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Feeding Biology of the Antarctic Brittle Star *Ophionotus victoriae* (Echinodermata: Ophiuroidea)

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Summary. The diet and feeding behavior of the brittle star *Ophionotus victoriae* were studied in 1981–1983. Frequency-of-occurrence and points methods were used to examine stomach contents of 2475 specimens from 19 stations representing seven general localities along the Antarctic Peninsula and South Sandwich Islands. Results of the two methods were in agreement and indicated this species is an opportunistic generalist with high diet plasticity. The most abundant component of the stomach contents was sediment but the diet derived from at least 13 phyla. Crustaceans, notably euphausiids and amphipods, were most important at some locations. Diet composition varied significantly between locations and years, but did not differ among brittle star size groups. Stomach content data and laboratory studies indicate that *O. victoriae* utilizes a variety of feeding methods but not suspension feeding.

Introduction

Little is known of the feeding energetics of Antarctic benthic organisms and only rarely has the trophic structure of benthic communities been analyzed (Dayton et al. 1974; Brand 1980). Natural diets of only the most ubiquitous bottom-dwelling invertebrates have been examined in detail. Available studies include Pearse (1965) for the asteroid *Odontaster validus*, Pearse and Giese (1966) for the echinoid *Sterechinus neumayeri*, Dearborn (1967) for the isopod *Glyptonotus antarcticus*, and Brand (1980) for a number of macroinvertebrates.

Asterozoan echinoderms are conspicuous members of most Antarctic Shelf communities. The bulk of information on diet composition consists of brief notes in taxonomic literature (Mortensen 1936; Fisher 1940; Fell 1961; Clark 1963). Dearborn (1977) synthesized current knowledge of the food habits of 30 asterozoan species and provided new stomach-content data for five of these. However, even for these species, little information is available on the factors which affect diet composition or feeding methods employed.

The present study was undertaken to examine the feeding ecology of the ophiuroid *Ophionotus victoriae* (Figs. 1/1, 1/2, 1/3). This circumpolar species is extremely common along the Antarctic Peninsula and Scotia Arc. It inhabits a variety of substrates in depths ranging from 5 to 1266 m (Madsen 1967). Preliminary work (Dearborn 1977) indicated that *O. victoriae* can ingest a great diversity of food types from the substrate surface and may capture euphausiids and other crustaceans from the water column. Unpublished studies by Paul Dayton and colleagues using scuba in McMurdo Sound demonstrated the flexibility of arm tips in this species (Fig. 1/3) and the fact that *Ophionotus* includes seal feces in its diet (Fig. 1/4).

This investigation involves a detailed analysis of stomach contents of *O. victoriae* populations at several locations along the Antarctic Peninsula and South Sandwich Islands and laboratory experiments on the feeding behavior of live individuals.

Materials and Methods

Site Descriptions

Specimens and environmental data were obtained at a total of 19 stations at seven general locations along the Antarctic Peninsula and South Sandwich Islands between 1973 and 1982 (Table 1). During May of 1975, specimens of *Ophionotus victoriae* were collected by trawl aboard *ARA Islas Orcadas* at Candlemas and Saunders Islands and two sites near Visokoi Island in the South Sandwich Island chain. Benthic investigations along the Antarctic Peninsula were conducted during 1973, 1981 and 1982 aboard *RV Hero*. Material was collected primarily by 1.5 m beam trawl, but additional information was obtained from grab samples. Hauls of short duration were used to minimize contamination. In 1973, collections were made at Paradise Harbor. During 1981, *O. victoriae* were collected at Deception Island and the Argentine Islands and bottom photographs were taken with a remote underwater camera. Similar work at Deception Island, the Argentine Islands and Valdivia Point was undertaken in 1982.

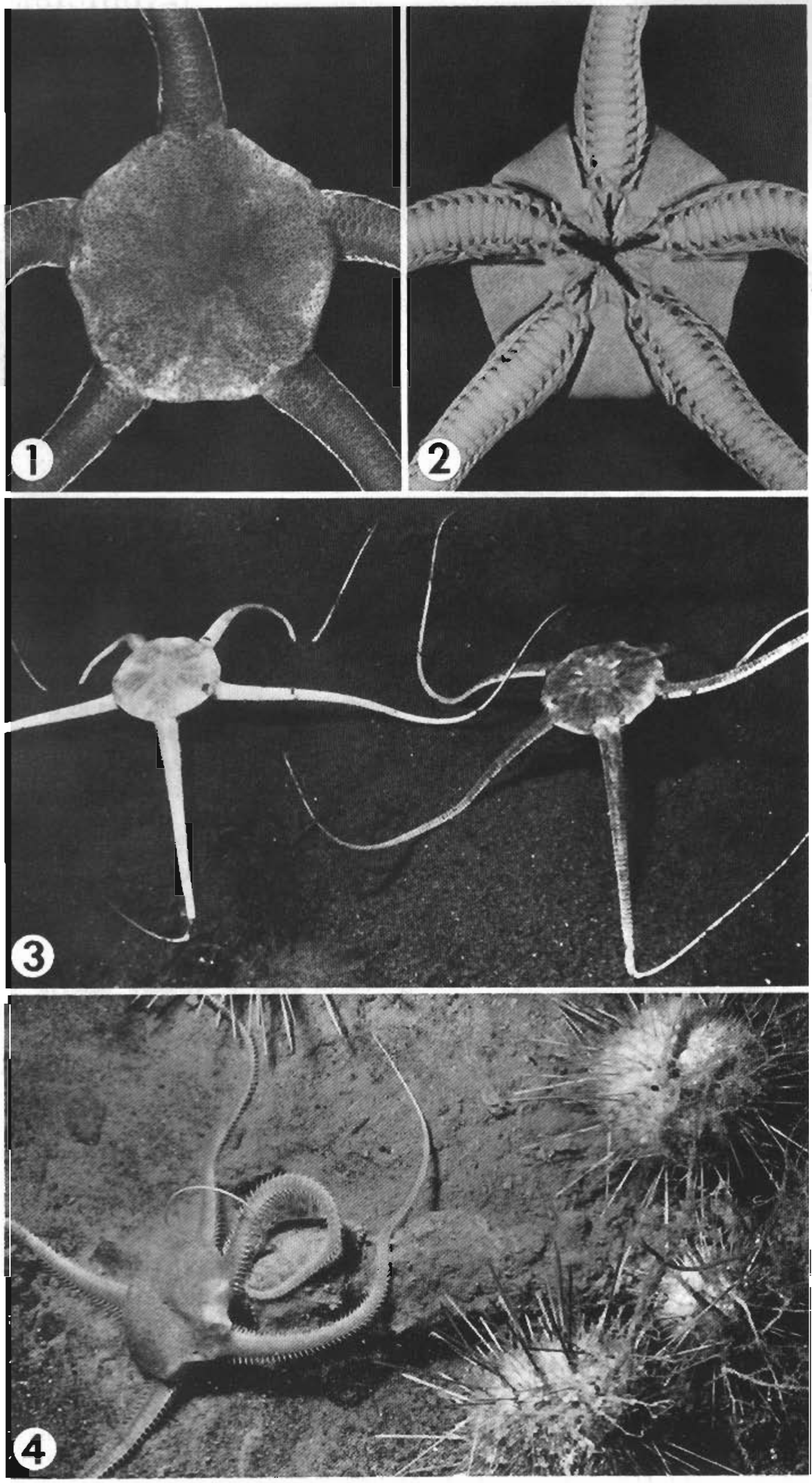

Fig. 1. *Ophionotus victoriae*. 1 Aboral view showing fragmentation of dorsal arm plates (disc diameter = 24.8 mm). 2 Oral view of the same specimen. 3 "Rowing" response. (Scuba photo by Paul K. Dayton, 9 January 1976, off Cape Chocolate, McMurdo Sound.) 4 Ingestion of seal feces using an arm coil. Several urchins, probably *Sterechinus neumayeri* at right. (Scuba photo by Edward O'Connor, 21 January 1976, off Garwood Valley, McMurdo Sound)

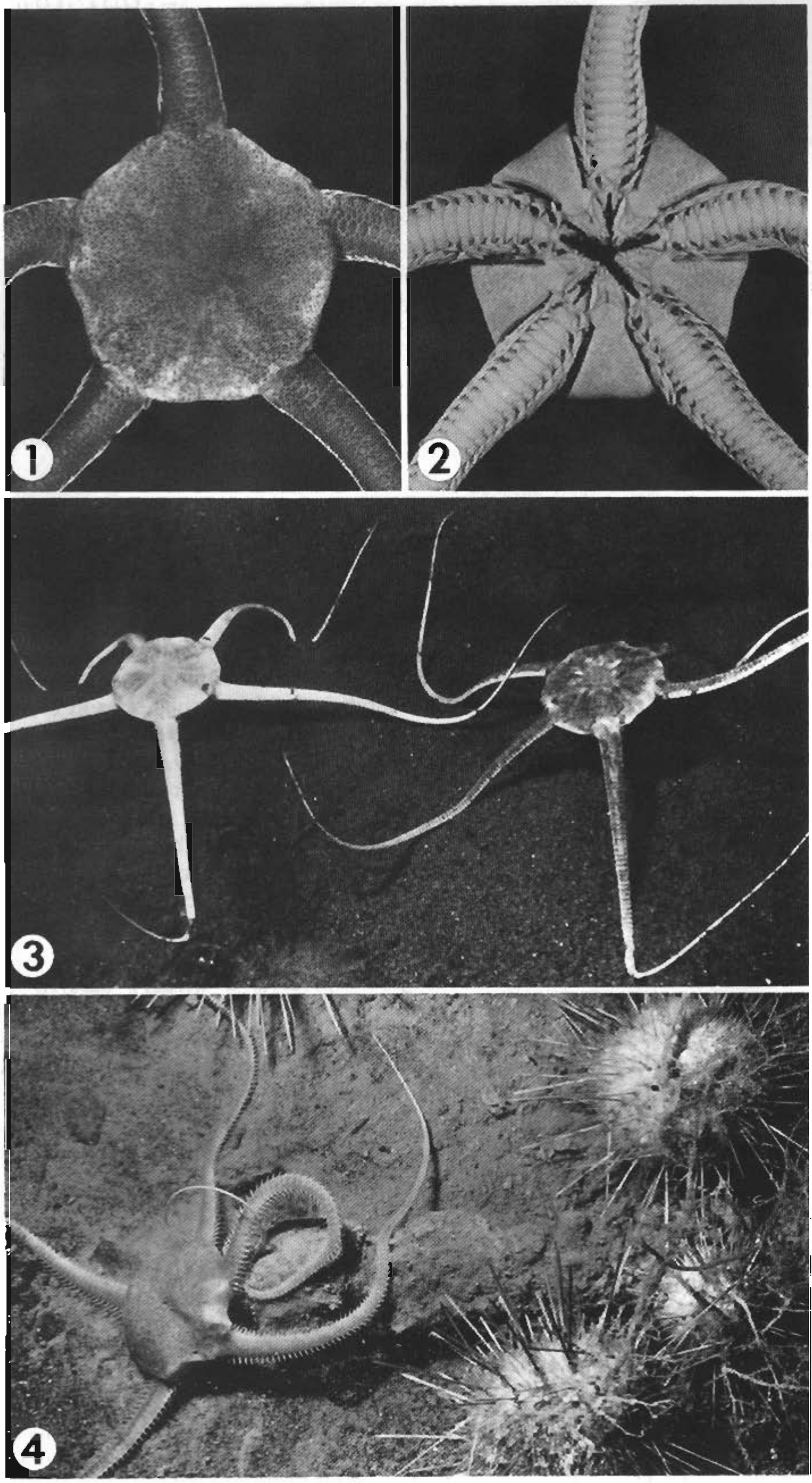

Fig. 1. *Ophionotus victoriae.* **1** Aboral view showing fragmentation of dorsal arm plates (disc diameter = 24.8 mm). **2** Oral view of the same specimen. **3** "Rowing" response. (Scuba photo by Paul K. Dayton, 9 January 1976, off Cape Chocolate, McMurdo Sound.) **4** Ingestion of seal feces using an arm coil. Several urchins, probably *Sterechinus neumayeri* at right. (Scuba photo by Edward O'Connor, 21 January 1976, off Garwood Valley, McMurdo Sound)

Food Habits

Specimens of *Ophionotus victoriae* retained for stomach analyses were fixed in 70% ethanol immediately after capture and returned to the University of Maine. Rapid sorting of specimens and fixation in ethanol nearly eliminated brittle star regurgitation once trawls were brought aboard the ship. Trawls of short duration (<5 min bottom time) minimized regurgitation during animal capture, but the possibility of this could not be excluded completely.

Prior to dissection the disc diameter (DD), or greatest distance between arm base and opposite interradius, was measured to the nearest 0.1 mm. Animals were dissected by cutting around the disc perimeter and folding back the aboral surface to expose the gut lining. Stomach contents were examined with a Wild M5 dissecting microscope. Food items were identified to the lowest taxon possible.

The diets of *O. victoriae* populations were estimated by two methods, one giving frequency of occurrence of food items and the other, a points method, giving volumetric contributions of food items. All animals were analyzed by the first procedure. Presence or absence of food was noted to determine the number of animals feeding. Frequency of occurrence of individual food items was then expressed as a percentage of feeding animals. Except for all specimens from Station 53 and some from Station 39, *O. victoriae* from 1975, 1981, and 1982 cruises were also analyzed by a points method modified from Brun (1972). To assess stomach fullness, points were allotted according to the scale 0, 1, 2, 4, 8, 12 and 16. A score of 16 was assigned to a completely full gut, 0 to an empty gut, 1 to a trace amount of material and 2, 4, 8 and 12 to appropriate fractions of a full stomach. Components of the bolus were then scored on the same scale. Total points for all food items in an individual approximated 16 regardless of animal size or bolus volume. For example, a half-filled stomach containing three quarters euphausiid remains and one quarter sediment would receive scores of 8, 12 and 4 for fullness, euphausiids and sediment, respectively. Trace amounts of several additional foods would cause the total value of the contents to exceed 16. To determine diet composition, the

Table 1. Summary of sampling stations. Single positions are given for vertical work. A single position for a trawl station is given when the ship moved more or less in a circular pattern during the operation because of local ice conditions or navigation problems near land

Cruise	Station no.	Date	Start position	Finish position	Location	Depth (m)	Gear
RV Hero 73-1	1946	11 March 1973	6452.8 S 6252.9 W	6453.2 S 6253.0 W	Antarctic Peninsula Paradise Harbor	264 – 272	0.6 m Blake Trawl
ARA Islas Orcadas 0575	39	23 May 1975	5701.2 S 2644.3 W	5701.2 S 2644.8 W	South Sandwich Islands Candlemas Island	97 – 101	3.0 m Blake Trawl
	53	26 May 1975	5741.4 S 2622.3 W	5741.8 S 2622.2 W	South Sandwich Islands Saunders Island	355 – 468	1.5 m Blake Trawl
	61	30 May 1975	5642.3 S 2700.4 W	5642.8 S 2700.8 W	South Sandwich Islands Visokoi Island	93 – 121	1.5 m Blake Trawl
	67	31 May 1975	5644.6 S 2702.7 W	5644.8 S 2704.4 W	South Sandwich Islands Visokoi Island	137 – 155	1.5 m Blake Trawl
RV Hero 81-2	5-1	15 February 1981	6514.2 S 6415.6 W	– –	Antarctic Peninsula Argentine Islands	51	Van Veen Grab (0.17 m^2)
	6	16 February 1981	6514.0 S 6415.2 W	– –	Antarctic Peninsula Argentine Islands	50 – 55	Small Otter Trawl
	9	16 February 1981	6514.2 S 6415.6 W	– –	Antarctic Peninsula Argentine Islands	55 – 56	Benthos Camera
	11	17 February 1981	6514.1 S 6415.2 W	– –	Antarctic Peninsula Argentine Islands	50 – 60	Large Otter Trawl
	16	22 February 1981	6259.3 S 6034.2 W	6259.0 S 6033.9 W	Antarctic Peninsula Deception Island	50 – 80	Large Otter Trawl
RV Hero 82-4	2	13 March 1982	6259.0 S 6033.8 W	– –	Antarctic Peninsula Deception Island	48 – 65	1.5 m Blake Trawl
	3	15 March 1982	6514.0 S 6415.5 W	– –	Antarctic Peninsula Argentine Islands	56 – 60	Van Veen Grab (0.11 m^2)
	4	16 March 1982	6513.6 S 6414.7 W	6513.7 S 6415.0 W	Antarctic Peninsula Argentine Islands	49 – 58	1.5 m Blake Trawl
	21	23 March 1982	6421.4 S 6128.2 W	6421.7 S 6129.8 W	Antarctic Peninsula Valdivia Point	110 – 155	1.5 m Blake Trawl
	22	23 March 1982	6422.3 S 6128.3 W	6422.1 S 6129.3 W	Antarctic Peninsula Valdivia Point	60 – 152	1.5 m Blake Trawl
	23-1	23 March 1982	6422.0 S 6128.8 W	– –	Antarctic Peninsula Valdivia Point	137.5 – 148.5	Benthos Camera
	43	03 April 1982	6259.3 S 6034.3 W	– –	Antarctic Peninsula Deception Island	94 – 95	Van Veen Grab (0.11 m^2)
	44-1	03 April 1982	6259.2 S 6034.6 W	– –	Antarctic Peninsula Deception Island	60	Van Veen Grab (0.11 m^2)
	44-4	03 April 1982	6259.2 S 6034.6 W	– –	Antarctic Peninsula Deception Island	71 – 74.5	Benthos Camera

sum of all points awarded each food category was expressed as a proportion of the sum of all points for all food categories combined.

Sediment taken from the stomachs of *O. victoriae* sampled at Station 4 was examined for the presence of organic material. Sediment grains were mounted on aluminium stubs, coated with 400 Å of a gold/palladium mixture, and examined with an AMR 1000 A scanning electron microscope.

Factors affecting diet composition were examined after the natural diet of *O. victoriae* was estimated. Results from frequency-of-occurrence and points methods were used to compare diets between locations, between years at a single location, and between animal size classes at a location. Only data from the RV Hero 1981 and 1982 stations were used in these comparisons in order to minimize sampling depth and handling variability. Any food type which occurred at least at three of the general locations was included in these analyses.

Because points method data were nonnormally distributed, rank values were compared using the Kruskal-Wallis test as performed by the NPAR1WAY procedure of the Statistical Analysis System (SAS 1979). Separate tests were run for each food to determine whether all populations were homogeneous with respect to the contribution of that item. Variability between size groups at a single location was tested in a similar fashion. The entire size range of *O. victoriae* examined (4.6 – 40.5 mm) was divided into small (4.6 – 13.5 mm), medium (13.6 – 22.5 mm), large (22.6 – 31.5 mm) and extra large (31.6 – 40.5 mm) size groups. Separate tests were conduced for each station to determine whether the mean scores of each food showed significant between size-group variation. Foods showing significant variability with the above tests were subjected to the multiple pairwise comparisons test described by Conover (1980). Paired combinations of year, location, or size group rank sums revealed where specific differences in the volumetric contribution of a food item occurred.

An analysis of variance on frequency data was conducted using the general linear models procedure of SAS. For every food, arcsine-transformed proportions from four size groups from various stations were subjected to a two-way ANOVA without replication. Differences in frequency of occurrence of items for specific station combinations were tested with the Duncan's multiple range test. Paired size group comparisons were not made.

Spearman rank correlation coefficients were used to compare results obtained by frequency-of-occurrence and points methods. Ranks of the frequency and volume percents of 28 food categories from each 1981 and 1982 station were compared using the CORR procedure of SAS.

Feeding Behavior

During February, 1982, postural orientations of six intact specimens of *O. victoriae* were observed in the laboratory at Palmer Station. Animals were collected on 6 February in the vicinity of *RV Hero* Station 22. All specimens were maintained in running seawater systems aboard *RV Hero* and at Palmer Station, and were starved for at least two days prior to experiments. Animals were observed in a specially constructed flow-through aquarium (102 × 30.5 × 30.5 cm). Ends of the tank were equipped with PVC couplings to diffuse and regulate the rate of inflowing water. A unidirectional current could thus be maintained over a bottom distance of 35 cm. Current velocity was determined by timing the movement of water between two points on a rule placed at the bottom of the tank. The measurement of water currents was facilitated by injecting table cream into the aquarium; an idea suggested by Fontaine (1965).

Orientation of *O. victoriae* in variable currents was examined for five velocities: 0, 2 – 4, 8 – 9, 13 – 15 and 18 – 20 cm/s. Animals were observed on a clean plexiglass bottom and on sediment sieved through a 1 mm mesh. At each speed, toluidine blue was used to study the distribution of mucus on body surfaces which might signal the use of suspension feeding. This dye stains mucus light purple and was introduced in concentrations sufficient to color the water pale blue.

Additional observations of live *O. victoriae* were made in 1983. Specimens were obtained on 5 March at Port Foster, Deception Island and feeding studies were conducted within 48 h at the Palmer laboratory. Behaviors were investigated by introducing moribund or freshly killed krill into a holding tank containing *O. victoriae*.

Description of Study Sites

South Sandwich Islands

Candlemas Island (Sta. 39, 1975), 97 – 101 m on north shelf of island. Bottom type was difficult to judge from the trawl sample although it appeared to consist of volcanic sand and gravel with a few small rocks and some mud.

Saunders Island (Sta. 53, 1975), 355 – 468 m. Substrate was primarily brown-black muddy sediment with smaller amounts of basaltic gravel and sand. Few sessile invertebrates.

Visokoi Island (Sta. 61, 1975), 93 – 121 m off southeast side of island. Substrate consisted of rocks mixed with sand and mud. Foliaceous bryozoans, siliceous sponges and a small number of thecate hydroids provided a vertical component to the community.

Visokoi Island (Sta. 67, 1975), 137 – 155 m off southeast side of island. The substrate was apparently coarse basaltic gravel. Few sessile invertebrates were present.

Antarctic Peninsula

Paradise Harbor (Sta. 1946, 1973), 264 – 272 m. Bottom sediments and fauna were not well sampled, but the location was apparently a level bottom with mud and rocks.

Argentine Islands (Sta. 5-1, 6, 9 and 11, 1981; Sta. 3 and 4, 1982), 49 – 60 m, north of Grotto Island. Grab samples and trawl contents revealed a bottom of silt and clay overlaying fine sand. Sediment was well packed and well sorted and polychaetes, bivalves, and animal tubes were apparent. A few sessile forms were seen in bottom photographs, but most epifaunal organisms were motile. The proximity of numerous icebergs and the above data suggest that the benthos may have been subject to ice scouring.

Deception Island (Sta. 16, 1981; Sta. 2, 43, 44-1 and 44-4, 1982), 48 – 95 m, within Whalers Bay. Grabs, trawls and bottom photographs (Fig. 2/1) indicated a substrate of volcanic rocks, gravel, and mud. Tube dwellers were apparently absent. Photographs showed comparatively high densities of only two echinoderm species and patchy occurrences of ascidians (Fig. 2/1).

Recent volcanic activity at Deception Island has been well documented (Baker et al. 1969; Baker and McReath 1971) and effects of two eruptions on bottom type and faunal composition have been examined (Gallardo and Castillo 1968, 1970; Gallardo et al. 1977). In our bottom photographs, high sedimentation was evident from the turbidity of water and the accumulation of sediment on benthic organisms. Disturbances from the effects of vulcanism at this site appear to be ongoing.

Valdivia Point (Sta. 21, 22 and 23-1, 1982), 60 – 155 m in unnamed bay west of Valdivia Point. The bottom was a mixture of large and small rocks and mud. Photographic surveys (Fig. 2/2) and trawls indicated an irregular topography with alternating level patches of soft bottom and rocky slopes. Sessile forms were abundant,

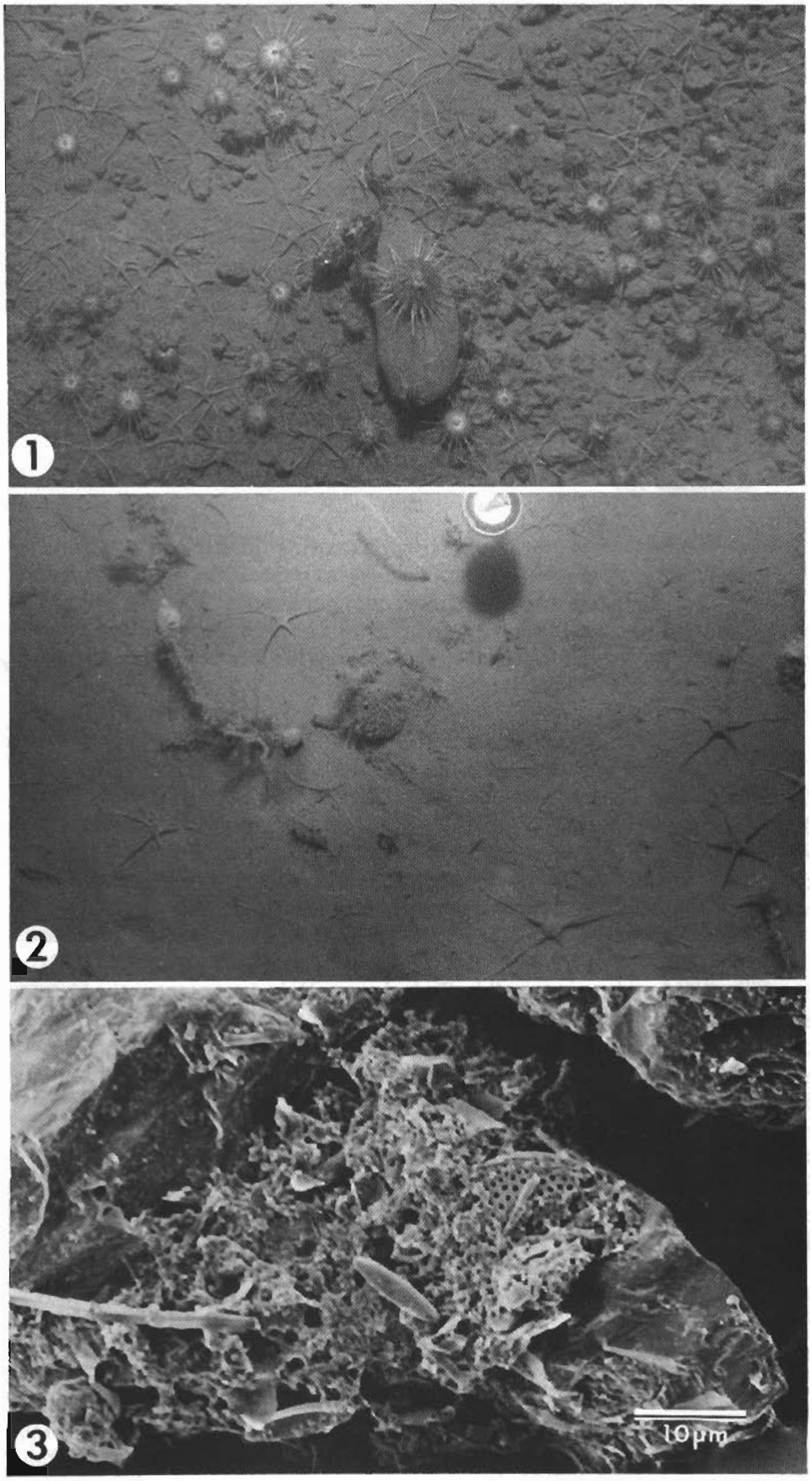

Fig. 2. Bottom photographs and sediment grain. **1** Whalers Bay, Deception Island, 71 – 74.5 m. Numerous specimens of *O. victoriae* and *Sterechinus neumayeri* and one specimen of a solitary ascidian (*center*) are visible. Total bottom area = 0.3 m². **2** Off Valdivia Point, 117.5 – 148.5 m. *Ophionotus victoriae* and solitary and colonial ascidians are apparent. Compass is visible at top of frame. Total bottom area = 0.7 m². **3** Scanning electron micrograph of sediment grain taken from the stomach of *O. victoriae* showing associated organic material, which includes: crustacean appendage (*lower left*), pennate diatoms (*center*) and fragment of a circular diatom (*right center*).

Table 2. Summary statistics from stomach analyses of *O. victoriae*

Variable		*ARA Islas Orcadas* (South Sandwich Islands)				*RV Hero* (Antarctic Peninsula)					
		1975				1973	1981		1982		
	Total	Sta. 39	Sta. 53	Sta. 61	Sta. 67	Sta. 1946	Sta. 11	Sta. 16	Sta. 2	Sta. 4	Sta. 22
Number examined	2475	182 + 173[a]	20[a]	105	233	109[a]	437	400	200	200	416
Size range (disc diameter in mm)	4.6 – 40.3	14.9 – 31.7	14.0 – 39.0	12.6 – 40.3	20.8 – 36.5	7.0 – 25.4	13.2 – 38.5	4.8 – 26.2	4.6 – 23.8	5.0 – 35.8	5.0 – 37.0
Mean size (mm)	22.5	25.7	29.3	27.4	28.0	16.0	28.7	13.9	14.1	25.4	21.0
Percent feeding	78.4	65.4	85.0	91.4	85.8	73.4	89.0	86.8	78.5	53.0	76.2
Percent feeding which contain more than one food	62.8	73.7	52.9	76.0	49.5	50.0	75.8	57.1	56.7	55.7	58.4
Mean number of foods per feeding animal	2.1	2.6	1.6	3.4	2.1	1.7	2.3	1.9	1.6	1.9	2.0
Mean fullness (points method only)	5.8	3.4	–	3.8	2.2	–	6.9	7.9	6.1	4.2	6.6

[a] Analyzed for frequency of occurrence only

especially on hard irregular substrates. Well-established populations of sessile, suspension-feeding invertebrates and abundant krill swarms in the vicinity of this station suggested high overall productivity and little disturbance by ice.

Results

Food Habits

A total of 2475 specimens of *Ophionotus victoriae* were examined for stomach contents and 1941 (78.4%) of these contained food (Table 2). Animals from Stations 6 and 11 were combined as Station 11 and those from Stations 21 and 22 as Station 22 for all analyses, giving 10 discrete populations.

The majority of animals with stomach contents fed on more than one food type. However, the mean number of foods per animal approached or exceeded three at only two stations. Mean fullness varied widely but never exceeded one half of the observed maximum fullness. At the low extreme, only four of the 200 feeding animals at Station 67 were more than one quarter full. Except for Station 4, stations from 1981 and 1982 showed higher mean fullness than earlier stations. Station 4 material was fixed in a weak formalin and freshwater solution prior to preservation which may have caused some regurgitation.

The diet included members of at least 13 phyla (Table 3). Items were separated into 28 food categories for further analysis. Frequency and volume percent results for these categories are listed in Tables 4 and 5. A brief description of the food types follows.

Sarcodina (Foraminifera). The occurrence of foraminiferans varied from 0 – 70.4% depending on the population (Table 4). At Deception Island, numbers per individual ophiuroid rarely exceeded four, but at the Argentine Islands one individual contained approximately 125 calcareous forams. They generally occurred mixed with sediment.

Porifera. Actual fragments occurred rarely. Sponge spicules, some of which were identified as hexactinellid spicules, were most commonly seen. With the exception of Station 39, frequency of occurrence was highest where trawl contents showed a well developed sponge fauna (Table 4).

Cnidaria (Hydrozoa). All seven occurrences were fragments of hydroid colonies.

Mollusca. Bivalves occurred with the highest frequency, and *Cyamiocardium denticulatum, Cyamiomactra laminifera* and *Yoldia eightsi* were the predominant species. Most molluscs appeared to be juveniles, many with poorly calcified shells. Broken valves were common and only rarely did soft tissue remain. Although found at most locations, molluscs were never a major food source by volume.

Annelida (Polychaeta). Polychaete material occurred with relatively high frequency (Table 4) but never contributed much to the volume of stomach contents (Table 5). Occurrences were usually marked by setae and tubes. Although tissue was sometimes present, fresh, intact worms were the exception. Only three individuals could be keyed to the generic level (Table 3).

Arthropoda (Crustacea). Crustaceans were the dominant animal group in *O. victoriae* stomachs, occurring in 37.7% of all individuals and constituting an average of 24.8% of the contents by volume. These figures reached highs of 83.3% and 61.9%, respectively at Valdivia Point (Tables 4 and 5). Both pelagic and benthic forms were present. The condition of crustaceans varied from fresh, intact animals to isolated broken appendages.

Aside from unidentifiable fragments, Euphausiacea dominated the crustacean category. For all *O. victoriae* examined, euphausiids were the second most important item by volume at 10.5% (Table 5). They occurred in more than 10% of the stomachs at each of three locations in the South Sandwich Islands, and were the dominant food class by occurrence (51.4%) and volume (43.2%) at Valdivia Point. Krill were rarely intact and

Table 3. Foods identified from the stomach contents of *O. victoriae* sampled at 10 sites along the Antarctic Peninsula and South Sandwich Islands

Sarcodina	Amphipoda
Foraminifera	Caprellidea
Porifera	Gammaroidea
Hexactinellida	*Ampelisca macrocephala*
Cnidaria	*Colomastix fissilingua*
Hydrozoa	*Gammaropsis* sp.
Nemertea	*Pontogeneiella* sp.
Nematoda	*Pachychelium oculatum*
Mollusca	Other Lysianassidae
Gastropoda	Eusiridae
Rissoa sp.	Other Crustacea
Subonoba sp.	Bryozoa
Bivalvia	Cheilostomata
Adacnarca limnopsoides	Echinodermata
Cyamiocardium denticulatum	*Labidiaster annulatus*
Cyamiomactra laminifera	*Ophionotus victoriae*
Yoldia eightsi	*Promachocrinus kerguelensis*
Leptonidae	*Sterechinus neumayeri*
Annelida (Polychaeta)	Other Ophiuroidea
Aglaophamus sp.	Other Crinoidea
Eteone sp.	Other Echinoidea
Spirorbis sp.	Ascidiacea
Polynoidae	
Sabellidae	
Other Polychaeta	Fecal pellets
Arthropoda (Crustacea)	Miscellanea
Ostracoda	algal tissue, fish scales,
Copytus elongatus	chitin, diatoms, eggs
Myodocopida	Unidentified organic material
Podocopida	Sediment
Copepoda	
Calanoida	
Harpacticoida	
Decapoda	
Euphausiacea	
Euphausia superba	
Mysidacea	
Antarctomysis maxima	
Antarctomysis ohlinii	
Cumacea	
Eudorella sp.	
Leuconidae	
Tanaidacea	
Isopoda	
Asselloidea	
Arcturidae	
Munnidae	
Valvifera	

fresh. Tissue was often present but the body was usually torn or fragmented. In some instances, only disarticulated appendages from one or more individuals were apparent. Several examples were keyed to *Euphausia superba*, but other species may have been present.

Two other crustacean groups were important. Amphipods composed one quarter of the stomach contents at Stations 39 and 61 (Table 5), but at other stations their contribution was small. State of preservation varied as in the euphausiids, and only one individual of each of the keyed genera and species was found. Mysids were locally significant at the Argentine Islands. Virtually all individuals from all stations keyed to *Antarctomysis maxima*. The remaining crustacean taxa occurred infrequently and in small amounts.

Echinodermata. Ophiuroids were present in stomachs from all but two stations, but their volume contribution was never large (Table 5). Arm fragments were most common. The only prey species identified with certainty was *O. victoriae*. At Deception Island, one brittle star (DD = 18.8 mm) contained the intact discs of two *O. victoriae*, each with a disc diameter of 5.8 mm.

Echinoids, primarily *Sterechinus neumayeri*, were restricted to animals from Antarctic Peninsula stations and only occurred in significant quantities at Deception Island. There they replaced crustaceans as a primary constituent of stomach contents. Spines and fragments of tests were common. Soft parts were not always present. Encrusting bryozoans were found on urchin spines in two instances.

All nine occurrences of asteroid fragments consisted of pedicellariae, ossicles and spines of *Labidiaster annulatus*. Crinoid fragments were identified as *Promachocrinus kerguelensis*.

Fecal pellets. Ovate pellets were found in stomachs from all but one location. At Paradise Harbor they occurred in 56.2% of feeding animals (Table 4) and one individual contained almost 80 pellets. Small size and number per ophiuroid meant that fecal pellets usually contributed little to the volume of stomach contents.

Miscellanea. Items are listed in Table 3. None of these contributed significantly to the diet.

Sediment. Sediment occurred in 48.6 – 99.2% of feeding ophiuroids depending on location (Table 4). Volumetrically, it was the most important item for one half of the populations analyzed. Figure 2/3 shows the organic coating often present on individual sediment grains. The color and consistency of samples indicated that "sediment" might sometime be derived from fecal pellets or the gut contents of a digested prey item.

Large amounts of sediment might be ingested as a consequence of handling other foods. This was addressed by calculating the percentage of sediment-containing stomachs which contained other foods. At Valdivia Point, sediment was accompanied by other foods in 93.9% of its occurrences, lending support to the above statement. At Deception Island, values of 52.4% and 53.5% for 1981 and 1982 meant that one half of the animals that ingested sediment ingested it alone. Argentine Islands samples gave intermediate values of 70.5% and 76.0% in 1981 and 1982.

A summary of the diet of *Ophionotus victoriae* as estimated by the points method is given in Fig. 3.

Spearman coefficients showed high correlation (0.93 – 0.99) between frequency-of-occurrence and points-method results. The relative importance of each food in the diet was thus defined similarly by the two methods.

All foods tested by the analysis of variance showed that frequency of occurrence of food items varied signifi-

Table 4. Percent frequency of occurrence of major food categories in the stomachs of feeding *O. victoriae*

Food type	Total	*ARA Islas Orcadas* (South Sandwich Islands)				*RV Hero* (Antarctic Peninsula)					
		1975				1973	1981		1982		
		Sta. 39	Sta. 53	Sta. 61	Sta. 67	Sta. 1946	Sta. 11	Sta. 16	Sta. 2	Sta. 4	Sta. 22
Foraminifera	27.2	2.6	–	7.3	8.5	–	70.4	19.9	50.9	24.5	15.1
Sponge fragments	8.8	19.0	–	44.8	24.5	7.5	–	–	–	–	9.1
Hydroid fragments	0.4	–	–	2.1	–	1.2	–	–	–	–	1.3
Nemertea	0.3	–	–	–	–	–	0.8	–	–	–	0.6
Nematoda	0.3	0.4	5.9	1.0	–	–	–	–	1.3	–	–
Mollusca	2.6	2.2	–	–	1.0	5.0	4.1	0.9	–	7.5	4.1
Polychaeta	12.0	4.7	–	7.3	4.5	5.0	23.9	15.8	–	9.4	13.9
Crustacea (Total)	37.7	71.6	52.9	68.8	22.0	18.8	14.4	14.1	1.3	58.5	83.3
Ostracoda	0.6	0.4	–	3.1	3.0	2.5	–	–	–	–	–
Copepoda	0.3	0.4	–	–	–	–	0.5	0.6	–	–	–
Euphausiacea	12.3	13.8	23.5	24.0	2.0	5.0	–	0.3	–	7.5	51.4
Decapoda	0.1	0.4	–	–	–	–	–	–	–	–	–
Mysidacea	3.4	1.3	–	–	1.0	2.5	4.9	–	–	34.9	1.3
Cumacea	1.3	0.4	–	–	–	–	–	6.1	–	3.8	–
Tanaidacea	0.4	–	–	2.1	0.5	–	0.8	–	–	1.9	–
Isopoda	1.1	6.5	–	4.2	1.5	–	–	–	–	–	–
Amphipoda	7.8	34.9	–	41.7	5.5	2.5	0.8	0.3	–	2.8	3.2
Crustacea (unident.)	18.5	44.0	35.3	46.9	13.0	8.8	8.5	7.5	1.3	18.9	29.0
Bryozoa	0.3	0.4	–	4.2	–	1.2	–	–	–	–	–
Echinodermata (Total)	9.5	4.3	5.9	8.3	16.5	–	2.6	28.8	7.5	2.8	2.5
Asteroidea	0.5	–	–	2.1	1.5	–	–	–	–	–	1.3
Ophiuroidea	3.3	2.6	5.9	6.2	8.5	–	1.8	6.6	1.3	–	0.9
Echinoidea	5.5	–	–	–	–	–	0.8	25.6	6.3	2.8	0.3
Crinoidea	0.3	0.4	–	–	2.5	–	–	–	–	–	–
Echinodermata (unident.)	1.0	1.3	–	1.0	8.0	–	–	–	–	–	–
Ascidiacea	0.2	–	–	1.0	–	–	–	–	0.6	–	0.3
Fecal pellets	10.4	11.6	–	5.2	8.0	56.2	8.5	2.0	1.3	15.1	16.1
Miscellanea	5.5	9.9	23.5	13.5	9.0	13.8	–	9.2	0.6	1.9	0.9
Unidentified organic material	6.7	27.6	–	25.0	7.5	5.0	1.0	1.4	0.6	4.7	2.8
Sediment	82.7	76.7	70.6	99.0	98.0	50.0	99.2	97.7	94.3	52.8	48.6

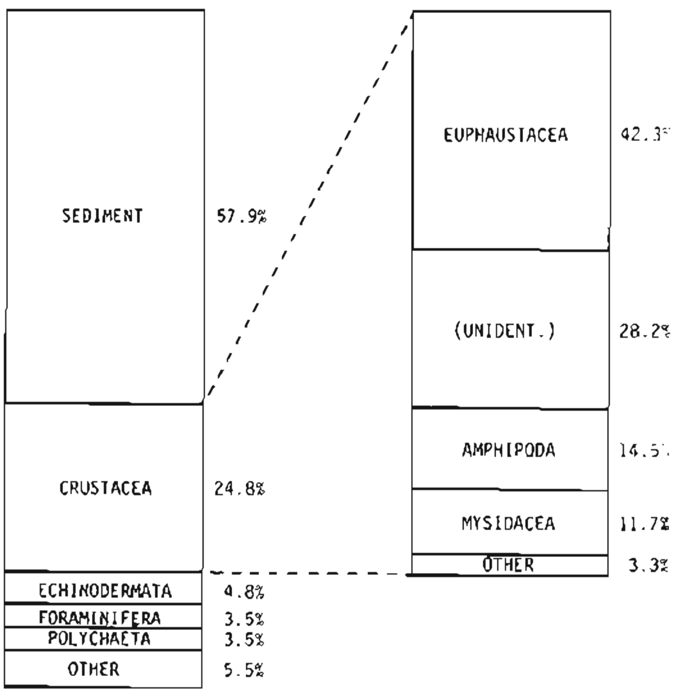

Fig. 3. Overall diet composition of *O. victoriae* with components of the major animal food group identified. (N = 1941 feeding ophiuroids)

cantly between stations. Duncan's test results indicated, depending on the comparison, that 33 – 89% of the food categories varied in occurrence between populations at the locations (Table 6). Diets were most similar between populations at the Argentine Islands and Valdivia Point. Only one third of the foods varied significantly in this comparison. Argentine Islands and Deception Island populations were least similar.

Volume contributions of fewer food types varied between years and locations. Four of 10 foods showed no significant variation over all five stations (Kruskal-Wallis test). Of those six foods with heterogeneous values (Table 7), only the three most important in any paired comparison showed clear differences ($P < 0.01$) in abundance. These top items constituted 66.7% to 98.5% of the diet depending on the station so that a large proportion of the diet varied annually and geographically.

The contributions of only five foods varied significantly among *Ophionotus* size groups. These foods included foraminiferans, mysids, euphausiids, echinoids and sediment. Of 150 paired comparisons (six size-group combinations, five stations, five foods), only four showed significant ($P = 0.01$) differences. This suggests little influence of brittle star body size on the taxonomic groups represented in the stomach contents.

Table 5. Percent composition by volume of *O. victoriae* stomach contents. Trace amounts were not considered in volume calculations. Only populations analyzed by the points method are included

Food type	Total	ARA *Islas Orcadas* (S. Sandwich Isl.)			*RV Hero* (Antarctic Peninsula)				
		1975			1981		1982		
		Sta. 39[a]	Sta. 61	Sta. 67	Sta. 11	Sta. 16	Sta. 2	Sta. 4	Sta. 22
Foraminifera	3.5	–	–	–	6.9	2.0	7.1	3.6	2.9
Sponge fragments	0.3	0.3	0.5	2.0	–	–	–	–	0.6
Hydroid fragments	–	–	0.2	–	–	–	–	–	0.2
Nemertea	0.3	–	–	–	0.6	–	–	–	0.6
Nematoda	–	–	0.2	–	–	–	0.4	–	–
Mollusca	0.8	0.5	–	0.4	1.2	0.1	–	4.0	1.0
Polychaeta	3.5	2.5	1.2	2.9	1.3	2.8	–	5.9	8.7
Crustacea (Total)	24.8	52.3	60.0	10.0	5.9	3.0	0.2	46.7	61.9
Ostracoda	–	–	–	–	–	–	–	–	–
Copepoda	0.1	0.7	–	–	0.1	0.3	–	–	–
Euphausiacea	10.5	10.4	13.0	3.0	–	–	–	4.9	43.2
Decapoda	–	–	–	–	–	–	–	–	–
Mysidacea	2.9	–	–	1.6	3.3	–	–	27.7	1.0
Cumacea	0.4	0.2	–	–	–	1.4	–	1.0	–
Tanaidacea	0.1	–	–	0.4	0.1	–	–	0.2	–
Isopoda	0.2	2.1	0.8	–	–	–	–	–	–
Amphipoda	3.6	22.3	24.2	3.2	0.6	–	–	1.4	1.7
Crustacea (unident.)	7.0	16.6	22.0	1.8	1.8	1.3	0.2	11.5	16.0
Bryozoa	–	–	0.3	–	–	–	–	–	–
Echinodermata (Total)	4.8	0.9	2.5	6.4	0.8	15.2	3.3	1.6	1.2
Asteroidea	0.1	–	–	–	–	–	–	–	0.6
Ophiuroidea	1.4	0.9	2.5	2.7	0.7	3.2	0.7	–	0.6
Echinoidea	3.0	–	–	–	0.1	12.0	2.6	1.6	–
Crinoidea	0.1	–	–	1.1	–	–	–	–	–
Echinodermata (unident.)	0.2	–	–	2.6	–	–	–	–	–
Ascidiacea	0.1	–	0.7	–	–	–	0.1	–	0.2
Fecal pellets	2.0	1.4	0.7	1.9	1.2	0.6	–	7.5	4.4
Miscellanea	0.6	0.6	1.0	3.4	–	0.4	0.1	0.7	0.3
Unidentified organic material	1.5	3.7	1.8	4.6	0.3	0.8	0.1	2.5	1.9
Sediment	57.9	37.8	31.1	68.1	81.8	75.1	88.8	27.5	16.1

[a] Only 182 animals of the 355 examined were analyzed by the points method

Table 6. Results of Duncan's multiple range test on all foods occurring at the majority of sampling locations using frequency-of-occurrence data. A comparison was not made if the mean of the two percentages in the pair did not exceed 1.0%. (* = $0.05 > P > 0.01$, ** = $P < 0.01$)

Food type	Annual variation		Geographical variation			
	1981 population vs. 1982 population		1981	1982		
	Argentine Isl.	Deception Isl.	Argentine Isl. vs. Deception Isl.	Argentine Isl. vs. Deception Isl.	Argentine Isl. vs. Valdivia Point	Deception Isl. vs. Valdivia Point
Foraminifera	**	**	**	**	NS	**
Mollusca	*	–	**	**	*	**
Polychaeta	**	**	NS	**	NS	**
Euphausiacea	**	–	–	**	**	**
Mysidacea	**	–	**	**	**	–
Amphipoda	NS	–	–	**	NS	**
Ophiuroidea	*	**	**	–	–	NS
Echinoidea	NS	**	**	NS	NS	NS
Fecal Pellets	*	NS	**	**	NS	**
Sediment	**	NS	NS	**	NS	**

Table 7. Multiple paired comparisons for foods showing significant between-station variation by the Kruskal-Wallis test using points method data. Numbers in parentheses indicate the average ranks of food items for the particular combination. A comparison was not made if the mean of the two percentages in the pair did not exceed 1.0%. (* = $0.05 > P > 0.01$, ** = $P < 0.01$)

Food type	Annual variation		Geographical variation			
	1981 population vs. 1982 population		1981	1982		
	Argentine Isl.	Deception Isl.	Argentine Isl. vs. Deception Isl.	Argentine Isl. vs. Deception Isl.	Argentine Isl. vs. Valdivia Point	Deception Isl. vs. Valdivia Point
Foraminifera	** (3)	** (3)	** (3)	** (3)	NS	** (3)
Euphausiacea	NS	–	–	NS	** (1)	** (2)
Mysidacea	** (2)	–	NS	** (2)	** (3)	–
Echinoidea	–	** (2)	** (2)	NS	–	NS
Fecal pellets	NS	–	–	*	NS	*
Sediment	** (1)	** (1)	NS (1)	** (1)	** (2)	** (1)

Feeding Behavior

Ophionotus victoriae maintained in running seawater aquaria in 1982 did not feed well and showed a high degree of arm autotomy. These phenomena were noted by Lowe and Crawford (1976) and led to their abandonment of work with live members of this species. During the present study, qualitative observations were made on six intact and relatively fresh specimens in 1982.

Orientation of ophiuroids into currents was similar whether the substratum was plexiglass or sediment.

0 cm/s (no detectable unidirectional current). Posture was variable. Most commonly the disc and proximal one-half to two-thirds of each arm were held against the bottom. Arms were elevated distally, curving upward so that the arm tips were 3 – 5 cm off the bottom. Occasionally all five arms supported the disc and elevated it 4 – 7 cm above the substrate.

2 – 4 and 8 – 9 cm/s. Orientation was similar for both velocities and for small (DD = 16.4 mm) and medium-sized (DD = 24 – 27 mm) ophiuroids. The disc remained against the substrate. Either two or three arms were directed toward the current source. In the latter case, one arm was pointed directly into the current. The proximal one-half to two-thirds of each arm was elevated slightly (4 – 5 mm) or not at all. Distal segments were elevated at approximately 45° angles, with arm tips rarely more than 2 cm from the substrate. Arm tips were curved downstream in a horizontal plane, or if oriented directly into the current, swept upward and downstream in a vertical plane.

13 – 15 cm/s. Animals showed the same posture as above except that no arms were oriented directly into the current. Arm tips were curved further downstream. Occasionally, animals "rowed" to the aquarium sides or into an upstream corner where current velocity was reduced.

18 – 20 cm/s. Only the most downstream arm was elevated. Small animals began to slide along the bottom.

Throughout these studies, the injection of toluidine blue into the aquarium revealed no significant mucus on body surfaces of *O. victoriae*.

During the 1983 season, moribund or freshly killed krill introduced into tanks containing *O. victoriae* initiated strong responses. Brittle stars moved toward the krill in virtually all instances, and responded from distances greater than 10 cm from the food source. In several cases, two or more brittle stars responded to the same euphausiid resulting in considerable interaction until one of the brittle stars ingested the food.

Discussion

Populations of *Ophionotus victoriae* were found in a variety of habitats along the South Sandwich Islands and Antarctic Peninsula. Substrates varied from level mud to gravel and rock bottoms with irregular topography. Several communities appeared to be disturbed relatively infrequently and included well-established sessile forms such as sponges, ascidians and bryozoans. Mobile deposit feeders were more conspicuous at other locations which were subject to disturbances from icebergs and vulcanism.

Stomach contents and feeding behaviour of *Ophionotus victoriae* suggest that this species is extremely opportunistic. With the exception of Station 4 at the Argentine Islands, the proportion of feeding individuals was higher than for many ophiuroids (Litvinova and Sokolova 1971; Litvinova 1979; Feder 1981) including Dearborn's (1977) values for this species. The discrepancy may be a result of handling differences which could lead to regurgitation or, in the present study from including foods with trace occurrences. However, a high number of feeding animals is expected if the brittle star is euryphagous (Litvinova and Sokolova 1971; Deschuyteneer and Jangoux 1978). The chance that a carnivore or other more selective feeder will encounter an acceptable food is comparatively low, resulting in a higher incidence of empty guts.

Ophionotus victoriae utilizes a variety of feeding modes. Necrophagy is common and has been demonstrated in the field by Arnaud (1970). Cannibalism occurs with variable frequency, confirming Dearborn's (1977) observations on this species and complementing Morison's (1979) conclusions for *O. hexactis*. *Ophionotus victoriae* can be an active predator on a variety of invertebrate prey (Tables 3 and 4). For example, both field and laboratory data show that it can capture moribund euphausiids which move at the substrate surface. Capture of crustaceans from the water column may also be possible. Morison (1979) stated that actively swimming amphipods are frequently caught by *O. hexactis*. Marr (1962) implied that active euphausiids might also be available to benthic predators in the Antarctic because krill were taken from depths exceeding 1000 m, and because they may spawn on or near the substrate surface in near-shore areas. However, if krill are captured directly from the water column, the paucity of fresh euphausiids in stomachs suggests that it is rare. In addition to these methods, *O. victoriae* is a nonselective deposit feeder and detritivore. Sediment, sponge spicules, fecal pellets, eggs, algae, and diatoms are ingested when available. The poor condition of many food items (e.g. broken bivalve shells, disarticulated crustacean appendages) often implies a detritiphagous habit rather than a predatory or carnivorous one.

Suspension and filter feeding were not observed in *Ophionotus victoriae*. Arm and tube foot orientation and mucus secretion in response to currents are common among suspension-feeding ophiuroids (Buchanan 1964; Fontaine 1965; Martin 1968; Pentreath 1970; Warner and Woodley 1975), but were not seen in this species. With increased current velocity individuals remained flat against the substrate or moved out of the current. Similar phenomena have been noted for *Ophionotus hexactis* (Morison 1979). In *O. victoriae* arm podia were relatively inactive in currents and rarely extended beyond the length of arm spines. Podial capture and transport of fine particulates seem unlikely.

Concomitant with its detritiphagous habit, *Ophionotus victoriae* shows extreme diet plasticity. High stomach content variability between sampling locations and years reflects changes in the availability of foods in the environment. Seasonal variation in the diets of generalist feeders has already been demonstrated for several Antarctic benthic invertebrates (Brand 1980). For *O. victoriae* populations, differences may be attributed to seasonal fluctuations in the abundance of community members (Dearborn 1965; Lowry 1975) or to the sampling of separate localized patches in different years.

Brittle star size did not appear to be a factor in determining diet composition. All food categories were represented in the diets of both small and large *O. victoriae*. Quantitative sampling of the environment was not undertaken, so the complete exclusion of an available food by all *O. victoriae* because of size limitations cannot be ruled out. Foods for which size thresholds might be expected (e.g. bivalves) were uncommon in the diet or small in size when taken. In any case, a high occurrence of fragmented items suggests that although all animals utilize the same food types, larger animals might simply ingest larger fragments.

Whether or not this species consumes energy-rich foods probably depends on the local abundances of all potential foods. Apparent low food-source diversity at Deception Island resulted in a high proportion of sediment in stomachs. The nutritional value of sediment and associated organic material to ophiuroids is unknown, but it is taken frequently by species other than *O. victoriae* (Morison 1979; Feder 1981) and is clearly important to some deposit feeders (Hargarve 1970; Lopez and Levinton 1978). Large quantities of foraminiferans were often associated with high sediment intake, and poor quality foods such as *Ophionotus* and *Sterechinus* fragments were also ingested. In other areas, crustaceans were more significant diet components. Krill were most important in the diet of the Valdivia Point population. Survey work in the vicinity of this station in the Gerlache Strait (Siegel 1982), and a high incidence of feeding humpback whales near this station indicate high euphausiid concentrations in the overlying water. The high frequency of amphipods in stomachs from Station 61 at Visokoi Island paralleled the large number of amphipods taken in trawls at this site. In every case, an increased proportion of euphausiids, amphipods or mysids reduced the contribution of sediment and other low-energy items.

Given the opportunistic nature of *O. victoriae*, appropriate methods of stomach analysis are limited. Frequency of occurrence is the simplest technique and gives a general description of the types of food eaten. It may be the only reasonable method when some regurgitation has occurred (Morison 1979), but we do not feel this was a serious problem in the present study. Its disadvantage is that it tends to overestimate the importance of small but frequently occurring items.

Numerous quantitative methods have been proposed and the salient features of many of these have been reviewed by Hynes (1950) and Hyslop (1980). When mastication of food occurs (Williams 1981), or when animals ingest detritus and prey fragments as in this study, counts of prey numbers or direct volume and weight determinations are inappropriate. A points method is well suited to this condition and has been applied to a variety of organisms (Swynnerton and Worthington 1940; Brun 1972; Williams 1981). Although somewhat subjective, this technique is not time-consuming, gives a relative measure of the bulk of food items and does not give a false impression of extreme accuracy. Subjectivity is at least partially overcome by large sample sizes (Hynes 1950).

The relative importance of each food item to the diet of *O. victoriae* was evaluated similarly by frequency-ofings of Hynes (1950) for stickleback fish and Williams (1981) for portunid crabs. However, the points method still has the advantage of estimating the bulk of each food item. Small organisms such as foraminiferans may occur in stomachs frequently but contribute little to the volume of the food bolus.

Regardless of the method used, diet determination on the basis of stomach contents has been criticized because it may inaccurately assess the actual nutritional importance of some foods. Different retention times and assimilation efficiencies of different foods may change the ranked importance of these foods from that determined by stomach analyses. Christensen (1970) realized this and measured residence times for important diet constituents of the predatory asteroid *Astropecten irregularis*. However, such determinations on fresh intact prey are inappropriate to the study of an animal which may ingest large quantities of detritus. Assimilation efficiencies have been calculated for some deposit feeders (Hargrave 1970; Kofoed 1975) but no such work was attempted for *O. victoriae*.

In spite of methodological limitations, several generalization can be made concerning the diet of *Ophionotus victoriae*. The species is extremely catholic and derives food from numerous invertebrate and several non-animal sources. Although sediment constitutes much of the stomach contents, food types fluctuate greatly between locations and years, and energy rich sources such as krill become important when available.

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