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Population structure and feeding deterrence in three shallow-water antarctic soft corals

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Abstract *Alcyonium paessleri* and *Clavularia frankliniana* are numerically abundant soft corals in the nearshore (12 to 33 m depth) benthic communities of eastern McMurdo Sound. They are much less abundant in western McMurdo Sound where a third species, *Gersemia antarctica*, co-occurs in low numbers. The body tissues of these three species are comprised mainly of organic material (53 to 70% dry wt), which is primarily derived from NaOH-soluble protein and refractory material. The energetic contents of the whole-body tissues of *A. paessleri*, *C. frankliniana* and *G. antarctica* are 15.9, 17.3, and 14.5 kJ g⁻¹ dry wt, respectively. The mean biomass per individual is 1.81, 0.008, and 45 g dry wt for each respective species. Based on population densities of 7.3, 1337.3, and 0.04 soft corals m⁻² for *A. paessleri*, *C. frankliniana* and *G. antarctica*, respectively, the population energetic densities are estimated to be 210.1, 185.1, and 26.1 kJ m⁻². Despite the relatively rich energetic content of the tissue and apparent vulnerability to predators, very little predation occurs on these soft corals. Two potential predators, the antarctic sea stars *Perknaster fuscus* and *Odontaster validus*, exhibited significant chemotactic defensive tube-foot retractions to hexane, chloroform, methanol, and aqueous methanol extracts of each soft coral. In addition, whole-body tissue of each soft coral was rejected by the demersal fish *Pseudotrematomus bernacchii* and the cryopelagic fish *Pagothenia borchgrevinki*. In contrast, whole soft-coral tissues sequentially extracted in four increasingly polar solvents were readily ingested by these antarctic fishes, indicating that sclerites do not play a significant role in deterring predators. Our results indicate that these antarctic soft corals contain bioactive compounds which deter common predatory seastars and fishes.

Introduction

Soft corals are among the dominant members of tropical Indo-Pacific hard-bottom communities and may account for a significant portion of total biomass (Tursch and Tursch 1982; Dinesen 1983; Huston 1985). Their potential as an accessible food source, often in nutrient-limited systems, suggests that numerous predators should consume soft corals (Grigg et al. 1984); however, the reported incidence of predation on soft corals is extremely low (Pawlik et al. 1987; Sammarco and Coll 1988). Those predators which do occur are mostly species-specific soft-coral specialists (Coll et al. 1983; Lasker 1984; Vreeland and Lasker 1989; Wylie and Paul 1989). Predation can exert tremendous selective pressure on the evolution of defensive mechanisms in organisms (Kettlewell 1956; Whittaker and Feeny 1971; Van Alstyne 1988). One apparent adaptation to predation in soft corals is selection for secondary metabolites that have feeding-deterrent properties (Pawlik et al. 1987; Paul 1992; Sammarco and Coll 1992). However, recent evidence has shown that prey nutritional quality (high protein content) can counteract the effectiveness of defensive compounds in marine algae and invertebrates (Duffy and Paul 1992). As such, to fully appreciate the complexities involved in predator-prey relationships, particularly those involving feeding-deterrent strategies, it is imperative that individual and population energetic content be considered (Paine 1971).

The shallow benthic community of McMurdo Sound, Antarctica, is composed of a diverse assemblage of sessile and sluggish invertebrates, many of which exhibit chemical bioactivity (Winston and Bernheimer 1986; McClintock 1987; McClintock et al. 1990, 1991, 1994 a, b, c; Heine et al. 1991). Evolutionary selection for chemical defense in antarctic benthic organisms may be facilitated by the extreme environmental stability which has persisted over geological time (Dayton and Oliver 1977; Pearse et al. 1991; Dayton et al. 1994) and a community structured primarily by biological interaction such as predation and competition (Dayton et al. 1974). The alcyonacean, *Alcyonium*

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paessleri May and the stoloniferan, *Clavularia frankliniana* Roule are conspicuous members of shallow (≤ 33 m depth) hard-bottom communities on the eastern side of McMurdo Sound along the coast of Ross Island (Dayton et al. 1970). Although numerically abundant, both species are avoided by asteroids, the dominant predators of sessile invertebrates (Dayton et al. 1974) as well as demersal fishes (Slattery 1994). *C. frankliniana* is preyed upon by the opisthobranch *Tritoniella belli* and two species of pycnogonids, *Colossendeis megalonyx* and *C. robusta* (Dayton et al. 1970; Slattery 1994). The pycnogonid *C. megalonyx* is the only known predator of *A. paessleri* (Slattery personal observation).

In contrast, the western portion of McMurdo Sound is characterized primarily by soft-bottom communities and comparatively low levels of primary productivity (Dayton and Oliver 1977; Dayton et al. 1986). The distribution and abundance of *Alcyonium paessleri* and *Clavularia frankliniana* is limited to the relatively rare hard substrata. However, the large (≥ 1 m height) nephtheid soft coral *Gersemia antarctica* Kukenthal is occasionally found in the soft sediment communities anchored to scallop shells, small rocks, or clay substratum (Slattery 1994). An unidentified species of pycnogonid, perhaps *Thavmastopycnon* sp., is the only known predator of *G. antarctica* (Slattery 1994).

The objectives of this study were: (1) to compare the distribution and abundance of soft-coral populations at Arrival Heights (Eastern McMurdo Sound) with Explorer's Cove (Western McMurdo Sound); (2) to determine the biochemical composition and energetic content of soft corals as a means of evaluating their nutrient and energy availability to higher trophic levels; and (3) to determine if *Alcyonium paessleri*, *Clavularia frankliniana* and *Gersemia antarctica* are defended against potential predators by noxious compounds.

Materials and methods

Population studies

Soft-coral collections and standing-crop estimates were made using SCUBA during October–November 1989, October–February 1992, 1993, and September–February 1993–1994 at two locations in McMurdo Sound, Antarctica (Fig. 1). The depth distribution and abundance of *Alcyonium paessleri* and *Clavularia frankliniana* were documented at Arrival Heights, a site ≈ 500 m north of McMurdo Station ($77^{\circ}51' S$; $166^{\circ}39' E$), at depths ranging from 1 to 33 m. In addition to these two species, the distribution and abundance of *Gersemia antarctica* was documented in Explorer's Cove ($77^{\circ}34' S$; $163^{\circ}35' S$), ≈ 1 km northeast of the Commonwealth Stream mouth, at depths ranging from 12 to 33 m.

At the Arrival Heights site, a weighted 20 m transect line was haphazardly positioned parallel to shore along seven depth contours beginning at 12 m and repeated at 3 m increments to a depth of 30 m. A 1 m^2 quadrat was positioned at five predetermined random points along the transect line at each of the depth contours in October–November 1989, October–November 1992 and September–November 1993. In order to sample the benthos between 1 and 12 m and below 30 m, the 1 m^2 quadrat was haphazardly positioned in ten locations at each depth. The numbers of *Alcyonium paessleri* colonies were counted in each quadrat. To facilitate counts of *Clavularia franklin-*

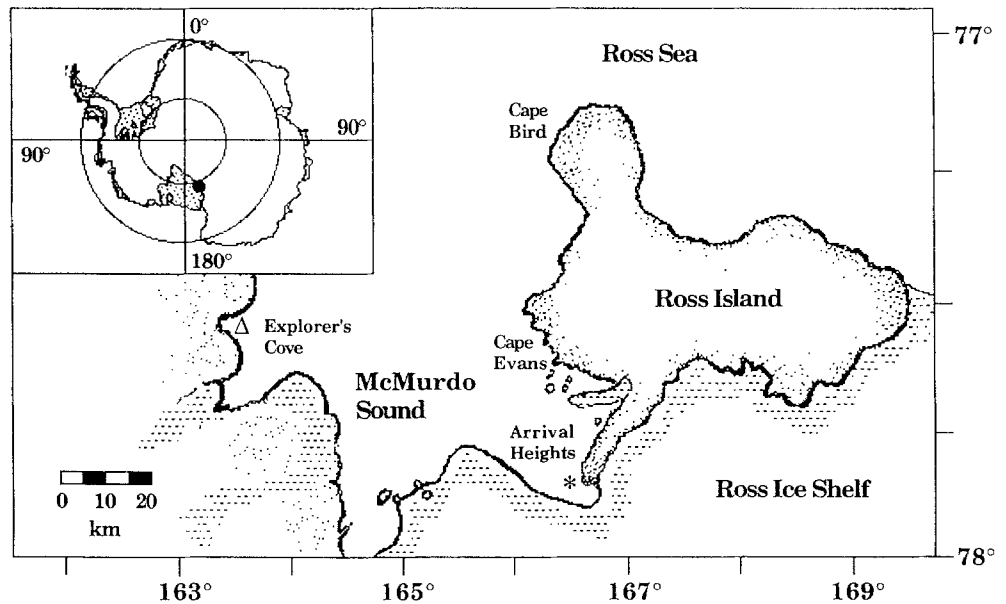
iana, which consists of small (≤ 2 cm) modular polyps arising from anastomosing stolons, a photoquadrat measuring 0.023 m^2 was obtained using a Nikonos camera equipped with a 35 mm lens and close-up kit system. Three photoquadrats were subsampled at random points within each random quadrat along each transect line. Photographs were projected onto a screen equipped with grid lines and the numbers of *C. frankliniana* polyps were counted. The average number of polyps from the three subsamples were converted to a per m^2 basis. An estimate of the average number of *C. frankliniana* polyps per colony was obtained from rocks ($n=83$), covered by a single stolon mat (i.e. a distinct colony), collected haphazardly at Arrival Heights.

At the Explorer's Cove site a 20 m belt transect was utilized to sample populations of all soft corals in November 1992 and October–November 1993. Divers swam parallel to shore, along the same 3 m incremental depth gradients sampled at Arrival Heights, and counted all soft corals falling within 1 m of the transect line. An additional 33 m-depth transect was counted. The total number of colonies or polyps counted in each transect was then divided by the area sampled to estimate the number of soft corals per m^2 . Sampling was not possible shallower than 12 m depth in Explorer's Cove due to ice conditions. Subsamples of *Alcyonium paessleri* and *Clavularia frankliniana* from the Arrival Heights site and *Gersemia antarctica* from the Explorer's Cove site were collected for population size frequencies and morphometric regression analyses. These data provided a means for estimating the mean number of soft corals in a population, the average biomass of each soft coral, and ultimately the energetic equivalents of each soft-coral population. The wet weight of each colony or modular polyp was recorded after a standardized period of handling (3 min), which resulted in deflation of the hydrostatic skeleton, retraction of the individual polyps or colony, and expulsion of excess water. The retracted height of *C. frankliniana* polyps and *G. antarctica* colonies was recorded to the nearest millimeter. Due to its amorphous body form, the volume, instead of height, of retracted *A. paessleri* colonies was regressed against total colony wet weight.

Biochemical and energetic analyses

The biochemical composition of *Alcyonium paessleri*, *Clavularia frankliniana*, and *Gersemia antarctica* was determined for lyophilized whole-body tissues of each colony. Ten colonies of *A. paessleri* were weighed, lyophilized, reweighed and ground with a Wiley mill. *C. frankliniana* polyps ($n \geq 50$) from the same stolon were pooled to provide sufficient tissue for biochemical assays; ten rocks covered with the soft-coral colonies were sampled to provide replicates. Stolons were not included in the analyses. Due to the sparse population of *G. antarctica*, only three colonies were sampled and similarly prepared for biochemical analyses. Ash weights were determined gravimetrically by placing whole-body tissues in a muffle furnace for 4 h at $500^{\circ}C$. NaOH-soluble protein and TCA-soluble carbohydrate were determined using standard colorimetric techniques (Bradford 1976 and Dubois et al. 1953, respectively). Briefly, 10 to 15 mg samples were extracted in either 1 N NaOH (18 h) or 5% TCA (1 h). An aliquot (protein: 100 μl ; carbohydrate: 2 ml) of either sample was removed and developed in a protein-dye reagent kit (BioRad Laboratories, Hercules California) or 5% phenol and sulfuric acid (1:5 v/v). Samples were visualized spectrophotometrically at $\lambda = 595$ (proteins) or 490 (carbohydrates). Lipid was determined gravimetrically using the technique of Freeman et al. (1957). Briefly, 50 mg samples were extracted (15 min) in chloroform:methanol (2:1 v/v) and partitioned with distilled water. The nonpolar fraction was transferred to pre-weighed dram vials, evaporated to dryness, and reweighed. Refractory material was estimated by subtraction, and for the purposes of energetic quantification was assumed to represent insoluble protein (Lawrence and Kafri 1979). The energetic composition of the soft-coral colonies was calculated indirectly by multiplying appropriate coefficients (Brody 1945) by each of the organic components. The total energy content of the whole-body tissue was calculated as the sum of the energy values attributable to each organic component.

Fig. 1 Map of McMurdo Sound, Antarctica showing location of study sites at Arrival Heights (*) and Explorer's Cove (Δ). Inset shows location of McMurdo Sound (\bullet) in relation to Antarctic continent



Extraction techniques

Crude organic extracts of *Alcyonium paessleri*, *Clavularia frankliniana*, and *Gersemia antarctica* were prepared from lyophilized whole-body tissues. Twenty grams of dry tissue pooled from a minimum of three colonies was sequentially extracted in 200 ml of hexane, chloroform, methanol, and aqueous methanol (30% deionized H₂O) for a period of 8 h. To maximize extract collection, tissue samples were re-extracted twice and solvents were pooled. Organic solvents were then evaporated to dryness using a rotary evaporator. Each fraction was weighed to determine the amount of extract per unit dry tissue weight. To determine the percent concentration of sclerites in whole tissues, the extracted tissue samples were dried, digested in 200 ml of bleach, rinsed (five times in deionized H₂O and once in acetone, Van Alstyne et al. 1992) and redried. Sclerites were then weighed and compared to ash-weight concentrations and examined under a compound microscope to determine their probable function (Lewis and Von Wallis 1991).

Feeding-deterrence assays

The common omnivorous seastars *Perknaster fuscus* and *Odontaster validus* (Dayton et al. 1974; Dearborn 1977; Slaterry personal observations) were utilized in a chemotactic tube-foot assay against extracts of *Alcyonium paessleri*, *Clavularia frankliniana*, and *Gersemia antarctica*. Sloan (1980) indicated that the terminal chemosensory tube-feet of seastars respond to feeding stimuli with stereotypic behavioral patterns. The retraction response of the chemosensory tube-feet of seastars has been shown to provide a quantitative measure of deterrence to sponge extracts containing bioactive compounds (McClintock et al. 1994b). Both seastar species ($n=7$ to 10 individuals each) were collected near the Arrival Heights study site (20 to 35 m depth) and maintained for 15 d in tanks with ambient, continuous-flow seawater before use in tube-foot assays.

Soft-coral extracts were embedded in inert silicone at a concentration consistent with the percent dry weight of each extract in each species and applied as a thin surface film to the tips of glass rods. A negative control, consisting of CuSO₄ embedded in inert silicone grease at a 0.1 M concentration, was used to verify tube-foot activity against a standard. A positive control, to confirm feeding stimulation, was prepared by embedding a 1:1 (wt:wt) ratio of hexane, chloroform-, methanol-, or aq methanol-extracted fish tissue (*Pseudotrematomus bernacchii*) in silicone. In addition, silicone-coated glass rods provided a control for the carrier matrix, and uncoated

glass rods were used to control for mechanical agitation of individual tube-feet. Seastars were placed on their aboral surface in glass finger-bowls containing 1.5 liters filtered seawater (fsw) at -1°C . To maintain water temperature, each glass bowl was set in a continuous-flow water bath of ambient seawater (-1.8°C) and monitored with a digital thermometer. Experimental and control probes were gently placed in contact with a single extended tube-foot. The response of the tube-foot and period of retraction (i.e. the length of time the tube-foot was withdrawn from the stimulus), when applicable, were recorded for up to 60 s. Each *P. fuscus* was subjected to ten experimental or control trials in random sequence before being replaced by a new seastar. *O. validus* were replaced whenever they righted themselves (after ≈ 3 to 6 trials). Each experimental trial and control was replicated 15 times.

The demersal fish *Pseudotrematomus bernacchii* and the cryopelagic fish *Pagothenia borchgeviniki* (which occasionally forages demersally; Foster et al. 1987) were utilized to test palatability of whole-colony tissue and to evaluate the role of sclerites as a morphological defense. Small cubes (0.5 cm³) of whole-colony tissue were cut from the tips of individual colonies ($n=10$) of *Alcyonium paessleri* and *Gersemia antarctica*. Individual polyps (≤ 1 cm height) were removed from ten separate colonies (i.e. distinct stolons) of *Clavularia frankliniana*. Control tissue consisted of similar-sized cubes cut from the muscle of the antarctic cod *Dissostichus mawsonii*. In addition, experimental tissues of each soft-coral species or control tissue were sequentially extracted as above to remove any non-polar or polar metabolites which might act as feeding deterrents, and washed in fsw. Ten experimentals (whole tissue or extracted tissue) from each soft coral and controls were offered in a random sequence to replicate fish ($n=10$) of either species. The percent of tissue ingested or rejected was recorded. Following random assignment of experimental and control tissues, a final control-tissue cube was offered to each fish to determine if the results might be biased by satiation; however, all fish ate the final control pellet.

Results

Alcyonium paessleri averaged 7.3 colonies per m² across all depths sampled at Arrival Heights and 0.02 colonies per m² across all depths sampled at Explorer's Cove. No significant differences ($P \geq 0.05$; Student's *t*-test) were noted

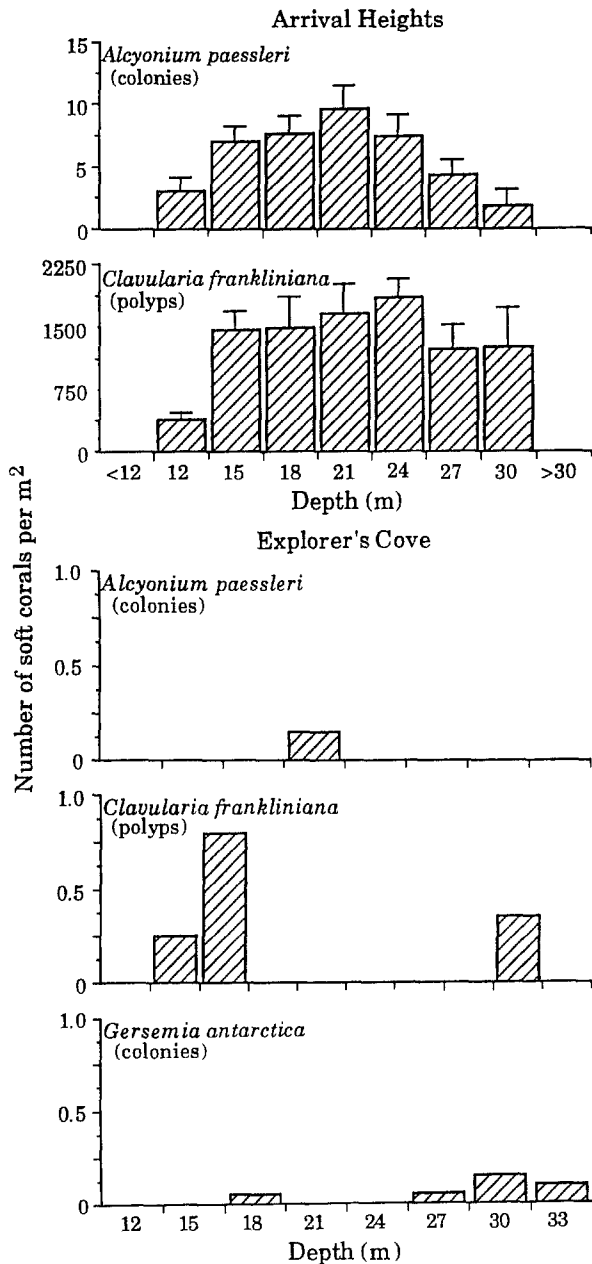


Fig. 2 *Alcyonium paessleri*, *Clavularia frankliniana* and *Gersemia antarctica*. Depth distribution and abundance at Arrival Heights and Explorer's Cove (*G. antarctica* were not found at Arrival Heights study site). Bars represent $\bar{x} \pm SE$ number of *A. paessleri* colonies and *C. frankliniana* polyps from five 1 m² quadrats at each of eight depth gradients and ten haphazard quadrats <12 m and >30 m at Arrival Heights, and mean number of *A. paessleri* and *G. antarctica* colonies and *C. frankliniana* polyps from a 20×1 m² belt transect from each of eight depth gradients at Explorer's Cove

in either population distributions or abundances between 1989 and 1992 so these mean values represent a pooled mean for both seasons (Fig. 2). Similarly, *Clavularia frankliniana* polyps were extremely dense at Arrival Heights and greatly reduced at Explorer's Cove (1337.3 and 0.18 polyps per m², respectively). Based on an estimate of 56.1 ± 47.6 ($\bar{x} \pm 1$ SD; range 0 to 162; $n=83$)

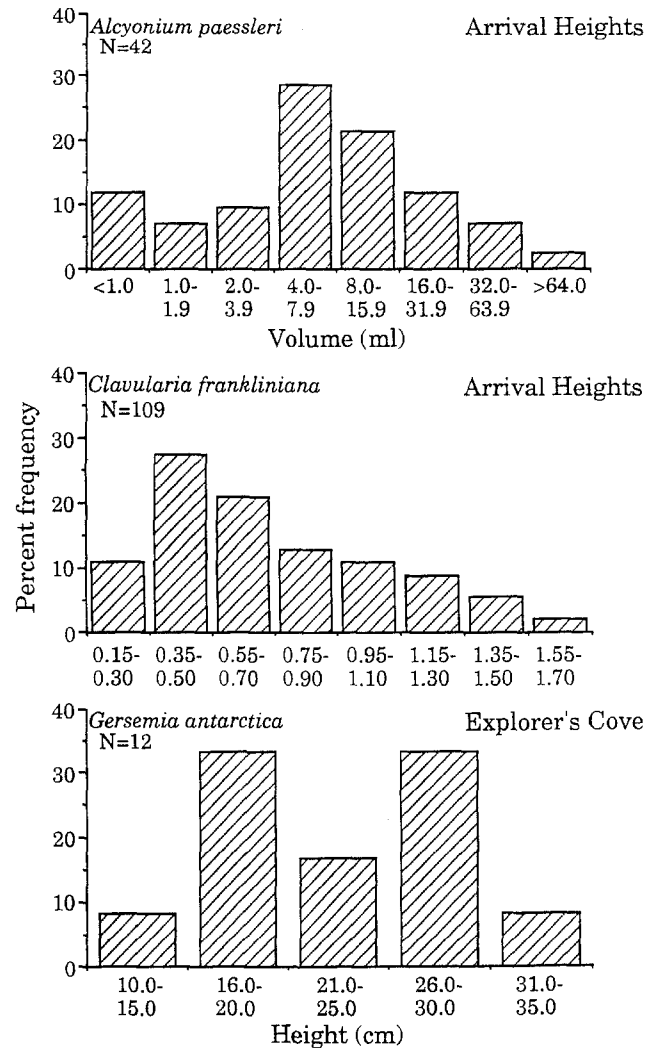


Fig. 3 *Alcyonium paessleri*, *Clavularia frankliniana* and *Gersemia antarctica*. Size-frequency distributions. Individuals censused were collected from similar depths (25 to 30 m) at either Arrival Heights (*A. paessleri* and *C. frankliniana*) or Explorer's Cove (*G. antarctica*). Note that *C. frankliniana* polyps were grouped (± 0.05 cm) due to resolution limitations on small individuals

C. frankliniana polyps per colony, Arrival Heights is probably populated by as many as 23.8 colonies per m². *Gersemia antarctica* was only found at Explorer's Cove and averaged 0.04 colonies per m² (Fig. 2). Disparate sampling techniques between seasons precluded pooling data for *C. frankliniana* and *G. antarctica*. Nonetheless, the mean values computed in 1993–1994 appear to be representative of all seasons.

The average height of *Clavularia frankliniana* and *Gersemia antarctica* was 8.3 mm and 22.0 cm, respectively. An average-sized *Alcyonium paessleri* colony displaced 11.9 ml fsw (Fig. 3). The population size-frequency histograms for *A. paessleri* and *C. frankliniana* suggest recent recruitment events, as cohorts of small individuals are present. A bimodal size distribution was noted in *G. antarctica* at New Harbor, although the sample size is too

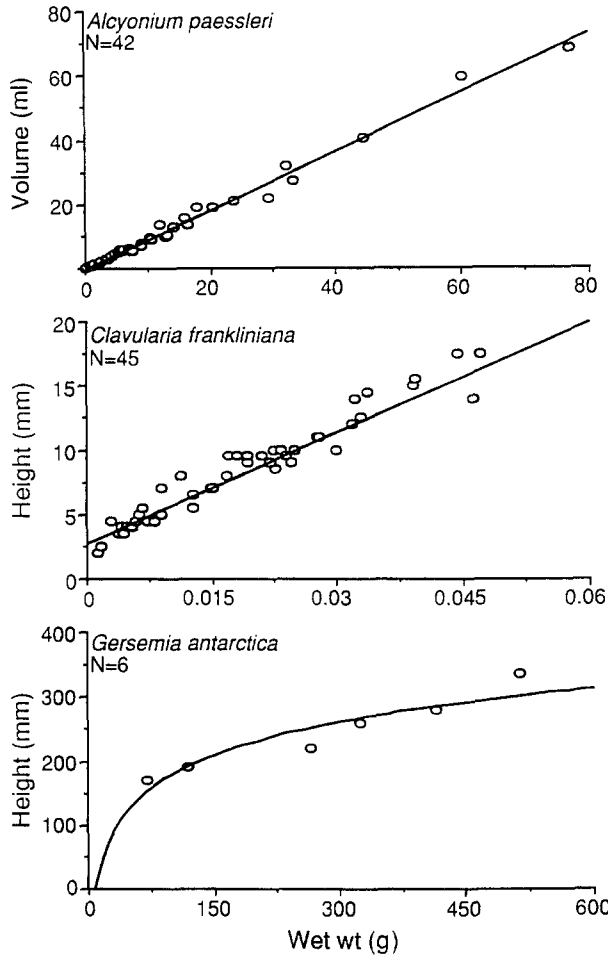


Fig. 4 *Alcyonium paessleri*, *Clavularia frankliniana* and *Gersemia antarctica*. Relationships between wet wt (g) and size. Size parameter measured for *A. paessleri* was volume, whereas height was measured for both *C. frankliniana* and *G. antarctica*

small to determine if this represents two specific age classes. The relationship between volume and wet weight is best described by a linear expression for *A. paessleri* [$y = -0.21093 + 0.91698(x)$; $r^2 = 0.99$; $n = 42$], and length vs wet weight for *C. frankliniana* and *G. antarctica* are best described by the linear equation [$y = 2.7167 + 0.030523 \cdot \log(x)$; $r^2 = 0.95$; $n = 45$] and the logarithmic equation [$y = -16.606 + 17.258 \cdot \log(x)$; $r^2 = 0.87$; $n = 6$], respectively (Fig. 4).

The biochemical composition of the whole-body tissues of *Alcyonium paessleri*, *Clavularia frankliniana* and *Gersemia antarctica* varied between species (Table 1). The total organic levels ranged from 53.0 to 69.8% dry wt and consisted primarily of soluble protein and refractory material. Inorganic material consisted almost entirely of sclerites (sclerite concentrations from digested tissues = 95, 99,

Table 1 *Alcyonium paessleri*, *Clavularia frankliniana*, and *Gersemia antarctica*. Proximate biochemical composition (% dry wt; $\bar{x} \pm SE$) of whole-body tissues. Samples of each specimen were collected from 25 to 30 m depth at either Arrival Heights (*A. paessleri* and *C. frankliniana*) or Explorer's Cove (*G. antarctica*)

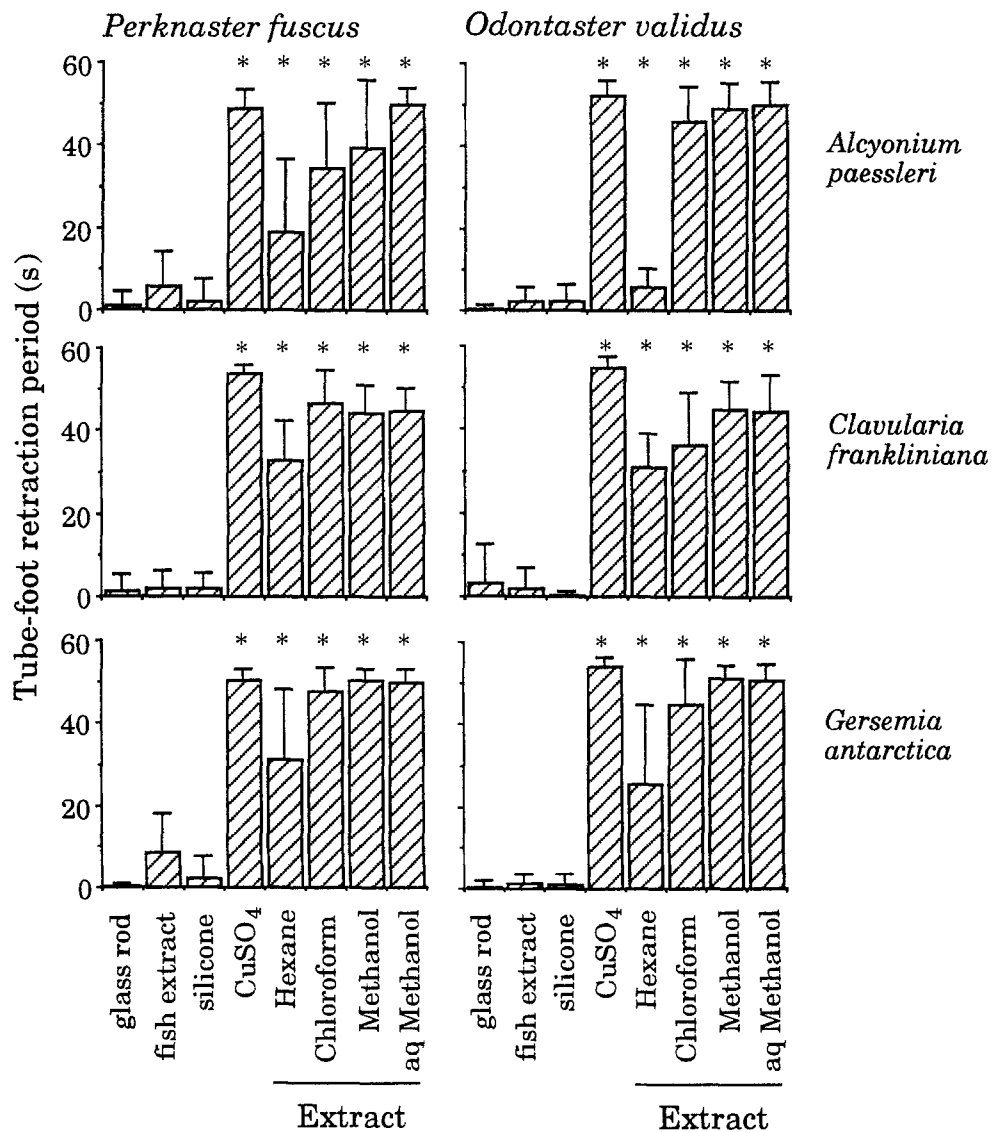
Species	(n)	Ash	Carbo- hydrate	Lipid	Protein	Refrac- tory
<i>Alcyonium paessleri</i>	(10)	38.8 ± 5.5	0.7 ± 0.1	8.4 ± 1.4	23.9 ± 1.5	28.2 ± 2.2
<i>Clavularia frankliniana</i>	(10)	30.2 ± 1.9	0.5 ± 0.0	5.2 ± 0.8	10.4 ± 0.7	53.8 ± 3.1
<i>Gersemia antarctica</i>	(3)	47.0 ± 3.3	0.6 ± 0.0	12.6 ± 1.5	20.7 ± 0.7	19.1 ± 3.1

Table 2 *Alcyonium paessleri*, *Clavularia frankliniana*, and *Gersemia antarctica*. Proximate energetic composition (kJ g^{-1} dry wt; $\bar{x} \pm SE$) of whole-body tissues. Samples of each specimen were collected from 25 to 30 m depth at either Arrival Heights (*A. paessleri* and *C. frankliniana*) or Explorer's Cove (*G. antarctica*)

Species	(n)	Carbo- hydrate	Lipid	Protein	Refrac- tory	Total
<i>Alcyonium paessleri</i>	(10)	0.12 ± 0.01	3.33 ± 0.22	5.66 ± 0.29	6.67 ± 1.13	15.94 ± 0.61
<i>Clavularia frankliniana</i>	(10)	0.09 ± 0.01	2.06 ± 0.01	2.46 ± 0.19	12.72 ± 0.73	17.33 ± 0.50
<i>Gersemia antarctica</i>	(3)	0.10 ± 0.00	4.98 ± 0.12	4.89 ± 0.35	4.52 ± 0.74	14.49 ± 0.75

and 96% of the ash dry weight for *A. paessleri*, *C. frankliniana* and *G. antarctica*, respectively). The sclerites of *A. paessleri* and *C. frankliniana* consisted of spindle-shaped spicules. The stalk of *G. antarctica* contained club-shaped spicules; however, the polyps were surrounded by needle-shaped sclerites. Levels of carbohydrate and lipid were comparatively low (<1% and 5.2 to 12.6%, respectively). Levels of refractory material in *C. frankliniana* were approximately double those recorded in the other two species. The total energy content (kJ g^{-1} dry wt) of soft corals was similar. However, the relative biochemical constituent sources varied in their contributions to energetic content (Table 2). Assuming that refractory material is composed of insoluble protein for purposes of energy calculations (Lawrence and Kafri 1979), proteins (soluble and insoluble) accounted for >65% of the total energy of each species. Lipid accounted for $\approx 20\%$ of the total energy content in *A. paessleri* and *G. antarctica*, but only half that in *C. frankliniana*. Average-sized colonies of *A. paessleri* and *G. antarctica* contain ≈ 28.8 and 652.5 kJ, respectively, while an average-sized *C. frankliniana* polyp would contain 0.14 kJ. The energetic contents of *A. paessleri* and *C. frankliniana* populations at Arrival Heights were 210.1, and 185.1 kJ m^{-2} , respectively. The energetic densities of populations in Explorer's Cove were significantly ($P < 0.001$; Student's *t*-test) lower (*A. paessleri* =

Fig. 5 *Perknaster fuscus* and *Odontaster validus*. Tube-foot retraction periods (s) when exposed to organic soft-coral extracts; bars represent $\bar{x} \pm SD$ time of tube-foot retraction for 15 replicates. Controls included glass rod, silicone only, silicone-embedded fish extract, and silicone-embedded CuSO_4 . Asterisks indicate statistical significance ($P \leq 0.05$) from silicone-embedded fish-extract control. Note that for illustrative purposes only hexane-extracted fish controls are presented



0.58 kJ m^{-2} and *C. frankliniana* = 0.03 kJ m^{-2}) than populations at Arrival Heights. Population energetic densities of *G. antarctica* in Explorer's Cove were 26.1 kJ m^{-2} .

Perknaster fuscus and *Odontaster validus* exhibited significantly longer tube-foot retraction periods ($P < 0.0001$ for all but the hexane fraction of *Alcyonium paessleri* where $P = 0.03$; ANOVA) when exposed to organic soft-coral extracts compared to controls (Fig. 5). There were no significant differences ($P \geq 0.05$; ANOVA) between sea star tube-foot retraction periods to organic extracts from each soft-coral species. The duration of tube-foot retraction in response to soft-coral extracts was not significantly different than for tube-feet exposed to CuSO_4 ($P \geq 0.05$; ANOVA).

Pseudotrematomus bernacchii and *Pagothenia borchgrevinki* rejected soft-coral whole-colony tissue significantly more often than control-fish tissue ($P < 0.05$; Student's *t*-test). Extracted whole-colony soft-coral tissues were ingested significantly more often than non-extracted whole-colony tissues ($P < 0.01$; Student's *t*-test), suggest-

ing that sclerites do not deter feeding (Fig. 6). There was no significant difference between ingestion of control tissues (fish and extracted-fish tissues) or extracted-colony tissue ($P \geq 0.05$; Student's *t*-test). Moreover, both species of fish responded to control tissues in a similar manner.

Discussion

The distribution and abundance of *Alcyonium paessleri* and *Clavularia frankliniana* at the Arrival Heights study site on the eastern side of McMurdo Sound appears to be largely regulated by physical factors. The upper depth limit of both species (12 to 15 m) is correlated with the lower boundary of a region strongly influenced by ice scour and anchor ice formation (i.e. Zone I; Dayton et al. 1970). Dayton et al. (1974) suggest that annual ice disturbance events, such as scour and anchor-ice uplift, effectively clear the substrata of sessile invertebrates that recruit during ice-free periods

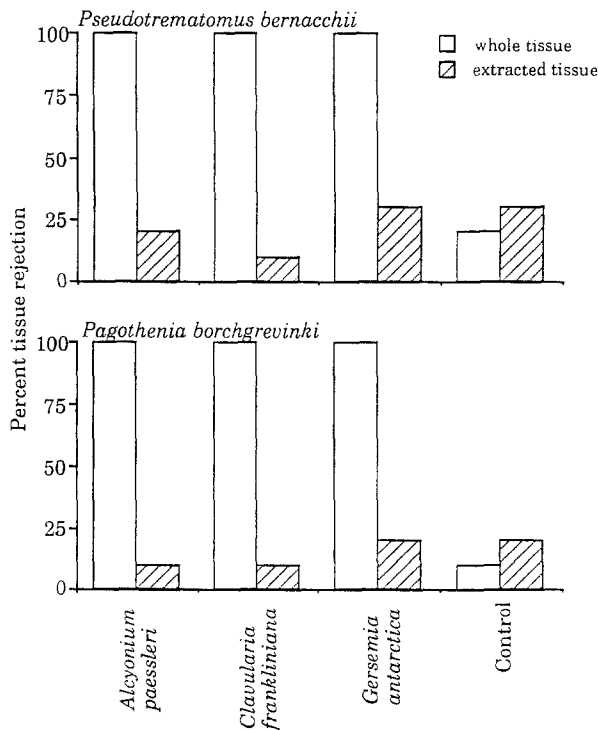


Fig. 6 *Pseudotrematomus bernacchii* and *Pagothenia borchgrevinki*. Percent rejection of pieces (0.5 cm³) of whole and extracted colony tissues of *Alcyonium paessleri*, *Clavularia frankliniana*, and *Gersemia antarctica*; bars represent percent rejection for ten replicates. Controls included extracted whole-colony tissue and muscle tissue (whole and extracted) from antarctic cod *Dissostichus mawsonii*

in shallow continental shelf waters of Antarctica. Recruits of *C. frankliniana* (<1 mm height) were observed during survey dives along the coast of Ross Island in depths shallower than 12 m during early October 1989 and 1993 (Slattery personal observations). However, subsequent observations revealed that these young polyps were removed from the substrate by anchor ice events within 2 to 4 wk. An alternative explanation for low population densities in shallow depths is that these areas are often characterized by the presence of motile predators, including pycnogonids, which may feed on soft-coral recruits (Slattery 1994).

The lower depth limits of *Alcyonium paessleri* and *Clavularia frankliniana* are coincident with the upper boundary of the sponge spicule mat and sponge-dominated community at depths \approx 33 m (i.e. Zone III: Dayton et al. 1970). The Arrival Heights study site was characterized by a relatively thin spicule mat (\approx 1 to 10 cm depth) spread across volcanic rubble at depths >27 m. *A. paessleri* and *C. frankliniana* occurred mostly on rare "patch reefs" formed where rocky substrate extended above the sponge spicule mat. Few soft-coral recruits were ever observed attached directly to the spicule mat (Slattery personal observation). This may be due to physical properties of the spicule mat which inhibit soft-coral attachment or to competitive exclusion by sponges (sensu Dayton et al. 1970). Additional factors which may indirectly influence the depth distribu-

tions of both species include local current patterns (Barry and Dayton 1988) and haloclines (Dayton et al. 1969), which might have an impact on the dispersal of soft-coral planula larvae (Pearse et al. 1991). At Arrival Heights, *A. paessleri* population density appears to have remained generally stable between 1989 and 1992. However, this population suffered dramatic localized mortality due to sedimentation in 1993 (Slattery and Bockus unpublished data). The *C. frankliniana* population remained stable over all seasons despite this sedimentation event.

In contrast to Arrival Heights, the study site at Explorer's Cove revealed no clear depth distribution pattern for either *Alcyonium paessleri* or *Clavularia frankliniana*. Both species were rare and restricted to hard substrata, including rocks, scallop shells (*Adamussium colbecki*), and dead echinoid tests (*Sterechinus neumayeri*). *Gersemia antarctica* were similarly rare; their distribution appeared to be patchy and localized within a small region of Explorer's Cove. Biological factors may be more important in structuring soft-coral populations on the western side of McMurdo Sound. Low infaunal population densities may be attributable to decreased water-column productivity associated with current patterns within the Sound that divert productivity and extended periods of sea-ice cover (Dayton and Oliver 1977; Barry and Dayton 1988). *Alcyonium paessleri* and *C. frankliniana* are both planktivorous (Dayton and Oliver 1977; Slattery 1994), while *G. antarctica* is also a deposit-feeder (Slattery 1994). Therefore, it is likely that limited productivity has an impact on the distribution and abundance of these species. Moreover, soft-coral predation by pycnogonids was observed more commonly in Explorer's Cove (Slattery 1994). Physical factors also impact the distributional patterns of soft corals on the western side of McMurdo Sound. For instance, we found individuals of *A. paessleri* and *C. frankliniana* partially buried under "glacial flour" or in the process of being crushed by flowing ice walls. The sluggish oscillatory current (≤ 1 cm s⁻¹) characteristic of Explorer's Cove (Barry and Dayton 1988), may decrease opportunities for current-driven larval dispersal and may contribute to the patchy distribution of *G. antarctica*.

The whole-body tissues of *Alcyonium paessleri*, *Clavularia frankliniana*, and *Gersemia antarctica* contained levels of organic material (g dry wt) similar to those noted for an antarctic echinoid, tunicate, and three gastropods (Pearse and Giese 1966; McClintock et al. 1991, 1992). Levels were higher than those reported for a variety of antarctic sponges (McClintock 1987) and antarctic echinoderms (McClintock and Pearse 1987). The comparatively high level of NaOH-insoluble protein (i.e. refractory material) in *C. frankliniana* may be indicative of increased amounts of connective tissue. *C. frankliniana* may rely on more pliable connective tissue for structural support, as opposed to sclerites, since boundary-layer drag forces have greater effects on smaller than on larger species (sensu Koehl 1982). The ash contents of all three soft corals are indicative of their relative sclerite content (Slattery 1994). *G. antarctica* contained the greatest levels of ash and consequently sclerites. The club-shaped morphology of the

stalk sclerites suggest a provision for colony rigidity. The needle-shaped morphology of *G. antarctica* polyp sclerites are suggestive of a defensive role (sensu Lewis and Von Wallis 1991). In contrast, the spindle-shaped sclerites of *A. paessleri* and *C. frankliniana* could have multiple functions including structural and defensive roles (sensu Lewis and Von Wallis 1991). Sclerites typically serve a structural function in soft corals (Kingsley 1984), but may also play a role in morphological defenses (Sammarco et al. 1987; Harvell et al. 1988; Van Alstyne et al. 1992). Dayton et al. (1974) suggest that antarctic sponge spicules would have little use against predatory seastars which extrude their cardiac stomach against prey tissue. Similarly, it is unlikely that soft-coral sclerites are effective deterrents of predation by antarctic seastars.

The energetic content of all three soft-coral species is relatively high (14.5 to 17.3 kJ g⁻¹ dry wt). McClintock (1987) reported energy contents ranging from 5.09 to 17.44 kJ g⁻¹ dry wt for 17 of the most common sponges from McMurdo Sound. In addition, the solitary antarctic tunicate *Cnemidocarpa verrucosa* contains ≈ 16.83 kJ g⁻¹ dry wt (McClintock et al. 1991), while the soft-body tissues of motile invertebrates, such as the nemertean *Parborlasia corrugatus* and three species of gastropod molluscs, contain slightly higher energy levels (≈ 20 kJ g⁻¹ dry wt; Heine et al. 1991; McClintock et al. 1992). Given the high densities of *Alcyonium paessleri* and *Clavularia frankliniana* between depths of 12 to 30 m at Arrival Heights, their effective population energetic density is substantially higher than that of other sympatric benthic marine invertebrates. Although Dayton et al. (1974) observed sponge standing-crops as high as 11 609 kJ m⁻², these high energetic densities occur below 33 m depth. Sponges appear generally unable to establish populations within the depth range dominated by cnidarians (Dayton et al. 1970). At Explorer's Cove, the population energetic levels of all three soft corals and most other sessile invertebrates are substantially lower. Western McMurdo Sound has dense populations of scallops, brittle stars, and infaunal deposit-feeders (Dayton and Oliver 1977; Dayton et al. 1986; Slattery personal observation). Nonetheless, among sessile invertebrates, it is likely that soft corals account for the highest energetic standing crop.

Organic extracts of *Alcyonium paessleri*, *Clavularia frankliniana*, and *Gersemia antarctica* elicited strong tube-foot retraction responses, indicative of feeding deterrence (Sloan 1980) in the antarctic seastars *Perknaster fuscus* and *Odontaster validus*. Tube-foot retractions were observed in response to all four organic fractions. As solvents vary in polarity, more than one metabolite may be responsible for seastar feeding-deterrent responses. In fact, studies of tropical gorgonians and soft corals indicate that they often contain multiple feeding-deterrent compounds which might act in a synergistic manner (Harvell et al. 1988; Wylie and Paul 1989; Fenical and Pawlik 1991). Selection for feeding-deterrent compounds in soft corals might be expected to increase learned avoidance by potential predators, particularly in conjunction with visual or olfactory cues (Gerhard 1991). *A. paessleri* and *G. antarctica* are

brightly-colored orange colonies which may release allelopathic compounds into the surrounding water (Slattery 1994). This is suggestive of a "predator warning system". Although seastars are among the most common benthic predators in southern polar waters (Dearborn 1977), it is conceivable that soft-coral feeding-deterrent compounds are the result of evolutionary selection in response to past fish predators which learned to avoid soft corals (Gerhart 1991). Extracted tissues of *A. paessleri*, *C. frankliniana*, and *G. antarctica* are not ichthyodeterrent, indicating that chemical compounds, removed during the organic extraction process, are responsible for predator deterrence. The presence of sclerites in extracted antarctic soft-coral tissue had no apparent effect in deterring potential predatory fish; however, it is possible that sclerites act in a cumulative manner in conjunction with bioactive compounds (Harvell et al. 1988; Van Alstyne et al. 1992).

The bioactive compounds in *Alcyonium paessleri*, *Clavularia frankliniana*, and *Gersemia antarctica* have not yet been identified; however, thin-layer chromatograms indicate the presence of closely-related compounds common to all three species (Slattery 1994). Chimyl alcohol and homarine, two bioactive compounds (Targett et al. 1983; McClintock et al. 1994 a, c), have been isolated from *C. frankliniana* (McClintock et al. 1994c; Slattery unpublished data). However, unless these compounds are sequestered at elevated concentrations in the epithelial tissues, they do not occur in sufficient concentrations to serve as feeding deterrents. Terpenoids, typically sesquiterpenes and diterpenes, are among the most common bioactive secondary metabolites isolated from alcyonarians (Tursch et al. 1978; Paul 1992). Nonetheless, the specific compounds responsible for feeding deterrence in alcyonaceans have rarely been identified (Wylie and Paul 1989; Sammarco and Coll 1992).

In summary, *Alcyonium paessleri*, *Clavularia frankliniana*, and *Gersemia antarctica* are energy-rich soft corals which occur in abundance in shallow benthic antarctic communities. Despite this rich energy resource, among the highest of shallow-water (<33 m) sessile antarctic invertebrates, few predators are observed to exploit soft corals as preferred prey. Predator-deterrence in these soft corals appears to be related to the presence of noxious bioactive compounds which render tissues unpalatable to seastars and fishes. The evolution of feeding-deterrent compounds may, in part, explain the numerical dominance of these soft corals in their respective communities.

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