



# Spatial and temporal variation in the abundance, distribution and population structure of epibenthic megafauna in Port Foster, Deception Island

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## Abstract

Abundance and spatial distribution of epibenthic megafauna were examined at Port Foster, Deception Island, five times between March 1999 and November 2000. Camera sled surveys and bottom trawls were used to identify and collect specimens, and camera sled photographs also were used to determine abundances and spatial distributions for each species. The ophiuroid *Ophionotus victoriae*, the regular echinoid *Sterechinus neumayeri*, and one or more species of Porifera were the most abundant taxa during this sampling period. Abundances of *O. victoriae* varied throughout the annual cycle, peaking in June 2000, and were correlated positively with sedimentation rates. In contrast, abundances of *S. neumayeri* were consistent throughout the sampling period, except for a peak in June 2000, during austral winter. Peak abundances for both species coincided with a large number of small individuals, indicating apparent recruitment events for *O. victoriae* and *S. neumayeri* during this time period. Poriferans, as a group, had statistically similar abundances during each sampling period. Low-abundance species tended to be aggregated on both small and large spatial scales, their distributions probably influenced by reproductive method, gregarious settlement, and food availability. The spatial distribution of *S. neumayeri* in June 2000 and *O. victoriae* was random across multiple spatial scales, perhaps in response to food availability and broad environmental tolerances, respectively.

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## 1. Introduction

The trophic relationship between the water column and benthic community has been described in four stages: particulate matter is suspended from the seafloor into the water column; nutrients stimulate bacterial and phytoplankton production, which stimulates zooplankton production; large suspended particles provide

food for planktonic and benthic grazers; and organisms not consumed sink to the seafloor to be utilized by the benthic community (Marcus and Boero, 1998). Changes in sediment flux may be seasonal, causing the underlying benthic community also to change seasonally. Densities of benthic organisms have been observed to increase when sedimentation rates increase (Grenz et al., 2000), and a positive correlation has been reported between increased rates of sedimentation and the activity of megafauna in the North Pacific (Smith et al., 1994; Kaufmann and Smith, 1997) and

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Mediterranean (Coma et al., 2000). Lauerman and Kaufmann (1998) also observed aggregation of mobile fauna during times of increased sedimentation in the North Pacific.

In addition to seasonal variation, there may be spatial variation in the benthic fauna. Spatial variability often is related to changes in substrate, but may be influenced by other factors, including depth, temperature, salinity, physical disturbance, and competition (Thrush, 1991; Snelgrove, 1998). Most obvious is the tendency for hard substrates to support encrusting or sedentary organisms, while soft substrates allow organisms to live within the sediment (Woodin and Jackson, 1979). Rosenberg et al. (1992) observed an increase in the number of individuals and biomass with depth along the Kattegat, Sweden. The increasing depth coincided with a decrease in wave action as well as variations in salinity and temperature.

In the Antarctic, seasonal variation is driven by solar radiation (Clarke, 1988). During austral summer, water temperatures may fluctuate at the surface and in shallow areas and a dense diatom bloom may occur, briefly increasing the typically low standing crop of this region (Clarke, 1988). This seasonal primary production may give rise to distinct seasonality in growth and reproduction for many benthic organisms (Clarke, 1988). Specifically, the ophiuroid *Ophionotus victoriae* and the regular echinoid *Sterechinus neumayeri* display bands that coincide with seasonal growth and have been used in age determination and growth studies (Brey et al., 1995; Dahm and Brey, 1998). Suspension feeders are believed to be sustained by the summer bloom for most of the year, but cease feeding for approximately two months during the austral winter (Barnes and Clarke, 1995).

Deception Island, one of the South Shetland Islands located west of the Antarctic Peninsula (Fig. 1), is part of an environment with low fluctuations in temperature and salinity (Arntz et al., 1994). Port Foster, the drowned caldera in the center of Deception Island, has sediments similar to those of the other South Shetland Islands (Sáiz-Salinas et al., 1997), yet the benthic community at Deception Island may be different from those elsewhere within the island chain.

Arnaud et al. (1998) grouped the benthic fauna of Port Foster separately from other islands in the South Shetlands and determined Port Foster to have a lower taxonomic richness (6 vs. 28 taxa) and higher mass ( $26.6 \pm 9.9$  vs.  $13.9 \pm 6.3$  g) than the other South Shetland Islands, based on 50-l subsamples from bottom trawls. However, Sáiz-Salinas et al. (1997) reported that macrobenthic assemblages from Port Foster were similar to those from Livingston Island and the Bransfield Strait.

Gallardo et al. (1977) found the ophiuroid, *O. victoriae*, the asteroid, *Odontaster validus*, and the echinoid, *S. neumayeri*, to be the dominant benthic fauna of Port Foster. Also present were ascidians, poriferans, and nemerteans (Sáiz-Salinas et al., 1997; Arnaud et al., 1998). Similarly, Gallardo and Castillo (1968), during collections 17 and 27 days after the eruptions in 1967, found decaying remains of *S. neumayeri* and *O. victoriae*, both of which were present in large numbers, suggesting that they dominated the community prior to the eruptions.

Although the benthic community of Port Foster has been characterized on several occasions, it is not known how the abundance and distribution of epibenthic megafauna vary spatially within Port Foster nor how the community varies throughout an annual cycle. This study examined the abundance and spatial distribution of epibenthic megafauna within Port Foster at five time points over the course of a 22-month sampling program. Quantitative photographic surveys and bottom trawls were conducted to identify and evaluate the abundance, composition and spatial distribution of epibenthic megafauna in Port Foster. The resulting information was used to examine temporal variation in the abundance and spatial distribution of epibenthic megafauna.

## 2. Methods

### 2.1. Site description

Deception Island is located at the southwestern end of the South Shetland Island chain (Fig. 1) and was visited by the R/V *Laurence M. Gould* on

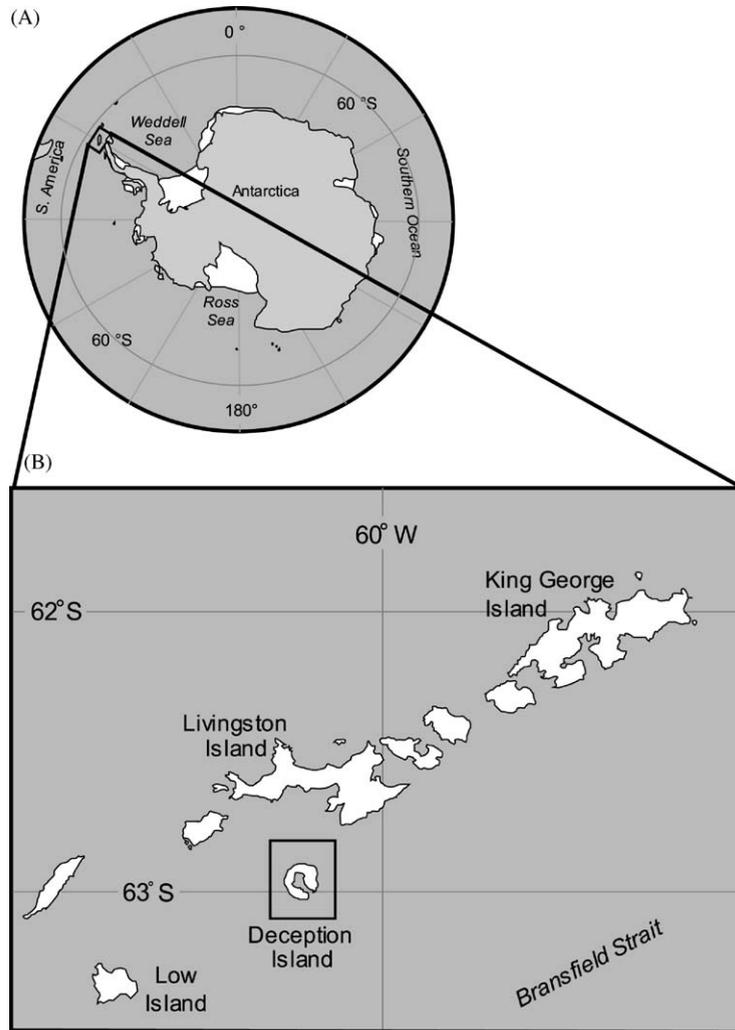


Fig. 1. (A) Map of the Antarctic continent and Southern Ocean. White regions indicate permanent oceanic ice sheets. Rectangle on the Antarctic Peninsula indicates the area depicted in Fig. 1b. (B) Map of the South Shetland Island region and Erupt study site including Deception Island, Livingston Island, and King George Island.

a series of five cruises between February 1999 and December 2000. These cruises took place during the following time periods: 22 February–17 March 1999, 25 October–16 November 1999, 5–27 February 2000, 16 May–15 June 2000, and 12 November–4 December 2000. Deception Island is a volcanically active island that has not erupted since 1970 (Baker et al., 1975; Smellie, 1988). The caldera exchanges water with the Bransfield Strait through a narrow channel (minimum width of 550 m) with a sill depth of 11 m (Smith et al.,

2003). The surrounding walls are covered with pyroclastic ash and lapilli-tuff, with layers of snow present from June through November. Gallardo et al. (1977) reported transport of these sediments by wind and water into Port Foster.

Sáiz-Salinas et al. (1997) described the bottom sediments as poorly sorted silty clays with high organic content and surface sediment pH values less than 7.0 for depths between 40 and 180 m. Gray et al. (2003) observed sediments dominated by gravel and coarse sand shallower than 80 m

depth, whereas silt and clay dominated sediments deeper than 80 m.

## 2.2. Camera sled deployments

A towed camera sled (Wakefield, 1990; Lauerman and Kaufmann, 1998) was deployed on four of the five cruises; no film was available during February 2000. The sled was equipped with a BENTHOS 372 35-mm camera and BENTHOS 382 100 W-s strobe and was towed behind the ship at a speed of approximately 1.5 knots. The sled was lowered to the bottom and towed through the center of Port Foster (Fig. 2) at a depth of 150–160 m along a transect 1500–2500 m in length (Table 1). The transects were conducted from NW to SE except for the transect in June 2000, which traveled SE to NW. During each transect the

camera, set at a height of 82 cm above the sea floor and an angle of  $22.5^\circ$  below horizontal, took pictures every 4.25 s to yield a series of photographs showing the floor of the caldera. Collections of animals were made with a semi-balloon trawl (6-m foot rope; 3.8 cm stretch mesh with 1.3-cm mesh cod-end liner) towed at approximately 1.5 knots along a transect of  $\sim 1000$  m length in a location similar to that of the camera sled. Specimens collected with the trawl were preserved in 10% seawater-buffered formalin and subsequently transferred to 80% ethyl alcohol.

## 2.3. Photograph analysis

Photographs were analyzed by projecting each frame onto the flat surface of an electronic digitizing pad. Organisms in each photograph

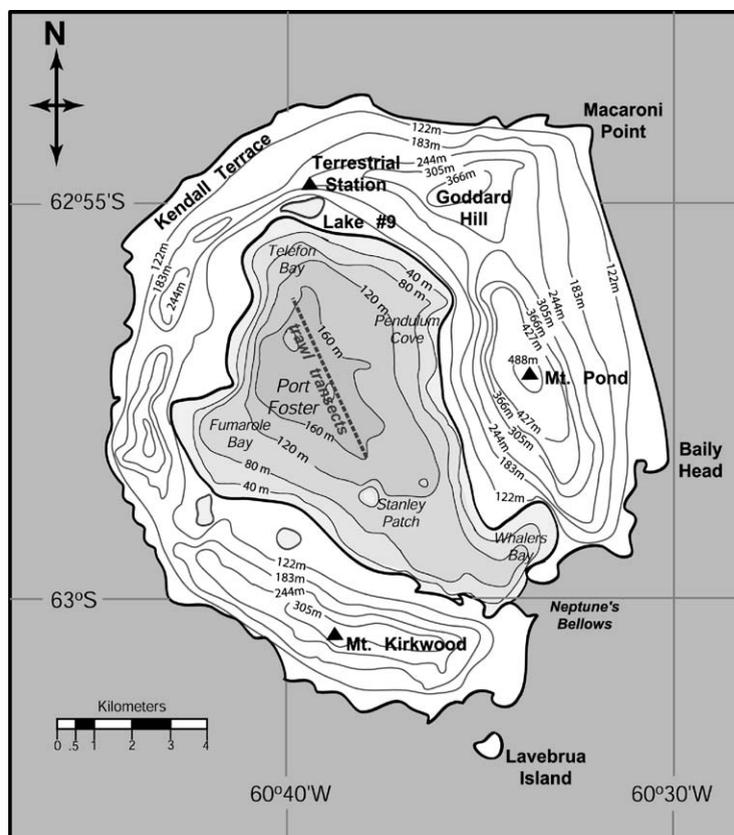


Fig. 2. Map of Deception Island showing the general transect used for the camera sled and trawls. Coordinates for the beginning and end of each camera sled transect are listed in Table 1.

Table 1

Summary data for the four camera sled transects through Port Foster, Deception Island

Date	Beginning position	Ending position	No. photos	Duration	Transect length (m)
4 Mar. 1999	62°57.925'S 60°38.257'W	62°56.754'S 60°39.821'W	563	42'33"	2086
6 Nov. 1999	62°57.924'S 60°38.103'W	62°56.759'S 60°39.179'W	651	48'56"	2531
5 Jun. 2000	62°58.410'S 60°37.661'W	62°57.695'S 60°38.300'W	432	33'51"	1485
28 Nov. 2000	62°57.986'S 60°38.201'W	62°57.157'S 60°38.938'W	559	42'02"	1738

were identified by comparing their appearance with specimens identified in trawl samples. The position of each individual was recorded electronically by a computer program that converted the pixels to seafloor coordinates using a perspective grid method (Wakefield and Genin, 1987; Lauerman et al., 1996). Lengths of individuals lying straight and flat on the sea floor also were recorded. For individuals that did not meet the “straight and flat” criterion, the center of the body was recorded as a point on the seafloor.

In the past, the amount of overlap between photographs has been used to calculate transect length (Lauerman et al., 1996). However, due to a lack of overlap between consecutive photographs, transect length was calculated using data from the ship's log and the time printed on the first and last photograph for each transect. The ship speed at the time on the beginning photograph was noted, as were the times and speeds recorded during the camera sled tow. The time elapsed between two consecutive recordings of ship speed was multiplied by the speed to determine the distance traveled for that portion of the tow. If there was a change in speed between two consecutive recordings, the change was assumed to be at a constant rate, allowing intermediate times and speeds to be interpolated from those recorded in the ship's log. Distances calculated for each portion of the tow were summed to provide the total distance traveled.

The density of each species was estimated using line-transect theory (Buckland et al., 1993) and the computer program DISTANCE (Laake et al., 1994). Line-transect theory assumes that only a narrow strip around the center line is censused accurately and that the probability of detecting an individual decreases with distance from the center

line. DISTANCE calculates an effective strip width (esw) and probability density function (pdf) on each side of the center line based on the detectability (visibility) of the species. The esw increases with increased visibility of a species, e.g., as a result of increased size or brighter color. The pdf describes the probability of detecting an individual at a given distance from the center line and also changes in response to visibility. Densities were estimated with DISTANCE when sufficiently large numbers (typically  $n > 40$ ) of a species were present to permit a pdf to be fitted reliably (cf. Lauerman et al., 1996).

During the analysis, the five species of Porifera were grouped together due to the inability to distinguish four of the species from each other in the photographs and the low densities of the fifth species, Demospongiae sp. H. The four species of Ascidiacea also were grouped together due to low abundances. Grouping these species of Porifera and Ascidiacea for the purposes of density estimation was justifiable since the visibility was similar among species within each group (cf. Kaufmann et al., 1989).

Density estimates for each species were compared among cruises using a Kruskal–Wallis nonparametric analysis of variance (Zar, 1999). Density differences between pairs of cruises were evaluated with a Mann–Whitney *U*-test.

#### 2.4. Spatial analysis

The spatial distributions of each species were determined over a range of spatial scales along each transect. Transects were divided into blocks of 1, 2, 4, 8, 16, 32, 64, and 128 photographs. The number of individuals in a single block was determined for each block size. Unpaired

photographs were not included in the analysis (e.g., March 1999 had 563 blocks of 1 photograph each, 281 blocks of 2 photos each, 140 blocks of 4 photos each, etc.). The distance covered between photographs was determined for each transect by using the maximum distance from the baseline (front of photograph) at which an organism was detected. Variance-to-mean ratios were calculated for each species along each transect at each block size. These values were compared to a two-tailed  $\chi^2$  distribution with  $n - 1$  degrees of freedom, where  $n$  represents the number of blocks considered in the analysis at that scale. Clumped distributions were indicated by  $p$  values greater than 0.975,  $p$  values less than 0.025 indicated an even distribution, and  $p$  values falling between 0.025 and 0.975 indicated distributions that could not be distinguished from random.

### 2.5. Specimen analysis

Measurements of specimens collected in the trawl were compared to the dimensions determined from the photographs. Specimens of *O. victoriae* and *S. neumayeri* collected in the trawls were measured with Vernier calipers to the nearest mm. The body diameter, excluding spines, of all the specimens of *S. neumayeri* were measured, as was the disk diameter of all the *O. victoriae* specimens from June and November 2000. For March and November 1999 and February 2000, *O. victoriae* specimens were selected at random until 200 individuals from each time period had been measured.

## 3. Results

### 3.1. Site description

The four photographic transects through Port Foster all traversed similar substrate that appeared as fine brown sediment in the photographs. The sediment surface included small clumps and divots, creating an irregular bottom on scales of centimeters to tens of centimeters. Sediments were determined to be oxygenated and moderately rich in organic matter. The sediments were primarily

composed of silt and clay sized grains, with varying amounts of sand-sized particles and less than 2% gravel. The sediment was composed of basaltic glass, plagioclase, cryptocrystalline opaques, and clinopyroxene (Gray et al., 2003). Rock outcrops and large clumps of macroalgae also were seen along each transect.

The transect in March 1999 primarily traversed a sediment bottom, as described above, with three outcrops of rock and occasional algal debris. Small details in the appearance of the sea floor were difficult to determine because of consistent turbidity, but the sediment qualitatively appeared to be fairly consistent across the entire transect. In November 1999 the water was much clearer and the substrate more diverse; many rock outcrops and algal masses were visible along the transect. Adding to the substrate diversity were reddish clumps of sediment or small rocks, likely to be weathered pieces of gravel composed of indeterminate cryptocrystalline secondary material (Gray et al., 2003), that were common in the first half of the transect. Also of interest were occasional patches of coarser sediment and an apparent trend for the sediment to become coarser as the camera sled progressed. The transect during June 2000 was similar to that of November 1999, however the number of rock outcrops was much lower and no weathered gravel was seen. In November 2000, the only substrate observed was the brown sediment that dominated all of the transects. No additional substrates, such as rock outcrops or algal masses, were seen. However, much of the transect was obscured by a persistent sediment cloud, particularly on the right side of each frame.

### 3.2. Density

A full list of the species seen in the photographs and analyzed for density is found in Table 2. *O. victoriae* was consistently the most abundant species identified in camera sled photographs, followed by *S. neumayeri* and Porifera (Fig. 3). *O. victoriae*, *S. neumayeri*, and ascidians all reached peak densities during June 2000 (11.76, 1.07, 0.11 ind m<sup>-2</sup>, respectively), while the density for Porifera was highest in November 1999 and 2000 (0.11 ind m<sup>-2</sup>). A density for the nemertean

*Parborlasia corrugatus* could be calculated only during March 1999 (0.02 ind m<sup>-2</sup>) because of low abundances in the remaining three transects (Table 3).

Table 2

Species observed in the camera sled photographs, as identified from trawl specimens

Taxon	Species	
Porifera	Demospongiae sp. H	
	Demospongiae sp. K	
	Poecilosclerida sp. D	
	? <i>Ectyodoryx</i> sp.	
	? <i>Mycale</i> sp.	
Cnidaria	<i>Artemidactis victrix</i>	
Nemertina	<i>Parborlasia corrugatus</i>	
Arthropoda, Crustacea	<i>Notocrangon antarcticus</i>	
Echinodermata		
	Asteroidea	<i>Odontaster validus</i>
	Ophiuroidea	<i>Ophionotus victoriae</i>
	Echinoidea	<i>Sterechinus neumayeri</i>
Asciacea		
	<i>Ascidia meridionalis</i>	
	<i>Bathypera</i> sp.	
	<i>Cnemidocarpa verrucosa</i>	
	<i>Molgula</i> sp.	

Species of Porifera were not identifiable in the photographs; those listed were found in the trawl samples.

Densities for *O. victoriae* were significantly different among transects (Kruskal–Wallis ANOVA,  $p < 0.05$ ), with no two transects statistically similar. *S. neumayeri* also showed a significant difference in density among transects ( $p < 0.05$ ), due to significantly elevated densities during June 2000. Densities observed on the other three transects (March 1999, November 1999 and 2000) all were similar to each other. Ascidian densities also differed significantly among transects ( $p < 0.05$ ). Only poriferans displayed statistically similar densities on all transects ( $p = 0.084$ ).

*O. victoriae* appeared to dominate the epibenthic species assemblage, comprising 89–96% of the total individuals observed (Table 3). *S. neumayeri* and poriferans were the next most dominant taxa, with 2–8% and 0.8–2% of the total individuals, respectively. *O. victoriae* and Porifera showed their lowest proportions and *S. neumayeri* its highest proportion during June 2000, largely as the result of a much higher abundance of *S. neumayeri* during this time period. The remaining species each comprised 1% or less of the individuals along each transect; combined, these species comprised 0.4–2.5% of individuals.

### 3.3. Diversity

Species diversity was evaluated with Shannon–Wiener ( $H'$ ) and log series ( $\alpha$ ) diversity indices

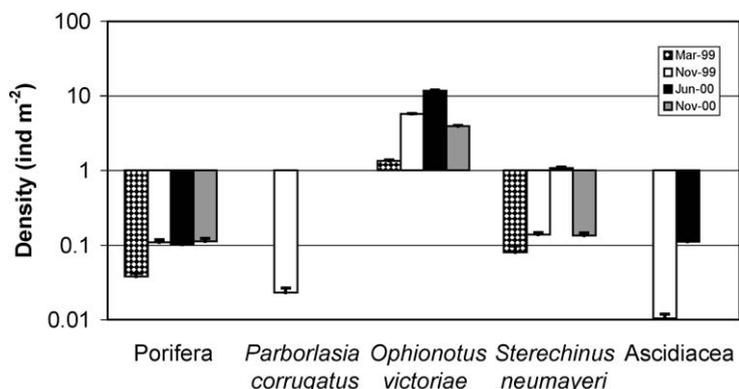


Fig. 3. Mean densities estimated by DISTANCE for five species of epibenthic megafauna from Port Foster. Error bars depict one standard error. Densities for *P. corrugatus* and Ascidiacea for November 1999 are too low to be seen on the graph; the numbers can be found in Table 2.

Table 3  
Summary of the estimated densities for each species observed in the camera sled photographs

Species	March 99	November 99	June 00	November 00
Porifera <sup>a</sup>	0.038 (0.021–0.055) [67, 2.2]	0.11 (0.09–0.13) [282, 1.3]	0.10 (0.08–0.12) [218, 0.8]	0.11 (0.09–0.14) [191, 2.4]
<i>Artemidactis victrix</i>	[4, 0.1]	[9, 0.040]	[1, 0.004]	[3, 0.04]
<i>Parborlasia corrugatus</i>	[38, 1.2]	0.023 (0.016–0.030) [83, 0.4]	[16, 0.06]	[10, 0.01]
<i>Notocrangon antarcticus</i>	[3, 0.09]	[2, 0.009]	[0, 0]	[0, 0]
<i>Sterechinus neumayeri</i>	0.08 (0.04–0.12) [133, 4.3]	0.14 (0.12–0.16) [521, 2.3]	1.07 (1.01–1.13) [2386, 9.0]	0.13 (0.11–0.16) [254, 3.2]
<i>Odontaster validus</i>	[6, 0.2]	[13, 0.06]	[4, 0.02]	[1, 0.01]
<i>Ophionotus victoriae</i>	1.32 (1.24–1.41) [2819, 91.1]	5.70 (5.50–5.91) [21541, 95.7]	11.76 (11.42–12.10) [23695, 90.3]	3.90 (3.72–4.08) [7417, 93.9]
<i>Ascidia meridionalis</i>	[0, 0]	[1, 0.004]	[1, 0.004]	[0, 0]
<i>Bathypera</i> sp.	[2, 0.06]	[1, 0.004]	[22, 0.08]	[3, 0.04]
<i>Cnemidocarpa verrucosa</i>	[0, 0]	[2, 0.009]	[0, 0]	[2, 0.03]
<i>Molgula</i> sp.	[24, 0.8]	[45, 0.2]	[190, 0.7]	[14, 0.2]
Combined Ascidiacea <sup>b</sup>	[26, 0.8]	0.010 (0.008–0.012) [49, 0.2]	0.11 (0.09–0.13) [213, 0.8]	[19, 0.2]
Total density	1.438 (1.360–1.516) [3096, 100]	5.983 (5.790–6.176) [22500, 100]	13.04 (12.73–13.35) [26533, 100]	4.14 (2.416–5.864) [7895, 100]
Minimum species richness	9	11	9	9

Each number is the mean density (ind m<sup>-2</sup>) calculated by DISTANCE. Numbers in parentheses represent 95% confidence intervals around each mean, and the numbers in brackets are the number of individuals observed and percent of total individuals for each transect, respectively.

<sup>a</sup>Grouped because it was not possible to distinguish among species in the photographs.

<sup>b</sup>Grouped due to an insufficient number of any one species.

(Magurran, 1988) for each camera sled transect (Table 4). Both indices showed low levels of diversity within the epibenthic community. According to the Shannon–Wiener index, diversity was lowest during November 1999 and 2000 ( $H' = 0.24$  and  $0.29$ , respectively) and highest during March 1999 and June 2000 ( $H' = 0.43$  and  $0.41$ , respectively). However, according to the log series index, diversity was lower in 2000 (June

$\alpha = 0.98$  and November  $\alpha = 1.14$ ) than in 1999 (March  $\alpha = 1.29$  and November  $\alpha = 1.23$ ).

### 3.4. Dispersion

Variance-to-mean ratios were used to detect departures from Poisson (random) distributions for five species (Table 5). *P. corrugatus*, poriferans, and ascidians displayed similar distribution

patterns among transects. *P. corrugatus* tended to be patchy on spatial scales up to approximately 100 m. On larger scales, above 150 m, a random

distribution was displayed. Porifera varied slightly from the pattern displayed by *P. corrugatus*, with aggregation occurring until approximately 70 m and random distributions on all larger scales examined (86–540 m). Ascidiacea displayed a patchy distribution on scales up to 228 and 68 m during November 1999 and June 2000, respectively. In November 1999, the distribution became random only on the largest scale (457 m), but in June 2000 the distribution progressed to evenness by 540 m.

Table 4

Diversity indices for each camera sled transect. Shannon–Wiener diversity was calculated using  $\log_e$ .

Index	Mar 99	Nov 99	Jun 00	Nov 00
Shannon–Wiener, $H'$	0.43	0.24	0.41	0.29
Log series, $\alpha$	1.29	1.23	0.98	1.14

Table 5

Summary of spatial analysis as determined by comparing variance-to-mean ratios to a  $\chi^2$  distribution

Cruise	Length (m)	Number of photographs	Porifera	<i>P. corrugatus</i>	<i>O. victoriae</i>	<i>S. neumayeri</i>	Ascidiacea
March 99	1.34	563	A	A	A	A	
	2.68	281	A	A	A	A	
	5.36	140	A	A	A	A	
	10.7	70	A	A	A	A	
	21.4	35	A	A	R	A	
	42.9	17	A	A	E	A	
	85.8	8	R	R	E	R	
172	4	R	R	E	R		
November 99	3.57	651	A	A	A	A	A
	7.14	325	A	A	A	A	A
	14.3	162	A	A	A	A	A
	28.6	81	A	A	A	A	A
	57.1	40	A	A	R	A	A
	114	20	R	A	E	A	A
	228	10	R	R	E	R	A
457	5	E	R	E	E	R	
June 00	4.22	432	A		A	A	A
	8.44	216	A		A	A	A
	16.9	108	A		A	A	A
	33.8	54	A		R	E	A
	67.5	27	A		E	E	A
	135	13	A		E	E	R
	270	6	R		E	E	R
540	3	R		E	E	E	
November 00	1.77	559	A		A	A	
	3.54	279	A		A	A	
	7.08	139	A		A	A	
	14.2	69	A		R	A	
	28.3	34	A		E	A	
	56.6	17	A		E	A	
	113	8	R		E	R	
227	4	R		E	E		

See text for description of methods used to determine spatial patterns. A—aggregated, R—random, and E—even distributions.

*O. victoriae* displayed a consistently aggregated distribution on scales less than 20 m for all transects except November 2000, for which a random distribution occurred at 14 m. In November 1999, the patchy distribution persisted through 29 m, a scale larger than the other transects. Random distributions were observed only once along each transect, 14–57 m, while even distributions were observed consistently among all transects on scales larger than 68 m. Fig. 4 depicts the distribution of *O. victoriae* along each transect. Patches of elevated abundance can be seen along each transect; however, *O. victoriae* were present in virtually all photographs from all transects.

*S. neumayeri* displayed a patchy distribution at distances less than 60 m, becoming random and even on larger scales. However, as with *O. victoriae*, aggregated distributions of *S. neumayeri* persisted during November 1999, through 114 m. The random distributions occurred most often between 86 and 172 m, while even distributions occurred mostly at length scales greater than 200 m. However, in June 2000, the distributions progressed from aggregated to even at smaller scales, with even distributions occurring at scales of 28 m. This trend is illustrated in Fig. 5c, where the abundance of individuals near the beginning of the transect was distinctly different from the other transects (Figs. 5a, b and d), coinciding with the altered distribution in June.

### 3.5. Size distribution

Body sizes varied significantly among time periods for both *O. victoriae* and *S. neumayeri*. For *O. victoriae*, mean sizes in photographs from March and November 1999 were larger than June and November 2000, and disk diameters were statistically different for each time period (Mann–Whitney *U*-test,  $p < 0.05$ ; Fig. 6a). However, direct measurements of collected specimens showed a different temporal trend. Animals acquired in November 2000 were significantly larger than those collected at any other time (Mann–Whitney *U*-test,  $p < 0.05$ ; Fig. 6b). Additionally, specimens from November 1999 were significantly smaller than those collected during March 1999 and February 2000.

Similarly, *S. neumayeri* measured in photographs appeared larger in transects from 1999 vs. 2000. Statistically, individuals present in photographs from March 1999 and November 2000 were similar (Mann–Whitney *U*-test  $p = 0.912$ ), while those from all other time periods were different from each other and individuals from June 2000 were smallest (Mann–Whitney *U*-test  $p < 0.05$ ). As with *O. victoriae*, measurements from specimens of *S. neumayeri* did not support the trends evident in the photographs (Figs. 6c and d). The sizes recorded from the two methods also were quite different. The film measurements for *S. neumayeri* ranged from 1.1 to 6.4 cm, while the specimens were 2.1–5.7 cm and statistically larger than individuals from photographs during each time period. Specimens collected during June 2000 were significantly smaller than those collected at any other time (Mann–Whitney *U*-test  $p < 0.05$ ). No significant differences in animal size were observed among other time periods.

Measurements from the photographs showed trends in the size of *O. victoriae* along each transect (Fig. 7). At the beginning of a transect, the majority of individuals measured were below the mean size for that transect. As the transects were traversed, the proportion of individuals below and above the mean sizes became more even. Larger individuals dominated photographs near the end of each transect. The transect from June 2000 showed a particularly large number of small individuals at the beginning of the transect, and this persisted through the first 100 photographs, unlike the other three transects, which showed a more even progression from small individuals to a predominance of large individuals.

The trends for the size of *S. neumayeri* along the transects (Fig. 8) were not quite so prominent as those of *O. victoriae*. Individuals were more evenly distributed around the mean size, but there still was a general increase in size as the transect was traversed. However, the transect from June 2000 showed a trend more like those seen for *O. victoriae*, with a large proportion of small individuals near the beginning and larger individuals near the end of the transect. Also in contrast to the general trend, the transect from March 1999

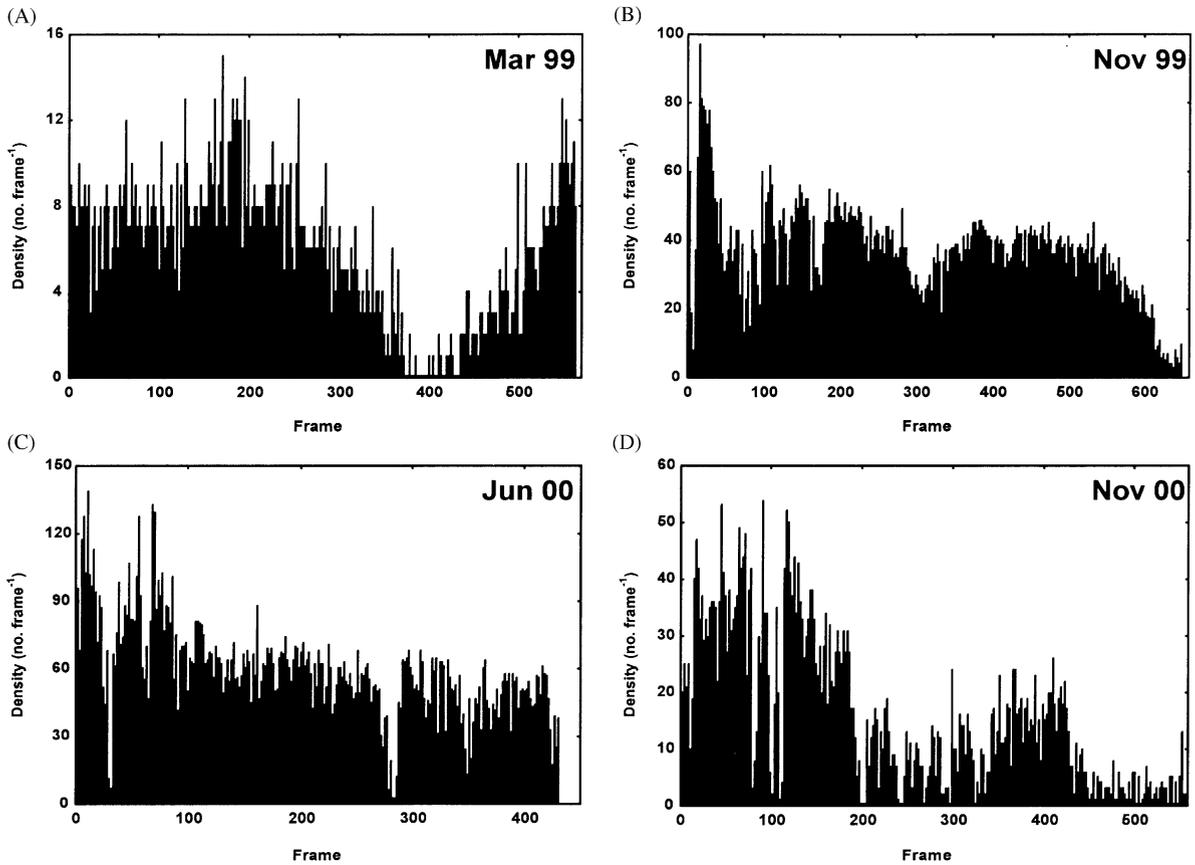


Fig. 4. Per-photograph abundance of *O. victoriana* in relation to distance along each transect. Note changes in vertical scale among panels, reflecting variation in abundance among time periods.

showed a preponderance of smaller individuals near the end of the transect.

Body size in both *O. victoriana* and *S. neumayeri* differed between estimates from transect photographs and direct measurements on preserved specimens collected with the benthic trawl (Fig. 5). In general, specimens measured in the laboratory tended to be larger than estimates from transect photographs during the same time periods. During March and November 1999, photographic measurements of *O. victoriana* were significantly larger than collected specimens, but during February and November 2000 specimens were significantly larger than photographic estimates (Mann–Whitney *U*-test,  $p < 0.05$ ). Specimens of *S. neumayeri* were significantly larger than

those from photographs in November 1999, June and November 2000 (Mann–Whitney *U*-test,  $p < 0.05$ ). The collection of only a single intact specimen during March 1999 precluded statistical analysis of size differences for this time period.

## 4. Discussion

### 4.1. Density

The dominance of the epibenthic community by *O. victoriana* and *S. neumayeri* supports published observations that these two species are dominant in Port Foster (Sáiz-Salinas et al., 1997; Arnaud

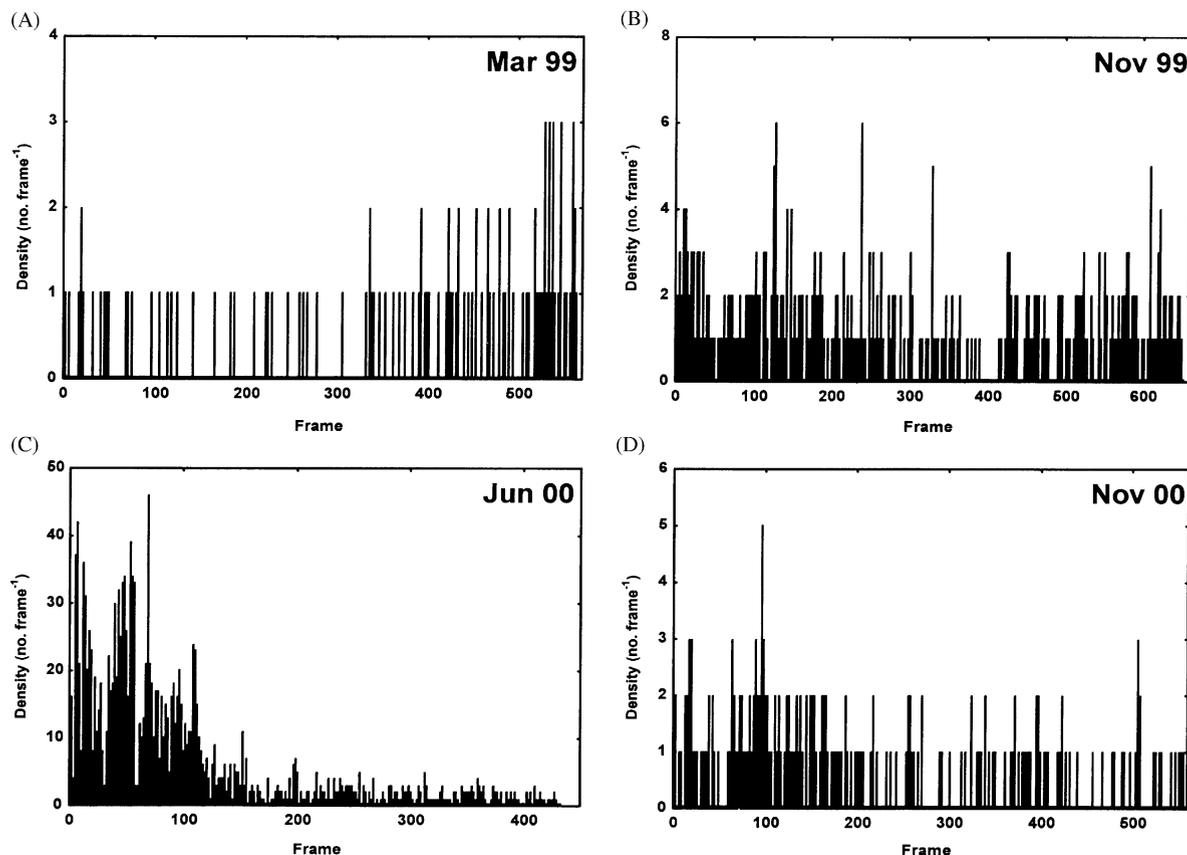


Fig. 5. Per-photograph abundance of *S. neumayeri* in relation to distance along each transect. Note changes in vertical scale among panels, reflecting variation in abundance among time periods.

et al., 1998). It is unusual that *O. validus*, which was reported as one of the dominant species by Gallardo et al. (1977), has not been so abundant in recent years. It is possible that during the camera sled tows individuals were beneath the sediment surface. However, no *sitzmarks* (characteristic depressions in the sediment; Kaufmann et al., 1989; Smith et al., 1993) were observed, and this explanation does not explain their absence compared to previous studies where similar trawls were used to sample the benthic fauna. It is possible that *O. validus*, despite the broad diet this species shares with *O. victoriae* and *S. neumayeri* (Fratt and Dearborn, 1984), was not as successful at reestablishing itself after the eruptions in 1970.

More than 50 different prey items have been identified from the guts of *O. victoriae*, including

sediment, juvenile ophiuroids, euphausiids, polychaetes, sponges, and copepods (Dearborn et al., 1972; Dearborn, 1977; Dearborn and Edwards, 1984; Fratt and Dearborn, 1984). *S. neumayeri* is believed to use diatoms as a main portion of its diet (Pearse and Giese, 1966; Dearborn et al., 1972), but also has been found to eat sponges (Brey and Gutt, 1991) as well as red algae, seal feces (Pearse and Giese, 1966), bryozoans, hydrozoans, scallops, amphipods, and foraminifera (McClintock, 1994).

Densities of *O. victoriae* differed significantly among transects and were correlated significantly and positively (Pearson correlation = 1.00,  $p = 0.01$ ) with sinking mass flux (Fig. 9; Baldwin and Smith, 2003) at depths of 20 and 50 m above bottom (mab). The lowest density, observed in

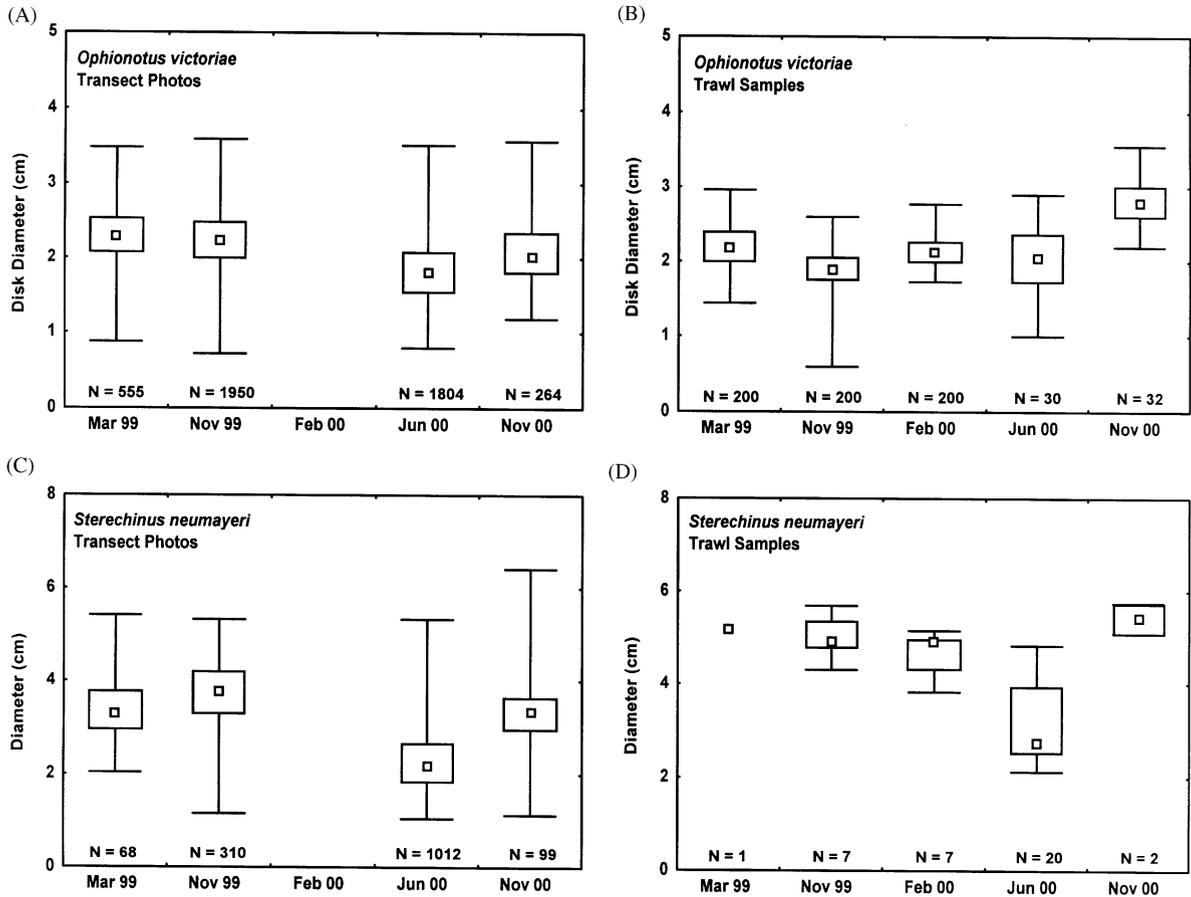


Fig. 6. Disk diameter and body diameter for *O. victoriae* and *S. neumayeri*, respectively. The small box represents the median size, the outer edges of the boxes are the 25th and 75th percentiles, while the vertical lines indicate minimum and maximum values. Panel A represents *O. victoriae* from photographs, panel B represents *O. victoriae* specimens, panel C represents *S. neumayeri* from photographs, and panel D represents *S. neumayeri* specimens.

March 1999, coincided with a time of low flux, while the November 1999 and 2000 densities were intermediate as was the mass flux (Baldwin and Smith, 2003). In June 2000, the peak density coincided with a time of increasing flux, but maximum flux rates for 2000 were not recorded until August, at a time when no benthic faunal samples were collected. This maximum density value also may have been influenced by the difference in transect location during this time period.

Densities of *S. neumayeri* were similar in all transects except June 2000 when densities were

nearly 10 times higher than in any other transect. Several factors may have been responsible for this dramatic change. Recruitment seems unlikely to explain the elevated densities in June 2000. The appearance of new recruits at this time of year would follow the known spring and summer spawning times for this species (Pearse and Giese, 1966; Yakovlev, 1984; Pearse et al., 1991), and individuals collected during June 2000 were significantly smaller than those from the other four sampling periods (Fig. 6c). However, the youngest specimens reported in previous studies were 4 years old (McMurdo Sound; Brey et al.,

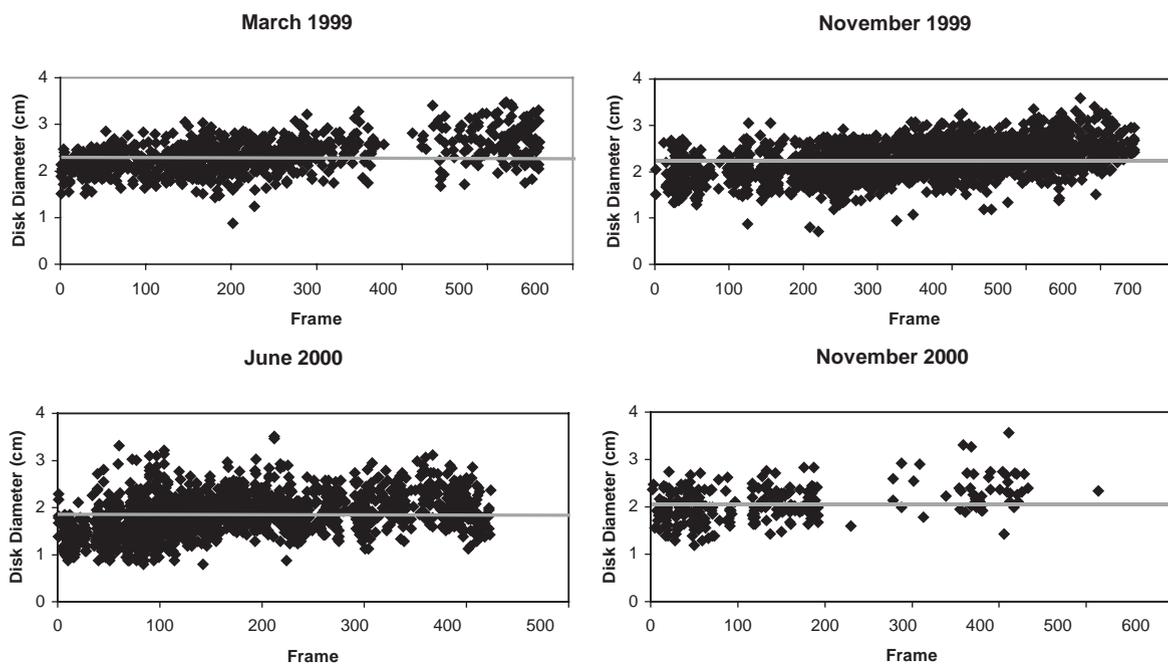


Fig. 7. Disk diameters of *O. victoriae* in relation to distance along each photographic transect. The horizontal gray line represents the mean disk diameter for each transect.

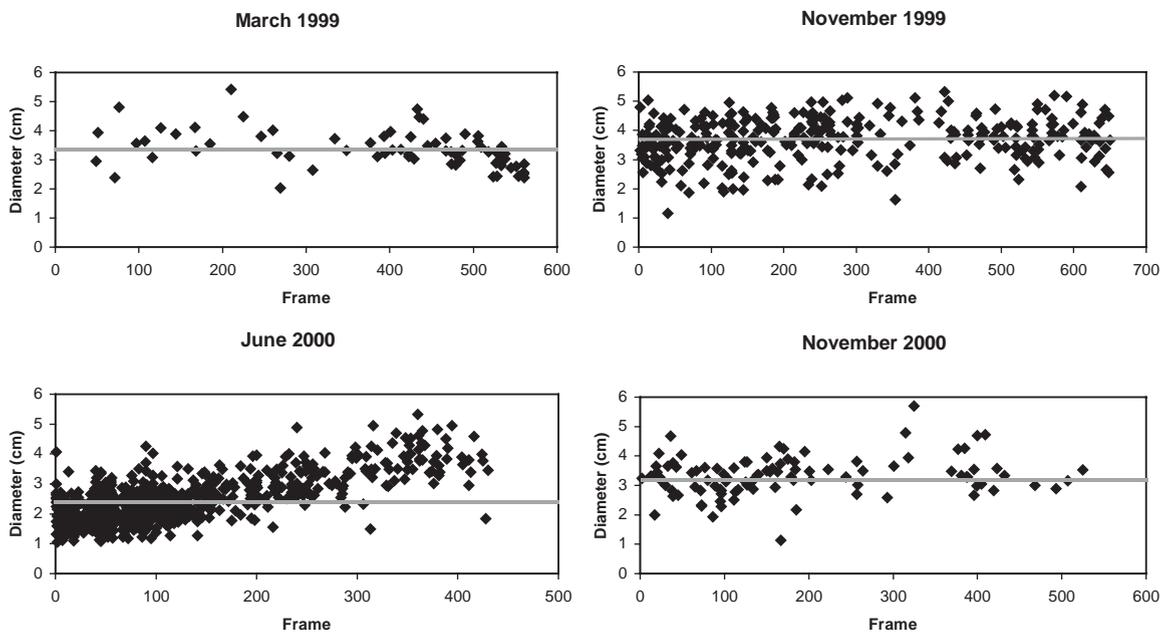


Fig. 8. Body diameters of *S. neumayeri* in relation to distance along each photographic transect. The horizontal gray line represents the mean body diameter for each transect.

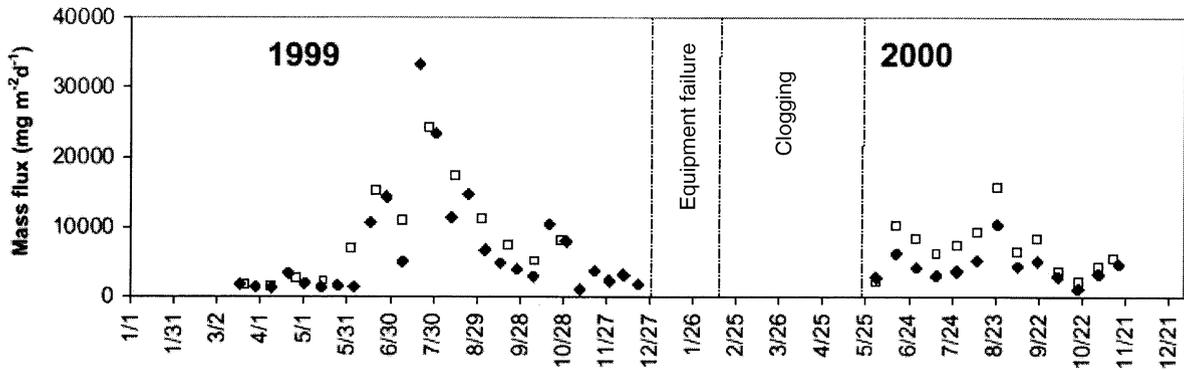


Fig. 9. Flux data for 20 mab (□) and 50 mab (◆) from Baldwin and Smith (2003).

1995), and it seems unlikely that the individuals contributing to the apparent population increase in Port Foster had recruited and grown to a diameter of several cm in a single season. Alternatively, the significant change in density may have been the result of spatial variability in the distribution of echinoids. The June 2000 transect was carried out in waters 130–160 m deep, in contrast to the other transects which took place at 160–170 m. This change in survey depth places the June 2000 transect closer to the depths dominated by regular echinoids (Arnaud et al., 1998).

Perhaps more importantly, the June 2000 transect was situated southeast of the other transects, which may have placed the camera sled in a portion of Port Foster with a community structure that differed from the community sampled during the other time periods. The significant increase in density during June 2000 also may have been a response to increased flux following a diatom bloom in March 2000 (Sturz et al., 2003). Diatoms represent a major dietary component for *S. neumayeri* (Pearse and Giese, 1966; Dearborn et al., 1972), and highly productive areas are believed to provide the best living conditions for *S. neumayeri* (Brey et al., 1995). Individuals from shallower portions of Port Foster may have congregated near the center in response to accumulation of sinking organic material in this area.

Densities of Porifera did not vary significantly throughout the annual cycle ( $p = 0.084$ ), despite the substantial temporal variation in the flux of

sinking particulate material (Baldwin and Smith, 2003). Although poriferans are filter feeders and rely on suspended particulate material for sustenance, their density did not correlate with changes in mass flux (Pearson correlation = 0.762,  $p = 0.449$ ). Densities were probably consistent because of the slow growth rates of Antarctic sponges (Dayton, 1979). The adults were not likely to grow much in the course of one year and any recruits were probably too small to be detected after only one year of growth, causing densities to remain constant throughout the study. Even the poriferan identified as a possible species of *Mycale* sp., a genus known to grow relatively quickly (Dayton, 1979), did not occur in abundances large enough to impact the poriferan community in Port Foster.

In comparison to other studies, it appears that the densities of *O. victoriae*, *S. neumayeri*, Porifera, and Ascidiacea at Deception Island were much lower than at other locations in the South Shetland Island chain (Table 6). However, densities of *O. victoriae* and ascidians in Port Foster were comparable to abundances measured in the Weddell and Lazarev Seas (Gutt and Starman, 1998). Poriferan densities were close to those found at depths of 120 and 170 m at Admiralty Bay, King George Island (Jażdżewski et al., 1986). The generally lower densities at Deception Island may be due, in part, to the limited exchange of water between Port Foster and the Bransfield Strait, which could limit the benthic fauna to resources already present within Port Foster. This

Table 6  
Densities of Antarctic epibenthic megafauna reported in the literature, in comparison to this study

Location (Ref.)	Depth (m)	Porifera	Ophiuroidea	Echinoidea	Ascidiacea	Total megafauna
Livingston Island (Sáiz-Salinas et al., 1998)	32–421	0.7	47.3	3.7	64	1236
King George Island (Jażdżewski et al., 1986)	120	0	50	17	27	1635
King George Island (Jażdżewski et al., 1986)	170	0	126	4	59	2829
Weddell and Lazarev Seas (Gutt and Starmans, 1998)	183–1162	2.79	9.63	N/A	0.10	46.0
Deception Island (this paper)						
March 1999	160	0.04	1.32	0.08	N/A	1.44
November 1999	160	0.11	5.70	0.14	0.01	5.98
June 2000	130–160	0.10	11.76	1.07	0.11	13.04
November 2000	167	0.11	3.90	0.13	N/A	4.14

Abundances are listed in  $\text{ind m}^{-2}$ . Jażdżewski et al. (1986) and Sáiz-Salinas et al. (1998) collected data with van Veen grabs ( $0.1 \text{ m}^2$ ) and Gutt and Starmans (1998), as well as the data from this study, were collected through photographic analysis.

is exemplified by lower concentrations of chlorophyll *a* during non-bloom times in Port Foster ( $0.2\text{--}0.5 \mu\text{g l}^{-1}$ ; Sturz et al., 2003) when compared to waters around the South Shetland Islands ( $2\text{--}10 \text{ mg m}^{-3}$ ; von Bodungen et al., 1986).

#### 4.2. Diversity

Epibenthic megafaunal diversity in Port Foster was low ( $H' < 1.0$ ) in comparison to other parts of the Antarctic. In the Weddell Sea and Bellingshausen and Amundsen Seas, Starmans et al. (1999) reported Shannon–Wiener values between 1.60 and 2.77 for organisms identified at either genus or species level. At a series of stations near Arthur Harbour, Antarctic Peninsula, Shannon–Wiener values from 2.03 to 4.92 were recorded for organisms identified at the species level (White, 1984). There are two major differences between Port Foster and other parts of Antarctica. One is the limited exchange of water between the caldera and the Bransfield Strait, which may not allow new species to invade and establish themselves as readily as in regions where the sources of water and larvae are greater. The other is habitat disturbance, which in much of the Antarctic is caused by ice, but in Port Foster is caused primarily by volcanic activity. Ice disturbances may occur on a smaller scale and less frequently than the volcanic activity experienced by Deception Island. For example, Gutt (2001) estimated that a square meter of Antarctic benthos should be affected by ice only once every 200–300 years,

whereas the eruption history of Deception Island indicates more frequent disturbance.

The 1967 eruption produced large amounts of dust, ash, bombs, blocks, and lapilli, a total volume estimated at  $0.05 \text{ km}^3$  (Baker et al., 1975). Much of Deception Island was covered with ash and lapilli, which subsequently was transported into Port Foster by snow melt, creating layers of pyroclastic material 1–150 cm thick. Soon after the 1967 eruption, Gallardo and Castillo (1968) performed three dredges that yielded a maximum of 753 individuals in a single haul, and grab samples, the richest of which was composed of deceased *S. neumayeri* and living and deceased *O. victoriae*. By 1973, the fauna again had become scarce after beginning to increase in abundance after 1971 (Gallardo et al., 1977). As late as 1975, deposition of secondary ash continued to alter the composition of the substrate (Gallardo et al., 1975). Thus, the effects of the most recent volcanic activity have been long-term, and may be still ongoing.

As for the dominant species, *O. victoriae* and *S. neumayeri* both have planktotrophic larvae (Poulin et al., 2002). Growth curves for both species suggest that growth slows with the number of bands present, representative of age (Brey et al., 1995; Dahm and Brey, 1998). However, annual growth values for individuals were not published. The maximum age determined for *O. victoriae* was 22 years (Dahm and Brey, 1998) and approximately 30 years for *S. neumayeri* (Brey et al., 1995), which indicates that at least one generation

of each species should have passed since the 1967 eruption. Such long-lived species are believed to be indicative of stable environments (Thorson, 1957), and the Antarctic is believed to have been geologically stable for a long period of time. High diversity levels at Deception Island have been attributed to mechanisms described by the stability–time hypothesis (Gallardo et al., 1977; Gallardo, 1987). However, low benthic diversity, as reported here, seems more typical of disturbed environments, such as the high stress location within the San Juan Archipelago described by Sanders (1969). At Deception Island, volcanic activity disrupts environmental stability and is likely to limit the types of organisms present to those that can withstand large-scale disturbance or species capable of recolonizing rapidly following an eruption or similar event.

Seasonal variation in diversity was observed in this study; however, different temporal patterns were detected with the two diversity indices used. The Shannon–Wiener index, which is more sensitive to species richness than the log series index (Magurran, 1988), indicated lowest diversity during November 1999 and 2000, probably in response to relatively high densities of *O. victoriae* compared to the other species observed (Tables 3 and 4). By comparison, the less biased log series index indicated lower diversity in 2000 vs. 1999. The lower diversity during 2000 coincided with a period of reduced sinking particle flux (Baldwin and Smith, 2003) that could have impacted the composition of the benthic community.

#### 4.3. Dispersion

All of the species examined exhibit patchy distributions to some degree. For the poriferans, aggregation is likely due to reproductive mode and gregarious settlement of the sessile individuals (Thorson, 1957, 1966; Thrush, 1991). A large proportion of Antarctic poriferans (80%) are viviparous or brood their offspring (White, 1984), reducing the potential for dispersal and resulting in a patchy distribution. Barthel and Gutt (1992) also found embryos released by the mother and free-swimming larvae to result in patchy distributions. Embryos are large and ready

to settle in the vicinity of the mother when released. Free-swimming larvae settle on a specific substrate, causing them to settle in groups, when they encounter the desired substrate. However, a preference for patches of hard substrate was not discernable due to the layer of fine sediment overlying the sea floor.

For ascidians, aggregation probably resulted from gregarious settlement that was not specifically related to hard substrates, as with the poriferans. The ascidians identified from Port Foster are either known to be solitary or are congeners of solitary species, all of which have been found to aggregate (Young and Vázquez, 1995; Kowalke, 1999). Young and Vázquez (1995) found that larvae settled around the bases of adults. Similarly, Havenhand and Svane (1989) found larvae of *Ascidia mentula* to settle preferentially near conspecifics, as has been reported for *Molgula complanata* and *Chelyosoma productum*.

*P. corrugatus* also appeared to be aggregated on both small and large scales. For this species, feeding behavior may have produced patchy distributions. *P. corrugatus* is a mobile, necrophagous scavenger, up to 1 m in length, and many individuals may converge on a single item (Presler, 1986), creating a clumped distribution. Although it was not possible to discern feeding in the photographs, there were frames with several individuals close together or entwined. These instances may have resulted from an undetectable food item, continued aggregation after feeding, or social behavior. The large-scale patchiness may have resulted from multiple feeding events.

*S. neumayeri* exhibited aggregated distributions for most of the sampling period, although more evenness was evident in June 2000. Brockington et al. (2001) observed dense aggregations of *S. neumayeri* during winter when they ceased feeding; after winter, feeding appeared to resume in response to increased benthic microalgal production. Since there was no mention of aggregation during times other than winter, it may be assumed that Brockington et al. (2001) observed a different dispersal pattern during times of feeding. The even distribution of *S. neumayeri* observed in June 2000 may have been in response to increased flux of

sinking particulate material, which probably included diatoms from the March bloom. The abundant individuals may have spread out through Port Foster to take advantage of the food supply. However, *S. neumayeri* appears to be unusual in becoming less aggregated when feeding, since aggregations of other urchins have been attributed to feeding behavior (Grassle et al., 1975). Also to be taken into consideration is the shallower depth (130 vs. 160 m) at which the transect began and the different position for the transect as a whole, compared to the other transects. This shift in position may have placed the transect in a portion of Port Foster that has a slightly different community composition and spatial distribution.

*O. victoriae* appeared to be less aggregated and more evenly distributed than the other species. *O. victoriae* also may inhabit a variety of substrates over a wide depth range (Fratt and Dearborn, 1984) and utilize a variety of food sources. This general use of habitat and resources should be reflected in spatial distributions that do not indicate dependence on patches of any single resource. However, some small-scale patchiness was observed, perhaps indicating a feeding aggregation in response to a recently dead organism on the sea floor. *O. victoriae* are known to move toward carrion in a captive setting (Fratt and Dearborn, 1984) and are likely to exhibit similar behavior in situ. The degree of small-scale aggregation within a particular transect may indicate the abundance of carrion during that time period.

#### 4.4. Size distribution

Individuals of *O. victoriae* measured in photographs and specimens were slightly smaller than published estimates of at least 4.0 cm (Dearborn, 1977; Fratt and Dearborn, 1984), but in agreement with Dahm and Brey (1998), who found the oldest specimen in their study area within the Weddell Sea to have a disk diameter of 3.25 cm. In June 2000, the specimens exhibited a broad size range (Fig. 6b) and individuals in photographs were smallest during this time (Fig. 6a). This was also the time when there was a large proportion of

small individuals at the beginning of the transect (Fig. 7c). The smaller *O. victoriae* individuals observed in this study are likely to be juveniles, as reported by Lovell and Trego (2003). The juveniles seemed to dominate at the shallower depths (e.g., 130 m at the beginning of the June transect), with larger individuals occurring in deeper areas (160 m depth typical of the transects in this study). This increase in size with depth is the opposite of findings by McClintock et al. (1988) for *O. validus*, which decreased in size with depth at East Cape Armitage, McMurdo Station. McClintock's findings were attributed to food availability, whereas the patterns described here may reflect social behavior.

Significant changes in size during the remaining time periods may have resulted from variations in sinking particle flux. There appeared to be a positive relationship between changes in size and sinking flux at 20 and 50 mab for *O. victoriae* (Pearson correlation = 1.00,  $p = 0.01$ ). However, Lauerman and Kaufmann (1998) did not observe consistent relationships between echinoderm distributions and the presence of particulate aggregates on the sea floor, since the source of particulate matter was highly patchy in space and time. Pfannkuche et al. (1999) found small inputs of organic matter to increase the biomass of organisms less than 100  $\mu\text{m}$ , but only temporarily, with biomass decreasing again when sedimentation ceased. Although there appeared to be a correlation between flux rates and body size in this study, this relationship was based on a very small data set, and a plausible mechanism for achieving these changes on seasonal time scales remains unclear.

Individuals measured in photographs and collected specimens of *S. neumayeri* had a broader size range than reported for specimens from Cape Evans, 40–60 mm (Brey et al., 1995). *S. neumayeri* were significantly smaller in June 2000 than at any other sampling time (Figs. 6c and d), and there was a large proportion of small individuals at the beginning of the transect (Fig. 8c). This pattern is most easily explained by a recruitment event. In McMurdo Sound, larvae of *S. neumayeri* have been found to feed in the water column between late December and March, during the peak in

phytoplankton abundance, and to recruit near the end of this period (Bosch et al., 1987). A diatom bloom occurred during March 2000 in Port Foster (Sturz et al., 2003), potentially allowing the larvae to remain in the water column until later in the season. Recruitment has been reported to coincide with an increase in benthic chlorophyll *a* concentration (Bosch et al., 1987). In Port Foster, the larvae may have recruited near June 2000 in response to benthic conditions. Again, it must be kept in mind that in June 2000 the transect was in a more southeasterly position and partially in shallower water.

The difference between sizes measured in photographs and directly from collected specimens most likely was due to the mesh size of the trawl. While the mesh size was large (3.8 cm net, 1.3 cm cod-end), specimens as small as those observed in photographs were collected (Fig. 6). However, smaller specimens may have been trapped by the numerous individuals already in the net, resulting in the collection of a few small animals among the predominance of large individuals. Another factor to be considered is the position of the camera in relation to the sea floor. The software in the digitizing program was set for a known camera angle and height, and changes in either of these values could have led to errors in determination of animal sizes and positions.

## 5. Conclusions

The epibenthic megafaunal community in Port Foster, Deception Island, was dominated by echinoderms, particularly the ophiuroid *O. victoriae* and the echinoid *S. neumayeri*. These two species comprised the majority of the megafauna in this area between March 1999 and November 2000. Abundances of these species were low compared to other shallow coastal sites near the Antarctic Peninsula, perhaps as a result of volcanic eruptions that disrupted the benthic community and caused mass mortality at this site in 1967 and 1970. The benthic community in Port Foster also was characterized by low diversity, likely as a result of the high latitude (Thorson, 1957) in combination with disturbance by volcanic

activity (White, 1984; Chave and Jones, 1991). Despite these factors, the species found at Deception Island were typical for Antarctic regions with similar substrates of mud, sandy-mud and occasional boulders (Picken, 1985).

Benthic fauna at Deception Island displayed seasonal variability in abundance, dispersion and body size. These patterns correlated well with variation in the sinking flux of particulate organic material (Baldwin and Smith, 2003). However, the small sample sizes used for this analysis caution against generalizing too broadly from these results. Spatial distributions of megafauna were patchy on a variety of spatial scales, perhaps in relation to the distribution of food resources as well as aspects of social behavior. Patchy distributions are characteristic of mobile megafauna (e.g., Starmans et al., 1999), and the species studied here displayed similar patterns to those reported elsewhere. As a whole, the slow-growing species found in the Antarctic do not display seasonal variation (White, 1984) but may experience sudden periods of proliferation (Arntz et al., 1994). It is difficult to separate the effects of proliferation from spatial heterogeneity, and although temporal variability was observed in this study, the data set does not permit a clear separation between spatial and temporal variability.

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