throughout the study area. Water temperature, recorded at 5 min intervals by data-logging thermometers anchored on the reef flat at 170 and 60 m offshore (Hobotemp Tidbits, Onset Computer Corp. Pocasset, Mass, USA), ranged from 26 to 38°C over the tidal cycle, occasionally reaching peaks of 40°C in shallow pools (measured by hand-held mercury thermometer) during mid-day low tides.

Density and size structure

The density and size structure of *Ophiocoma scolopendrina* at Tiwi Beach was estimated by stratified random sampling of the reef platform. Ophiuroids were counted and measured in 20×20 cm (400 cm^2) quadrats ($n=25$–31) haphazardly placed along each of five belt transects (~2 m wide) extending 50 m in an alongshore direction and spaced at 30 m intervals between 75 m and 195 m offshore (Stratum 1–5). Data were pooled across strata to describe the population. Disc diameter of ophiuroids was measured in 3 mm size classes by matching the disc against a template of seven squares increasing in dimension by 3 mm increments from 3 to 21 mm. In some cases ($<10\%$), individuals could not be extracted without damage from refuges in the substratum and were counted but not measured. The length of the longest (non-regenerating) arm and disc diameter were measured (1 mm accuracy with vernier calipers) in an additional sample of 116 individuals to determine the relationship between these metrics by linear regression. These ophiuroids were narcotized in an isotonic solution of magnesium chloride at a concentration of 72 gl^{-1} to facilitate measurement and prevent arm loss.

Feeding behaviour and exposure

Patterns of exposure and feeding behaviour of *Ophiocoma scolopendrina* in Stratum 3 (120–150 m offshore) were quantified by sampling ophiuroids at 1–2 h intervals throughout the daytime tidal cycle over five days. For each sample, all visible ophiuroids within ten haphazardly-placed quadrats of 400 cm^2 were classified according to three levels of exposure (low, medium, high) and three feeding modes (surface-film feeding, suspension feeding, deposit feeding) (Table 1). Ophiuroids were pooled over the ten quadrats to give sample sizes ranging from 33 to 118 individuals (mean = 82) per sampling interval per day. The percentage of individuals in each exposure level, and engaged in each type of feeding, was calculated for each pooled sample. The samples were then grouped in 2 h periods according to tidal stage and averaged across sampling days. Depth at fixed reference points (in Stratum 3) was recorded at the beginning and end of each sampling interval.

Table 1 Classification of degree of exposure and feeding mode of *Ophiocoma scolopendrina*

Exposure level	
Low	Disc hidden in a crevice or hole, at least 1 arm visible
Medium	Partly covered by vegetation, disc and some arms visible
High	Disc and most or all arms fully exposed
Feeding mode	
Surface-film	Arms sweeping the air-water interface
Suspension	Arms suspended in the water column
Deposit	Arms sweeping the substratum

The pattern of surface-film feeding was quantified in greater detail by increasing the sampling frequency during the first "wave" of incoming tide on four days. This wave is a shallow tidal front that forms once the rising sea begins to flood the platform. The front advances slowly (a few centimetres per second) towards shore, generally carrying with it a conspicuous layer of sea foam (Fig. 1a). On each sampling day, ten quadrats of 400 cm^2 were placed in areas of high ophiuroid density (6–22 individuals per quadrat). The proportion of individuals engaged in surface-film feeding and the water depth were recorded in each quadrat at approximately 12 min before, during, and 12 min after the first wave of the incoming tide. Data from each sampling interval were pooled over the ten quadrats on each day and averaged across sampling days.

The number of arms used in surface-film feeding was recorded by haphazardly sampling individuals at water depths of 2–4 cm as the incoming tidal front progressed over the platform. Data were pooled for samples taken on three sampling days giving a sample size of 414 individuals.

Analysis of particulate food sources

To compare the organic content of different particulate food sources available to *O. scolopendrina*, surface sediment, seawater, and sea foam were haphazardly sampled at daytime low tides within an area of ~10 m^2 in Stratum 1 (60–90 m offshore) over 3–5 days. Sediment was collected by scooping the top 3 mm of fine sand into a small plastic vial (3–13 g dry weight per sample). Seawater from shallow tide pools was collected in 60 ml syringes (0.4–1.8 l per sample) and filtered on glass-fibre (GF/C) filters. Foam was collected with an aquarium dip net and deposited onto glass-fibre filters (0.04–1.0 g dry weight of particulate residue per sample). The samples were dried and weighed, combusted in a muffle furnace at 500°C for 4 h, and then re-weighed to calculate ash-free dry weight and percentage of dry weight that is organic matter. Replicate samples on each day ($n = 4$–6) were averaged for each particulate food source and grand means were calculated based on daily averages.

Field experiments

Experiment 1

To examine environmental factors that may potentially regulate surface-film feeding in *O. scolopendrina*, naturally occurring individuals were enclosed in cylindrical plastic arenas (25 cm diameter, 10 cm height, 490 cm^2 of enclosed surface area) placed on flat sand and seagrass substrata in Stratum 2 (90–120 m offshore). The effect of the presence of sea foam, water flow and depth on feeding behaviour was examined by comparing *O. scolopendrina* in enclosed arenas to open-sided control arenas. Control arenas had solid 3 and 2 cm-high rims around the top and bottom, respectively, and three equal panels cut out of the sides, separated by three evenly-spaced 5 cm wide supporting walls such that 81% of the circumference between the two rims was open. They presented some of the potential artefacts of the fully enclosed (with solid sides) arenas, such as disturbance to enclosed ophiuroids and sediments during deployment. The base of each arena was driven 2–3 cm into the sediment. This temporarily sealed off enclosed arenas from the incoming tide while allowing water and foam to flow naturally through the open sides of control arenas. To test their efficacy as enclosures, a fluorescent red dye (Rhodamine B, Sigma Chemicals) was released around the outside perimeter of enclosed arenas immediately after deployment.

Five arenas were used in each of six experimental trials: three enclosed and two open arenas were positioned in random order perpendicular to the direction of the incoming tide with ~2 m spacing between arenas. The arenas were placed in areas with <2 cm of overlying water and relatively high ophiuroid density 5–10 min before the incoming tidal front washed over the area. Within 1 min after deployment, initial water depth, the total number of individuals (7–21 per arena), and the number that were surface-film feeding were recorded in each arena. Depth and the number of individuals surface-film feeding were then recorded at 20–60 s intervals as the front passed over the area, until all surface-film feeding ceased in the arenas. Replicates were discarded (no more than one per treatment per trial) if seepage around the base occurred in enclosed arenas or if water levels rose too rapidly in open-sided controls to attain a reliable count of feeding individuals. The percentage of individuals surface-film feeding at each sampling interval was calculated and averaged across two or three replicate arenas for each treatment in each experimental trial. A paired samples t test was conducted, based on these averages for each trial, to compare the depth and time (from the start of the experiment) at which surface-film feeding peaked and ended between enclosed and open treatments.

Experiment 2

To examine the effect of suspended particles in triggering surface-film feeding, experiments were conducted with three particulate materials: fine sand from the surrounding area, carmine particles, and sea foam collected near shore that was laden with organic material (giving it a brownish tinge). Enclosed arenas (with solid walls) were placed on the substrate at low tide approximately 30–60 min prior to the first wave of the flooding tide. The arenas were placed in the same general area as Experiment 1 but where there was sufficient water depth for surface-film feeding. Three arenas were used in each of three or four (for sea foam) trials: two were haphazardly selected to receive the experimental treatment and the third was used as a control. The total number of individuals and the number of individuals engaged in surface-film feeding in each arena was recorded before each trial.

The experimental treatment consisted of sprinkling approximately 3 ml of sea foam with associated particulate material, 100 mg of dry sand, or 20–30 mg of carmine particles onto the water surface enclosed by each experimental arena. These amounts were sufficient to disperse each of these particulate materials across the water surface within an arena. The maximum number of ophiuroids that were surface-film feeding during a 3 min interval after the introduction of particulate substances was recorded. The control treatment involved sprinkling seawater over the arena.

Replicate treatment or control arenas were pooled across experimental trials (which were conducted within a 30 min period on the same day) for each type of particulate material. The percentage of individuals that were surface-film feeding was compared between control and experimental treatments by t test, and among experimental treatments by 1-way analysis of variance.

Results

Density and size structure

Mean density of *O. scolopendrina* ranged from 7.9 to 12.8 individuals per 400 cm^2 among strata on the intertidal platform at Tiwi Beach (Table 2). The mean density pooled across all strata was 9.9 individuals per 400 cm^2 (or 248 individuals m^{-2}). The size-frequency distribution (as disc diameter) was similar among strata, and approximately normal about a modal class of 9 mm and class range of 3–18 mm for individuals pooled across all strata ($n = 1265$) (Fig. 2). The 3 mm size class

Table 2 Density of *Ophiocoma scolopendrina* (individuals/400 cm^2) in transects sampled at 30 m intervals offshore within each of five strata on the reef flat at Tiwi Beach, Kenya

Stratum	Distance offshore (m)	Density (/400 cm^2)	*n*
1	75	12.8 ± 5.6	27
2	105	10.0 ± 5.9	30
3	135	7.9 ± 4.0	29
4	165	10.3 ± 4.0	31
5	195	8.5 ± 4.3	25

Data are mean ± SD for *n* quadrats in each stratum

may have been under-sampled because small ophiuroids were particularly cryptic and difficult to collect for measurement. Regression analysis, based on a sample of 116 ophiuroids ranging from 4 to 18 mm in disc diameter, showed a strong linear relationship ($r^2 = 0.978$) between of arm length (L) and disc diameter (D): $L = 4.816D$. Thus the modal disc diameter (9 mm) gives a predicted arm length of 43 mm and the upper disc diameter class of 15 mm (excluding larger individuals which accounted for < 1% of the population) gives a predicted maximum arm length of 72 mm.

Feeding behaviour and exposure

The degree of exposure of *Ophiocoma scolopendrina* varied with tidal stage (Fig. 3a). Ophiuroids were most cryptic at or shortly before high tide, when 85–95% of the population was hiding in crevices or holes in the reef (Level 1, low exposure), and most exposed at low tide, when 32% was covered only by vegetation and 11% was fully exposed (Levels 2 and 3, medium and high exposure, respectively). Suspension feeding was the primary feeding mode across all 2 h tidal intervals (grand mean ± SD, 44 ± 14%), with the highest frequency of this feeding mode (65%) occurring shortly after high tide (Fig. 3b). The frequency of bottom feeding was low

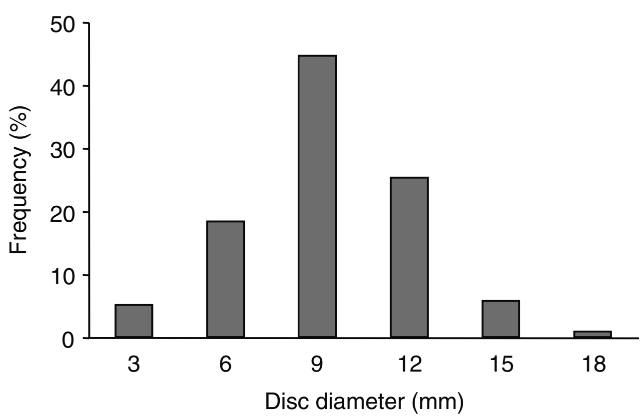


Fig. 2 Disc diameter class frequency (%) of *Ophiocoma scolopendrina* on the reef flat at Tiwi Beach, Kenya ($n = 1265$)

(< 10%) throughout the tidal cycle, with a minimum (1.4%) occurring around high tide. Surface-film feeding could occur only at low tide, when water depth was only a few centimetres.

Frequent sampling around the incoming tide indicated a burst of surface-film feeding in *O. scolopendrina* as the tidal front washed over the platform (Fig. 1b), with a mean of 47% of the population engaged in this mode of feeding (Fig. 4). The ophiuroids rapidly vacated their refuges to vigorously wave their arms along the air-water interface in an irregular pattern. Most used three arms (67%, $n = 414$) for surface-film feeding, and less often two (15%) or four arms (13%) (Fig. 5). While sweeping the water surface, they remained anchored to the substratum or vegetation with at least one arm, often turning the disc and arms entirely upside-down (Fig. 1c, d). The ophiuroids usually were fully exposed in this position. The activity lasted only a few minutes; the frequency of surface-film feeding declined to < 2% within 12 min of the passage of the tidal front. As water depth increased, contact with the surface decreased until only the very tips of the arms remained (Fig. 1e). Some ophiuroids prolonged the feeding period by ascending vegetation (Fig. 1f). Once contact was lost, they lowered their arms and retreated into refuges on the bottom. Thus, as the tidal front progressed along the reef platform it was tracked by a translating wave of ophiuroid arms, moving like a stadium full of exuberant arm-waving fans at sporting event.

Particulate food sources

The suspended particles in the seawater over the reef flat consisted of 74.7 ± 8.2% organic matter by dry weight (mean ± SD, $n = 4$), however these were extremely dilute at only 22.8 ± 6.3 mgl^{-1}. The surface sediment consisted of 5.3 ± 1.4% ($n = 17$) organic matter, and particles in sea foam delivered by the incoming tide were 43.4 ± 20.0% ($n = 32$) organic matter.

Field experiments

Experiment 1

In open-sided control arenas, surface-film feeding generally peaked immediately upon exposure to the first wave of the incoming tide and then dropped off quickly as water depth increased. The solid walls of enclosed arenas slowed the rise in water level within the arenas, as water seeped in through the porous substrate. Depth in enclosed arenas was consistently shallower, at any given time, than in the control arenas and surrounding environment (Fig. 6). Therefore surface-film feeding in enclosed arenas peaked later and was sustained longer than in open control arenas.

There was no significant difference between the enclosed and open arenas in the mean depth at which

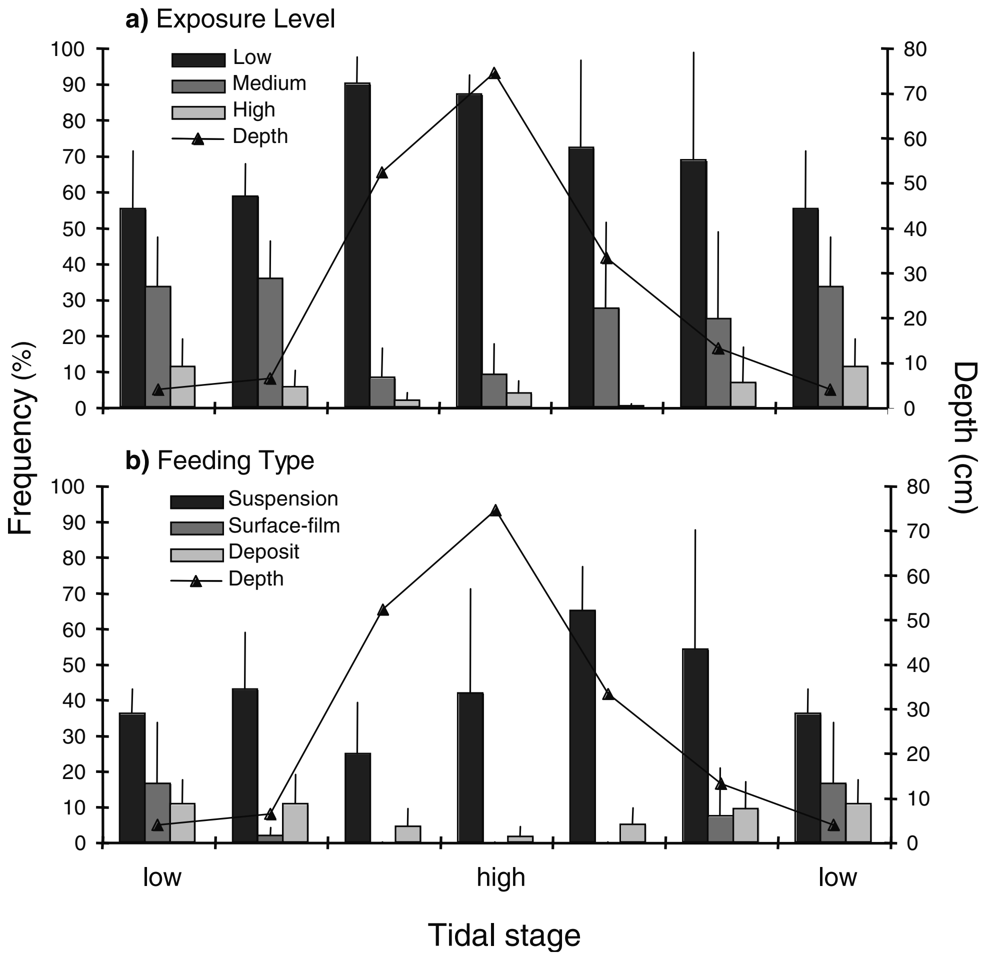


Fig. 3 Mean (+SD) frequency (%) of *Ophiocoma scolopendrina* in **a** three exposure levels (low, medium and high; Table 1), and **b** three feeding modes (suspension, surface-film, and deposit feeding; Table 1) at 2 h tidal stages on the reef flat at Tiwi Beach, Kenya. Values at the low tide interval are repeated for graphical clarity. Mean water depth at each tidal stage is also shown

surface-film feeding peaked or ended (Fig. 7a), although the timing of these events differed significantly between the treatments (peak: $t_5=3.723$, $P=0.007$; end: $t_5=3.62$, $P=0.008$) (Fig. 7b). The peak in frequency of surface-film feeding occurred at a mean depth (averaged across both treatments) of 2.3±0.4 cm (mean ± SD); most feeding had ended at a mean depth of 4.0±0.5 cm.

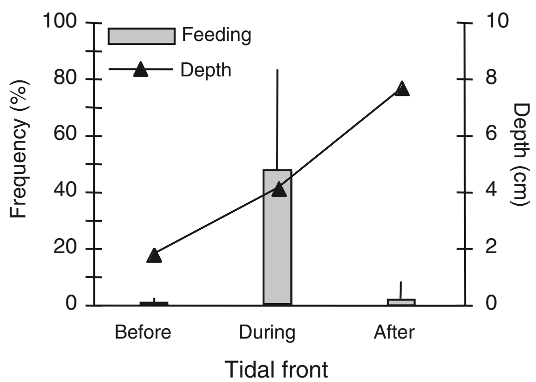


Fig. 4 Mean (+SD) frequency (%) of *Ophiocoma scolopendrina* engaged in surface-film feeding about 12 min before, during, and 12 min after passage of the flooding tidal front on the reef flat at Tiwi Beach, Kenya. Mean water depth at each tidal stage is also shown

Experiment 2

Surface-film feeding was triggered by addition to arenas of each of three types of particulate materials: sand, inert (carmine) particles, and organic material associated with

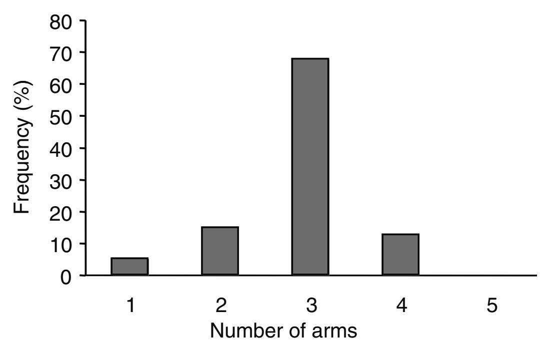
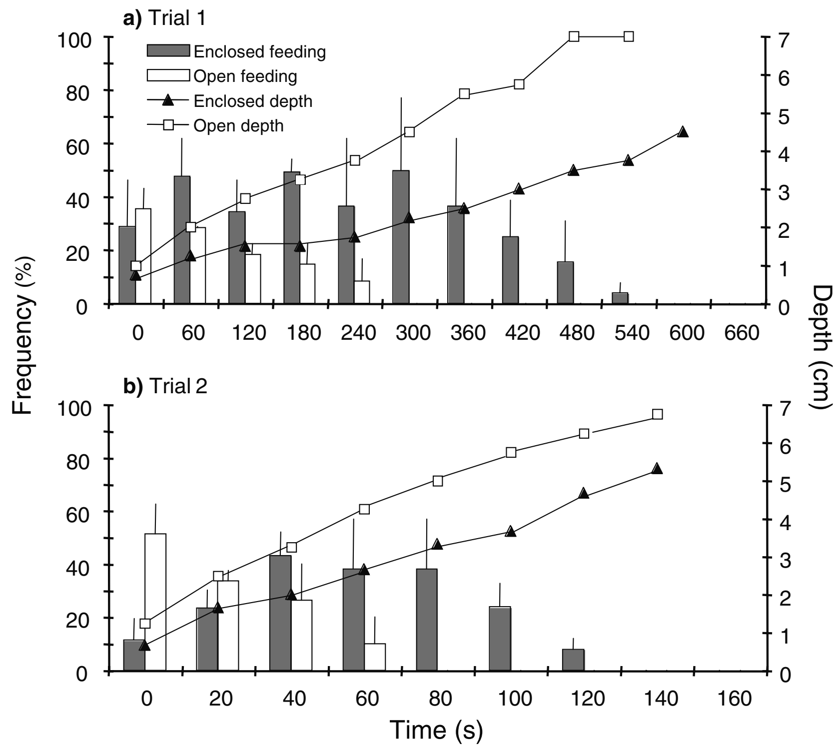


Fig. 5 Frequency (%) of the number of arms per individual of *Ophiocoma scolopendrina* used in surface-film feeding on the reef flat at Tiwi Beach, Kenya ($n=414$)

Fig. 6 Mean (+SD) frequency of *Ophiocoma scolopendrina* engaged in surface-film feeding over time (since contact with the first wave of the flooding tide) in open (control) and enclosed arenas during two representative experimental trials on the reef flat at Tiwi Beach, Kenya



the surface foam. Less than 2% of ophiuroids in experimental arenas were engaged in surface-film feeding before the addition of these materials. There was a significant increase in the percentage of individuals engaged in surface-film feeding in treatment arenas (40–60%) relative to the respective sea water controls (<5%) for each material tested (*t* test, $P<0.001$) (Fig. 8). The percentage of individuals that was surface-film feeding was significantly higher for the treatment with carmine particles than that with foam ($F_{1,\ 12}=4.1$, $P=0.015$). There were no significant differences between carmine and sand, or sand and foam treatments.

The carmine particles and dry sand were of similar consistency. Both formed a fine film of suspended

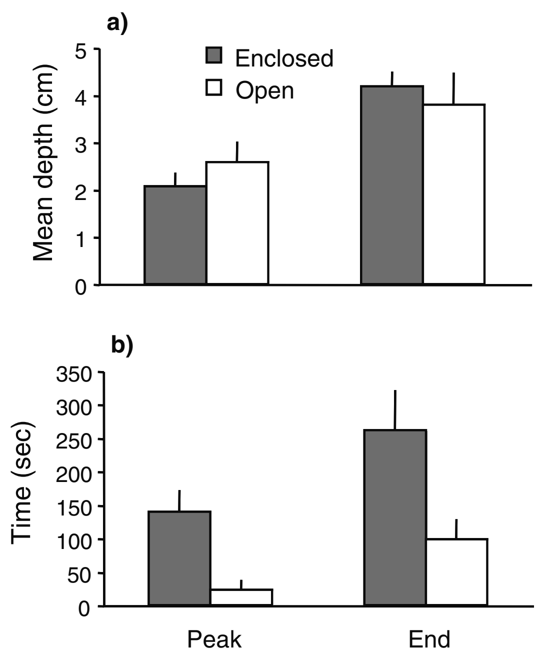


Fig. 7 Mean (+SD) **a** depth and **b** time (since contact with the first wave of the flooding tide) at the peak and the end of surface-film feeding by *Ophiocoma scolopendrina* in open (control) and enclosed arenas on the reef flat at Tiwi Beach, Kenya

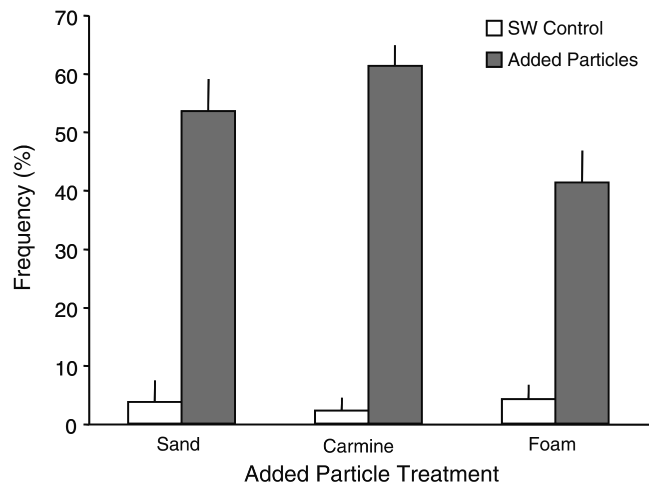


Fig. 8 Mean (+SD) frequency (%) of *Ophiocoma scolopendrina* engaged in surface-film feeding in arenas where particulate materials (sand, carmine particles, sea foam) were added, and in controls where only seawater was added, on the reef flat at Tiwi Beach, Kenya

particles on the water surface and dispersed evenly throughout the arena as they sank. Individuals throughout an arena responded similarly, sensing the sand or carmine particles with one or more arms, then coming fully out of hiding to feed. The collected particles were clearly evident in the ambulacral grooves as they were moved by tube feet from arm tip to mouth.

The foam used for this experiment was collected near the shoreline. It was considerably denser than the foam associated with the tidal front as it flooded the reef flat, and contained stringy agglutinations of organic material. The particles in the foam usually sank quickly to the bottom and did not distribute evenly within the arenas. Within seconds, individuals in an arena congregated where aggregates or strands of particulate material were precipitating from the overlying foam. These strands or clumps usually were grasped with one or more arms and delivered to the mouth by a curling action of the arms.

Discussion

Ophiocoma scolopendrina inhabits the upper intertidal zone on limestone reef platforms throughout the tropical Indo-Pacific region and the Red Sea (Ely 1942; Devaney 1974; Clark 1976; Chartock 1983). It is the most abundant ophiuroid in this zone, where it usually occupies small crevices in reef conglomerate or coral rubble. The average density of *O. scolopendrina* in our study (247 individuals m^{-2} across the reef flat and up to 320 individuals m^{-2} in one region) was higher than that previously recorded in other areas. Devaney (1974) reported that this species occurs in aggregations of up to 50 individuals m^{-2} in Southeastern Polynesia. At Enewetak, Marshall Islands, Chartock (1983) recorded a maximum density of 100 individuals m^{-2}, but densities of 20 individuals m^{-2} were more typical. James and Pearse (1969) noted that *O. scolopendrina* was the most conspicuous intertidal ophiuroid on the Egyptian coast of the Red Sea, but did not provide measures of abundance. The size range of *O. scolopendrina* at Tiwi Beach (from about 3–18 mm disc diameter) was similar to that recorded by Law (1995) in Fiji (1–22 mm) and Devaney (1974) in Polynesia (up to 25 mm).

Among the Ophiuroidea, surface-film feeding as an alternative microphagous feeding mechanism has been reported only in *O. scolopendrina*. This mode of feeding among intertidal ophiuroids can occur only at low tide when the air-water interface is within arms' reach. The phenomenon also has been observed in *Ophiocomina nigra*, but only in aquaria (Fontaine 1965). Because *O. nigra* is predominantly a subtidal species, this unusual feeding mechanism may be less important to its nutrition than it is to *O. scolopendrina*, a strictly intertidal species (Fontaine 1965).

Our observations of microphagous feeding behaviour in *O. scolopendrina* are consistent with previous descriptions for this species in similar habitats (Magnus 1962; James and Pearse 1969; Chartock 1983; Law 1995). Magnus (1962), in the first detailed study of surface-film feeding in *O. scolopendrina*, also noted that as the depth increased with the incoming tide, the ophiuroids lifted their arms higher in order to maintain contact with the surface. Clark (1921, in Ely 1942) described *O. scolopendrina* as using three arms for surface-film feeding, while using the other two to anchor the body in a crevice. Aside from brief bursts of surface-film feeding, *O. scolopendrina* also engages in suspension feeding with arms extended in the water column, and deposit feeding with arms sweeping the sediments (Magnus 1962; James and Pearse 1969; Chartock 1983). Suspension feeding was the primary feeding mode of *O. scolopendrina* in our study. Chartock (1983) also noted that ophiuroids at Enewetak switched to suspension feeding as depth increased with the incoming tide and surface-film feeding ceased. Deposit feeding was relatively infrequent in our study, especially around the low tide. In the Red Sea, however, Magnus (1962) observed that sweeping the substratum was the most common feeding method of *O. scolopendrina* during times of still water prior to surface-film feeding.

A sudden increase in surface-film feeding in *O. scolopendrina* with the incoming tide suggests an external trigger associated with this tidal event. A layer of sea foam, carried by the flooding tidal front, accumulates organic matter and progressively increases in thickness and discoloration as it moves shoreward across the reef platform. In Experiment 2, organic aggregates precipitating from sea foam (collected in a nearshore region of the platform) triggered surface-film feeding by *O. scolopendrina* when the foam was introduced to enclosed arenas. The ophiuroids curled their arms around larger food particles to bring them to the mouth, a method of feeding previously noted by Chartock (1983). In Experiment 1, surface-film feeding occurred in enclosed arenas that excluded foam, indicating that the presence of the foam itself, particularly before it becomes heavily laden with organic material, is not a necessary trigger for this feeding behaviour.

Water flow is known to stimulate suspension feeding in many species of ophiuroids (e.g. Pentreath 1970; Miller et al. 1992; Loo et al. 1996). In Experiment 1 however, the pattern of surface-film feeding activity was similar in control arenas (open to the ambient tidal flow) and enclosed arenas (without flow), except for a time lag in the enclosed ones. The mean depth at which surface-film feeding peaked and ended did not vary significantly between the treatments. This similarity in the pattern of feeding activity in both treatments suggests that increasing depth, even in the absence of tidal flow, can trigger surface-film feeding in *O. scolopendrina*, and that feeding ceases once the operative depth is exceeded. The peak in surface-film feeding occurred at a mean depth of 2.3 cm in Experiment 1, which is about half the modal arm length of the population (4.3 cm), and feeding ended at a mean depth of 4 cm as the surface moved beyond arms' reach of most ophiuroids. Magnus (1962) also noted that surface-film feeding in *O. scolopendrina* occurred at water depths less than 4–5 cm.

Experiment 2 indicated that surface-film feeding in *O. scolopendrina* also can be induced by the introduction of particles to the water column, without increasing water flow or depth. The ophiuroids were highly sensitive to small amounts of added sand and carmine particles, despite these having little or no nutritional value. Magnus (1962) observed similar results when he suspended sand and shavings from his razor on the water surface during the incoming tide. In Experiment 1, water percolating up through the porous reef substrate with the flooding tide may have resuspended fine particles within the enclosed arenas, although this was not visually detectable. Thus, *O. scolopendrina* may have responded to increased particle concentrations within the enclosed arenas in addition to increased depth. These potentially interacting stimuli could only be isolated under more controlled conditions in the laboratory.

Surface-film feeding associated with the flooding tide represents a very limited proportion of the activity budget of *O. scolopendrina*. Assuming an average duration of 2 min per tidal cycle (as measured in control arenas in Experiment 1, Fig. 7b) and two low tides per day, the daily investment in surface-film feeding may be as little as 4 min day^{-1} (=0.3%). In a few localized microhabitats, water flowing off of the reef allowed some ophiuroids to also engage in surface-film feeding during the ebbing tide, but this was relatively infrequent. The vigour of arm sweeping activity during short bursts of surface-film feeding suggests a rate of energy expenditure which exceeds that of passive suspension feeding and deposit feeding. Considering the high organic content of particulate matter associated with surface foam (43%), the rate of energy acquisition is presumably also highest during surface-film feeding. Although seston in the water column over the reef platform has a high organic content (75%), it is a very dilute food source for suspension feeding (23 mgl^{-1}), and surface sediments swept during deposit feeding have a low organic content (5%).

The restricted distribution of *O. scolopendrina* in the intertidal zone not only affords the ability to exploit the nutrient-rich water surface layer but also provides a refuge from predators that are excluded from these habitats at low tide. Potential predators of these ophiuroids include a variety of fish, which frequent intertidal reef flats at high tide (Law 1995). A large proportion of ophiuroids throughout the study area had regenerating arms indicative of fish predation, and individuals tethered in deeper water off the seaward edge of reef platform at Tiwi Beach were rapidly consumed by small wrasses and other reef fish (Scheibling unpublished data). Chartock (1983) discussed feeding and habitat as possible factors contributing to the adaptive radiation of the genus *Ophiocoma*, from predominantly bottom-feeding species in the subtidal zone, to more specialized species such as *O. scolopendrina* in the intertidal zone. Surface-film feeding in *O. scolopendrina* may have evolved in response to reduced predation pressure in intertidal habitats.

The high population density of *O. scolopendrina* recorded in our study, and elsewhere in the Indo-Pacific region, suggests this species represents an important trophic link in shallow reef ecosystems between producers of particulate organic material (such as corals) and higher-level consumers that prey on ophiuroids. At Tiwi Beach, the population of *O. scolopendrina* spanned more than 200 m of the 300 m wide reef flat. Given an average density of ophiuroids across this range of 247 individuals m^{-2} (Table 2), a 1 m section of flooding tidal front would pass over 49,400 individuals as it moved shoreward. Assuming only half the population in this swath (24,700 individuals) engages in surface-film feeding (Fig. 4) and each animal uses three arms (Fig. 2), this gives an estimate of 74,100 arms sweeping the surface film from every meter of tidal front on a single flood tide. Furthermore, following this burst of surface-film feeding, these ophiuroids continue to remove particles suspended in the rising water column, or deposited on the bottom, throughout the tidal cycle. In turn, they likely are consumed, either completely or partially (as arm tips), by fish that forage on the submerged reef flat at high tide. Additional studies that measure ingestion rates and secondary production of populations of *O. scolopendrina*, and losses due to predation, are needed to elucidate this species' role in reef trophodynamics. Until such information is available, estimation of the potential ecological importance of these ophiuroids remains a matter of ''arm-waving''.

Acknowledgements We thank Donald Macdonald and the Canadian Field Studies in Africa Program 2000 for enabling us to travel to Kenya and conduct this research. We are particularly grateful to Jessica Guidobono, Amanda Lane, Erin Myers, Susanne Pokotylo, and Carley Watson for their untiring assistance in the field. Two anonymous reviewers and Bruce Hatcher provided helpful advice on improving the manuscript. The research was supported by a Natural Sciences and Engineering Research Council Discovery Grant to RES.

References

Aronson RB (1991) Predation, physical disturbance, and sublethal arm damage in ophiuroids: a Jurassic-Recent comparison. Mar Ecol Prog Ser 74:91–97

Aronson RB, Harms CA (1985) Ophiuroids in a Bahamian saltwater lake: the ecology of a Paleozoic-like community. Ecology 66:1472–1483

Bourgoin A, Guillou M (1994) Arm regeneration in two populations of *Acrocnida brachiata* (Montagu) (Echinoidea; Ophiuroidea) in Douarnenez Bay, (Britanny: France): an ecological significance. J Exp Mar Biol Ecol 184: 123–139

Chartock MA (1983) Habitat and feeding observations on species of *Ophiocoma* (Ophiocomidae) at Enewetak. Micronesica 19:131–149

Clark AM (1976) Echinoderms of coral reefs. In: Jones OA, Endean R (eds) Biology and geology of coral reefs. VIII. Biology 2. Academic, New York, pp 95–123

Devaney DM (1974) Shallow-water asterozoans of Southeastern Polynesia. Micronesica 10:105–204

Ely CA (1942) Asteroidea and ophiuroidea of Hawaii. Bernice P Bishop Museum Bulletin 176:1–63

Fontaine AR (1965) The feeding mechanisms of the ophiuroid *Ophiocomina nigra*. J Mar Biol Assoc UK 45:373–385

James DB, Pearse JS (1969) Echinoderms from the Gulf of Suez and the Northern Red Sea. J Mar Biol Assoc India 11:78–125

Law, RA (1995) A comparative study of reproduction, growth, ageing and regeneration in three species of tropical Indo-West Pacific brittle stars (*Ophiocoma scolopendrina*, *Ophiocoma erinaceus* and *Macrophiothrix longipeda*). MSc Thesis. University of Otago, Dunedin, New Zealand

Lawrence JM (1987) A functional biology of echinoderms. John Hopkins University Press, Baltimore

Loo L-O, Jonsson PR, Sköld M, Karlsson Ö (1996) Passive suspension feeding in *Amphiura filiformis* (Echinodermata: Ophiuroidea): feeding behaviour in flume flow and potential feeding rate of field populations. Mar Ecol Prog Ser 139:143–155

Magnus DBE (1962) Über das "Abweiden" der Flutwasseroherfläche durch den Schlangenstern *Ophiocoma scolopendrina* (Lamarck). Verhandlungen der Deutschen Zoologishen Gesellschaft 11:471–481

Miller DC, Bock MJ, Turner EJ (1992) Deposit and suspension feeding in oscillatory flows and sediment fluxes. J Mar Res 50:489–520

Munday BW (1993) Field survey of the occurrence and significance of regeneration in *Amphiura chiajei* (Echinoidea; Ophiuroidea) from Killary Harbour, west coast of Ireland. Mar Biol 115:661–668

Ngusaru A (1997) Geological history. In: Richmond MD (ed) A guide to the seashores of Eastern Africa and the Western Indian Ocean islands. Sida/department for research cooperation, SAREC, Zanzibar, Tanzania, pp 7–18

Pentreath RJ (1970) Feeding mechanisms and the functional morphology of podia and spines in some New Zealand ophiuroids (Echinodermata). J Zool Lond 161:395–429

Warner GF (1982) Food and feeding mechanisms: Ophiuroidea. In: Jangoux M, Lawrence JM (eds) Echinoderm nutrition. AA Balkema, Rotterdam, pp 161–181

Warner GF, Woodley JD (1975) Suspension-feeding in the brittlestar *Ophiothrix fragilis*. J Mar Biol Assoc UK 55:199–210