AN ANTARCTIC FAST-ICE FOOD CHAIN: OBSERVATIONS ON THE INTERACTION OF THE AMPHIPOD *Pontogeneia antarctica* Chevreux WITH ICE-ASSOCIATED MICRO-ALGAE

By MICHAEL G. RICHARDSON *and* TERENCE M. WHITAKER

ABSTRACT. Sea ice provides a great variety of sites for micro-algal growth. During winter 1973, observations were made on the colonization of the coastal ice foot at Signy Island and on the feeding habits of *Pontogeneia antarctica* Chevreux associated with the micro-algal growth. Samples of amphipods and micro-algae were taken using SCUBA diving techniques.

The ice-associated micro-flora started development in early June with extensive growth of the blue-gree alga *Phaeocystis antarctica* Karsten. This was replaced, mainly by diatoms, with *Navicula glaciei* Van Heurck and *Nitzschia curta* (Van Heurck) Hasle predominant. With the formation of fast ice, the amphipod migrated from its summer habitat among the weed beds of the shallow water to the coastal tide-crack area. Here a protracted hatchling release started in August and both young and some adults fed on the developing micro-algal flora of the ice foot. *Pontogeneia antarctica* seems to be non-selective, consuming detrital, algal or crustacean material within a broad range of particle size. This omnivorous feeding, combined with protracted hatchling release and migration to the ice-associated food source present during most winters, increases the probability that young will survive in a variable environment.

Sea ice at Signy Island

At Signy Island in the South Orkney Islands (lat. 60°42·5′S., long. 45°36′W.), sea ice up to 1 m. in thickness is present for between 70 and 242 days every year. Inshore fast ice rarely breaks up before September; ice there lasts longer than the 148 day average offshore (White, 1977). Where the fast ice joins land at the top of a shallow sloping shore, a series of parallel shear cracks is generated by tidal movement. The ice inshore of the cracks eventually freezes solidly to the beach. In steeply shelving areas or against cliffs, fewer marginal tide cracks are formed but a massive ice structure forms underwater, completely sheathing the shore down to a maximum depth of 7 m. This ice bulge (Fig. 1) (the ice foot) originates from:

i. Marginal freezing in the splash zone during the period before the fast ice forms.
ii. Anchor-ice formation (Dayton and others, 1969) accentuated by cold brine draining back from the tide-crack overflow area (Whitaker, 1977; Whitaker and Richardson, in press).
iii. Creep induced by the accumulated weight of several metres of drift snow at the fast-ice margin. Downward deformation of this kind caused the formation of a bulge of composite origin, whose top consisted of infiltration ice (snow origin) and a basal section of more solid sea-water ice by July in 1972 and 1973. Fig. 1 shows a typical profile.

Ice-associated micro-algae

Micro-algal growth appears to be possible on any type of submerged marine ice substrate. Whitaker (in press) has tabulated most of the types of habitat present in winter at the South Orkney Islands. Infiltration ice, where snow is soaked by sea-water, appears to be peculiarly favourable for extensive micro-algal development. Dense concentrations of *Nitzschia closterium* (Ehrenburgh) Wm. Smith have been reported from the infiltration zone of pack ice, and *Navicula glaciei* from the tide-crack overflow infiltration ice at Signy Island (Whitaker, 1977; Whitaker and Richardson, in press). These solid but porous substrates resemble a benthic type of habitat.

Amphipoda associated with sea ice

Ice-associated amphipods occupy a central position in the cryopelagic food chain noted by Andriashev (1968, 1970) and El-Sayed (1971) where Crustacea grazing on micro-algae are

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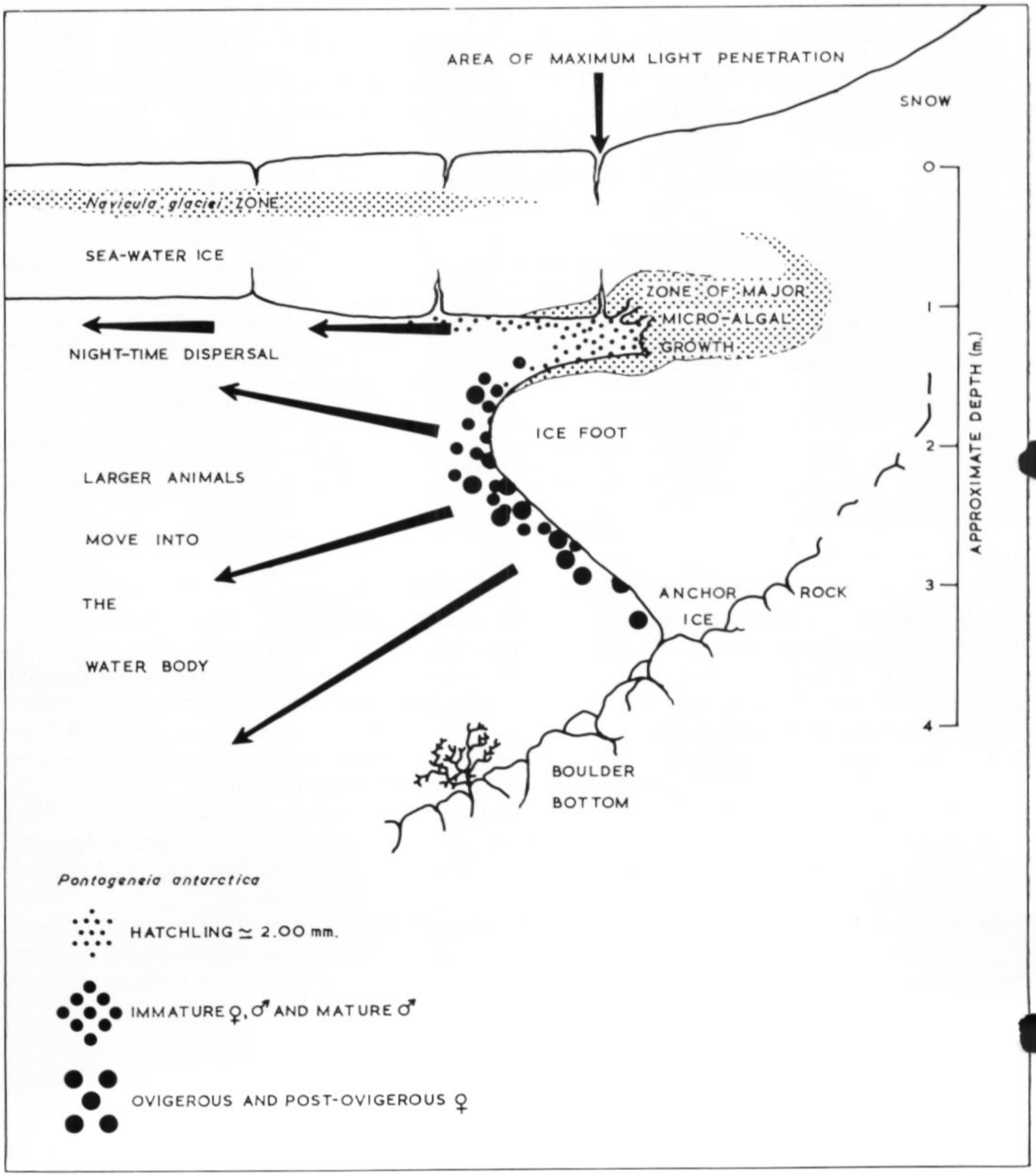

Fig. 1. Schematic section across the ice foot and tide-crack area, Knife Point, Signy Island, August 1972. Diurnal movements of the amphipod *Pontogeneia antarctica* are indicated by the arrows.

eaten by fish. The occurrence of ice-associated amphipods has been previously recorded from both Arctic (Barnard, 1959) and Antarctic ecosystems (Andriashev, 1968, 1970; Rakusa-Suszczewski, 1972), and these were noted at Signy Island in 1971–73.

During 2–3 weeks after initial fast-ice formation, amphipods began appearing in increasing numbers on ice surfaces, particularly at points where light penetration was high but sub-maximal: tide cracks, ice-foot areas and seal holes or man-made ice holes. Four species of amphipod were recorded at Signy Island from the immediate vicinity of sea ice. *Lepidopecreum cingulatum* Barnard, a detrital feeder, was observed sporadically in small numbers throughout the winter. *Paramoera walkeri* Stebbing and *Cheirimedon femoratus* (Pfeffer) occurred locally at the under side of the ice, late in the winter, actively preying on newly released young of *Pontogeneia antarctica*. This last species is the predominant herbivore of ice-associated micro-algae. Benthic samples indicate that up to 60 per cent of this species, including over 95 per cent of the ovigerous females, ascend from the macro-algal beds of *Desmarestia* and *Phyllogigas* (its habitat during the ice-free periods) to overwinter in the tide-crack area. This migration pattern is only exhibited in less than 20 m. of water.

The association between micro-algal growth and the amphipod was investigated during the winters of 1972 and 1973 at a site at Knife Point, Factory Cove, Signy Island.

The sample site

The ice foot at Knife Point forms on a steeply shelving, north-facing rocky shore, above a zone of packed boulders where there is a sparse growth of several species of *Desmarestia* and *Phyllogigas*. Below this is a level sandy bottom with larger weed beds. Fast ice formed during May in 1973, after an initial month of transient sea ice while ice was accumulating in the upper intertidal area. From this time until August, the ice foot was accumulating but, although much detrital material was incorporated apparently by the nucleation of congelation ice crystals around detritus in the water, no micro-algae were seen until 26 June. Radiant heating aided by periodic inundation of the tide-crack areas by melt water resulted in the gradual attrition of the ice foot from late September onwards. It collapsed finally on 28 November. A few portions persisted until several days after the break-up of fast ice on 6 December.

METHODS

Ice-associated micro-algae and amphipods were obtained by aqualung divers during the austral winter of 1973 (between June and November). The micro-algae were collected with small fragments of ice from the Knife Point ice foot using 100 ml. polythene bottles which were pushed into the relatively soft ice substrate. Amphipoda were captured during the same period by towing a net (mesh size 0·3 mm.) along the ice foot. Samples were taken within minutes to the laboratory. The ice was melted and centrifuged at 2,000 r.p.m. to concentrate particulate material. Sub-samples were examined under × 400 magnification and visual estimates were made on a 4-point scale of relative abundance of micro-algal species and associated material. Amphipods were hand sorted from net catches and killed by placing in warm filtered sea-water (+10° C). Specimens were examined either fresh, or after fixation and storage in 10 per cent formalin made with filtered buffered sea-water. The gut contents of small individuals (approximately 2 mm. in length) were examined from squash preparations. Guts from larger animals were removed by dissection before similar examination under ×100 and × 400 magnification. A total of 303 *Pontogeneia antarctica* was examined and approximately one-third of these were investigated fresh. Preservation was found to make examination of the smaller animals difficult and consequently all the preserved amphipod material examined consisted of large ovigerous or immediately pre- or post-ovigerous females. A measure of feeding activity of the females was obtained by estimating the amount of material present in the gut for a limited number of animals (180). Diurnal activity was recorded by a variety of methods: netting, traps, direct observation, and time-lapse flash cinematography (unpublished data of B. Kellett).

RESULTS AND DISCUSSION

The biology of Pontogeneia antarctica

Initially, the reason for the biennial alteration of habitat preference by the amphipod was not apparent. All age groups of the population were represented including adult males, ovigerous females and juveniles. There was little feeding in early winter, particularly amongst the ovigerous females, but a characteristic diurnal rhythm was also apparent with maximum swimming activity between 20.00 and 24.00 hr. local time. Many amphipods were eaten by the pelagic fish *Trematomus newnesi* Boulenger at the onset of winter (Richardson, 1975) but as ice formation progressed the amphipods hid in small pockets and pits in the ice surface. These small identations may have been excavated by the amphipods or they may have been produced passively by black-body conduction and localized melting, or by non-freezing in the immediate vicinity of the animals due to constant movement especially of the ventilating pleopods.

P. antarctica, like many polar invertebrates, has an extended embryonic development, 4·5–5 months long. The relatively large pink-orange ova are brooded by the female and, with the added presence of second-brood production, ovigerous females may be found throughout the greater part of the year. Most of the 2·0 mm. long hatchilings (which resemble adults) are released in late August. The mean fecundity for the species is $65 \cdot 4 \pm 19$ young per female. The habitat preference of these newly released young is markedly different from that of the adults and the intermediate juveniles. The young are positively phototropic and congregate at points where illumination is greatest, just under the tide cracks. This attraction to light can be readily shown in the laboratory. Hatchlings are thus instinctively attracted to the area where micro-algae grow best. Crustacean densities were up to 12,730 individuals m.$^{-3}$ ($8 \cdot 3$ g. m.$^{-3}$) in this area; hatchlings accounting for 97 per cent of the numbers and 54 per cent by weight. Their nocturnal dispersal was also different from that of the adult and juveniles, and is shown diagrammatically in Fig. 1.

Micro-algal growth

The micro-algae formed the majority of particulate material at the ice foot, although copepods, ciliates, flagellates, motile bacteria and detrital matter were also present. At least 44 species of micro-algae were found and of these at least 35 were diatoms. Two species, *Navicula glaciei* and *Nitzschia curta* formed over 90 per cent of the micro-algal material. Species recorded from each of the samples are shown in Table I. The species diversity of micro-algae increased to a peak of 22 species in the sample of 15 October, at which time it is probable that the population was also at its peak as major attrition of the substrate had not yet begun.

Few examples of species succession were observed, the process being mainly one of colonization. It is probable that micro-algal species, not recorded in later samples, persisted undetected in their original small numbers being masked by the very high numbers of the common diatoms. The most significant change observed was the early colonization by Cyanophyceae especially *Phaeocystis antarctica*, whose colonies were extremely abundant in June but blue-greens were not found at all after diatom growth was established by early August. This is in agreement with Bunt (1964), who suggested that *Phaeocystis antarctica* could be better adapted to conditions of low light than under-ice diatoms.

Analysis of gut contents

The problems of gut-content analysis are well known, but two further complications in this work were that one author familiar with micro-algal work did all the work on fresh material and the other more familiar with Crustacea did all the analyses on preserved material. Also, the smaller preserved animals could not be dissected. The specimens examined were therefore almost entirely adult and mainly ovigerous females. An exception was the 31 May sample taken before ovigerous females were present. Table II gives the gut-content analyses.

Crustacean material was identified by appendages, trophi or by epidermal setae and patterning. Digested or partly digested materials could often be used as an indication of the type of material eaten; purple, orange or pink fat droplets were always associated with crustacean remains and yellow or yellow-green fat droplets were usually associated with micro-algal

TABLE I

	26 Jun.	24 Jul.	1 Aug.	20 Aug.	13 Sep.	17 Sep.	5 Oct.	8 Oct.	15 Oct.	29 Oct.	12 Nov.	26 Nov.
CHRYSOPHYTA: BACILLARIOPHYCEAE												
Centrales												
Eucampia balaustium Castr.											+	
Charcotia actinochilus (Ehr.) Hust.	+			+					+	+	+	
Charcotia australis (Karst.) M. Peragallo								+				
Thalassiosira antarctica Comber		+		+	+	+	+		+	+	++	+
Thalassiosira sp. (65)			+	+								
Coscinodiscus bouvet Karst.								+				
Coscinodiscus oppositus Karst.									+	+		
Coscinodiscus oculoides Karst.								+				
Coscinosira antarctica Kozlova								+				
Corethron criophillum Castr. forma *hystrix*						+	+		+	+	+	+
Cocconeis imperatrix A. Schm.	+		+		+				+			
Chaetoceros schimperanum Karst.	+	++	+		+		+++	+	+	+	+	+
Chaetoceros sp. (32)		+					+					
Biddulphia striata Karst.							+					
Pennales												
Nitzschia curta (Van Heurck) Hasle	+++	++++	+++	+++	++	++++	++++	+++	+++	+++	++	+
Nitzschia cylindrus (Grun.) Hasle												
Nitzschia kerguelensis (O'Meara) Hasle			+									
Nitzschia lineata Hasle				+			++	+	+	+		
Nitzschia sublineata Hasle		+			+		+			+		+
(*Nitzschia*) *Fragilariopsis rhombica* (O'Meara) Hasle forma *minima* Kozlova						+						
Nitzschia closterium (Ehr.) W. Sm.				+					+			
Nitzschia bilobata W. Sm. var. *antarctica*		+++	+	++	+	+	+		+	+	++	+
Nitzschia sp. (42)	+++	++++		+	+	+	+	+	+	+	++	+
Navicula glaciei Van Heurck		++	+++	+	+	+	++		++++	++++	+++	++++
Navicula frequens Van Heurck			+		+		+	+	+	+		
Navicula sp. (77A)	+											
Amphiprora oestrupii Van Heurck			+	+	+		+	+	+			
Amphiprora sp. (44B)	+	+	++	+			+	+	+	+		+
Amphiprora kjelmanii Cl.								+	+	+		
Amphora sp. (18)					+		+	+	+	+		
Amphora sp. (76)	+											
Rhizsolenia inermis Castr. forma *rostrata* Heiden et Kölbe		+		+			+				+	
Licmophora spp.	+		+									
Gyrosigma attenuatum Sm. var. *antarctic* Frenguelli							+		+			
Grammatophora sp. (64)			+									
CHRYSOPHYTA: XANTHOPHYCEAE												
Heterochloridales												
Chloromeson sp. (83)									++	+	+	+
CHLOROPHYTA: CHLOROPHYCEA												
Volvocales												
Chlamydomonas sp. (89)					+							+
CYANOPHYTA: MYXOPHYCEAE												
Phaeocystis antarctica Karst.	++++	++	+									
Anabaena sp.		++										
Nostoc sp.			+									
PYRROPHYTA: DINOPHYCEAE												
Gymnodiniales												
Gymnodinium sp.									+	+		
Peridiniales												
sp. (85)									+	+		
WARNOWIACEAE												
sp. (106)									+	+		+
Dictyocha speculum (Ehr.)							+					
TOTAL SPECIES PRESENT	10	12	14	12	12	7	18	13	22	19	11	12
Copepoda							+		+			
Cilliates									+			
Flagellates (*Bodo* sp.)									++			+
Motile bacteria										+		+
Gregarine spores (?)	+								+			

+	Present.
++	Common.
+++	Abundant.
++++	Extremely abundant.

31 May	The ice foot forming; no diatoms, much detritus.
28 Nov.	Ice foot area collapsed.
6 Dec.	Fast ice broke up.

TABLE II. GUT ANALYSES

		13 May	31 May	25 June	24 July	20 Aug.	13 Sep.	17 Sep.	5 Oct.	15 Oct.	29 Oct.	26 Nov.	TOTAL
MICRO-ALGAE													
Charcotia actinochilus				+			+					+	
Thalassiosira tumida			+	+		+			+		+	+	
Coscinodiscus oppositus												+	
Cocconeis imperatrix		+	+++	++	++	++	++	++	+	++	++	++	
Chaetoceros schimperianum									+	++	+		
Nitzschia curta		++	++	+	+	+	+			+	+		
Nitzschia cylindrus			+			+						+	
Nitzschia lineata		+	+						+		+		
Nitzschia bilobata var. *antarctica* (40)				+	+				+	+	+	++	
Nitzschia sp. (42)			+	+		+		+	+	+	+	+	
Navicula glaciei		+	+	+	+	+	+	+	++	++	++	++	
Navicula frequens						+			+		+	+	
Amphora sp. (18)			+	+	+	+	+			+	+		
Licmorphora spp.		++	++	+	+						+	+	
Amphiprora spp.									+		+		
Nitzschia spp.		+	+		+	+	+	+	+	+			
Coscinodiscus spp.		+++	++	++	+	++	++	++	++	++	++	++	
Pennales spp.		+	+	+		+	+		+	+	+	+	
Centrales spp.						+	+						
Diatom fragments		++	+	++	+	+	+	++	++	++	++	++	
Chloromeson sp. (83)											+	+	
Dictyocha speculum			+	+	+				+	+	+	++	
Dinophyceae spp.								+					
Macro-algal fragments			+	+	+		+	+					
Chloroplast debris		+	++	++	++	++	++	++	++	++	++	++	
Detritus		+	+++	++	+++	++	++	++	++		++	++	
Mineral particles			+	+	+	+							
Crustacea		+	+	+	+	++	++	++	+		+	+	
Isopoda					+								
Amphipoda			+	+	+	+	+	+			+		
Copepoda			+	+	+	+	+	++	+		+	++	
Pontogeneia antarctica			+	+	+	++	++	++	+		++		
Oradarea bidentata				+									
Porifera fragments			+			+		+					
Spermatophores			+	+	+						+		
Fat droplets		++	+	+	+	+	+		+	++	+	++	
Gregarinda: Cephaloidea		++	++	++	+	+	+	++	+	+	+	+	
Nematode fragments											+		
Small ovae, not identified				+	+	+					+		
Bacteria												+	
Empty gut			+		+	+	+	+	+	++	+	++	
Number examined	Fresh	11	10	10	10	12	12	0	13	14	10	5	107
	Preserved	1	31	18	45	24	29	18	0	0	23	7	196
	Total	12	41	28	55	36	41	18	13	14	33	12	303

Percentage occurrences in gut samples

20	+
20–60	++
60	+++

material. Often omatidial elements could be found even when no other crustacean material was seen. Micro-algae vary greatly in their resistance to trituition. It is unfortunate that what may be common and readily identifiable in the gut may in fact be the residual material that is not easily assimilated. Animals containing many diatoms always had masses of green plastid debris which became greyish in the hind gut. Samples taken in June and July contained this material but very few broken frustules; this probably indicates the ingestion of *Phaeocystis antarctica.* This type of result is not shown in Table III, which compares the incidence of micro-algae in the gut samples and in the ice-foot samples (cf. Table I with Table II), because any doubtful identifications were placed in the appropriate class of incompletely identified material. Micro-algae in Table III can be easily divided into groups: those detected in the gut samples and those never seen in the gut. It is also possible to distinguish, in the former class, species which are more often seen in the gut samples than in nature. The explanation of these differences between species can be ascribed to two groups of factors: those influencing the chance of ingestion (abundance, size and shape) and those involving the probability of identification after possible ingestion (abundance, ease of identification and durability). A large, bulky or spiny micro-alga is likely to be difficult to ingest. If the alga occurs abundantly, and feeding is relatively indiscriminate, it has more chance of being eaten and there is more chance that an individual may remain in a recognizable condition (e.g. *N. glaciei* and *N. curta*). A compact or strongly silicified diatom may entirely escape breakage (e.g. *Amphora* sp.). The frustules of several diatom species are very distinctive and a species such as *Cocconeis imperatrix* can be recognized from very small fragments, but several of the *Nitzschia* (≡ *Fragillariopsis*) species (e.g. *N. curta, N. lineata, N. sublineata* and *N. cylindrus*) cannot be separated when much fragmented, and most are grouped as "*Nitzschia* species not identified" in Table II. Table IV is an evaluation of these factors for each of the micro-algal species recorded in the ice foot. The observed differences in Table III are closely mirrored by groups of factors in Table IV.

The examination of amphipod guts showed that plant, animal and detrital material was consumed and the relative proportions varied according to the availability of the ice-associated micro-algal food source (Table V). At the start of the winter many individuals ate mainly diatoms such as *Cocconeis imperatrix* (only present in the benthic flora at this time), macro-algal fragments and a large number of the brown platy detrital particles which were concentrated under the ice by the floating of ice crystals nucleating around them. From August onwards the ice-associated micro-algae became the most important food but cannibalism by the adults, a common occurrence in Crustacea, somewhat distorted the August figures. It seems probable that diatoms with maximum dimensions greater than about 60 μm. are not ingested but it is likely that such particles are not so much avoided as mechanically rejected by the trophi. Apparent concentration of several species in the gut can be accounted for either by their being relatively resistant to trituition or being easily recognizable (e.g. *Amphora* spp., *N. frequens, C. imperatrix, Licmophora* spp.), factors recognized by Nemoto (1968) with reference to diatoms in the gut of *Euphausia superba* Dana. The hatchling amphipods feed actively on the smaller components of the ice-associated flora, their staple diet being *Nitzschia curta* and *Navicula glaciei.* The importance of these smaller diatoms during the initial growth of the amphipod was demonstrated by the gross mortality of young hatchlings isolated in natural environments where only larger diatoms were available such as *Cocconeis imperatrix* A. Schm., which is easily utilized by adult amphipods.

A comparision of feeding activity was made between non-ovigerous females collected on 31 May 1973 and ovigerous females collected between 13 May 1973 and 29 October 1973. The results are shown in Table VI and Fig. 2. The "empty gut" category could be a result of different causes which makes statistical comparison of the two very different frequency distributions in Fig. 2 difficult. It is apparent, however, that the ovigerous females do not feed as intensively as non-ovigerous ones, but qualitative differences were not detected. The reduction of feeding by the ovigerous females, combined with different dispersal patterns of the adult,

TABLE III

	Date of sample	25 June	24 July	20 Aug.	13 Sept.	17 Sept.	5 Oct.	15 Oct.	29 Oct.	26 Nov.	
Species commonly detected in gut	*Navicula glaciei* Van Heurck	▧	▩	▩	▩	▩	▩	▩	▩	▩	*Common species; abundant in gut*
	Nitzschia sp. (42)	▧	▩	▩	▨	▩	▩	▩	▩	▩	
	Nitzschia bilobata W. Sm. var. *antarctica*	▧	▩	▨	▨	▨	▩	▩	▩	▩	
	Nitzschia curta (Van Heurck) Hasle	▩	▩	▩	▩	▨	▨	▩	▩	▩	
	Thalassiosira antarctica (Janisch) Hasle	▧	▨	▩	▨	▨	▩	▨	▩	▩	*Easily identified or durable species*
	Amphora spp.	▧	▧	▧	▩		▨	▩	▩		
	Navicula frequens Van Heurck			▧	▨		▩	▨	▩	▧	
	Cocconeis imperatrix A. Schm.	▩	▧	▧	▩	▧	▩	▧	▧	▧	
	Dichtyocha speculum (Ehr.)	▧	▧				▩	▧	▧	▧	
	Licmophora spp.	▩	▧						▧	▧	
	Chloromeson sp.							▨	▩	▩	
	Chaetoceros schimperianum Karsten	▨	▨		▨	▩		▩	▩		*Rare, large or species with low durability*
	Nitzschia lineata Hasle			▨			▩	▨	▩		
Species rarely detected in gut	*Amphiprora* spp.	▨	▨	▨			▩	▨	▩	▨	
	Charcotia actinochilus (Ehr.) Hust.	▩		▨				▨	▨	▨▧	
	Dinophyceae					▧		▨	▨	▨	
	Coccinodiscus oppositus Karsten							▨	▨	▨▧	
Species never detected in gut	*Nitzschia sublineata* Hasle		▨		▨		▨		▨	▨	
	Corethron criophillum Castr.					▨	▨	▨	▨	▨	
	Rhizosolenia inermis f. *rostrata* Heiden et Kölbe		▨	▨			▨				
	Phaeocystis antarctica Karsten	▨	▨								
	Gyrosigma attenuatum W. Sm. var. *antarctic* Frenguelli						▨	▨			
	Chlamydomonas sp. (89)				▨					▨	
	Chaetoceros sp. (32)		▨				▨				
	Anabaena sp.		▨								
	Nitzschia closterium (Ehr.) Wm. Smith			▨							
	Thalassiosira sp. (65)			▨							
	Nitzschia rhombica (O'Meara) Hasle f. *minima* Kozlova					▨					
	Biddulphia striata Karsten						▨				

▧	▩	▨
Detected in gut	Detected in gut and in ice foot	Detected in ice foot

TABLE IV. FACTORS INFLUENCING THE CHANCE OF INGESTION AND THEN OF IDENTIFICATION OF MICRO-ALGAE FOUND AT THE KNIFE POINT SAMPLE SITE

Micro-algal species	*Factors influencing ingestion*					*Factors influencing detection after ingestion*			
	Size, shape and abundance					*Identification and durability*			
	Small	*Common*	*Large*	*Bulky*	*Rare*	*Easy*	*High*	*Difficult*	*Low*
Navicula glaciei	×	×							×
Nitzschia sp. 42		×						×	×
Nitzschia bilobata var. *antarctica*	×	×						×	×
Nitzschia curta	×	×						×	×
Thalassiosira antarctica						×			
Amphora spp.	×						×		
Navicula frequens							×		
Cocconeis imperatrix						×	×		
Dictyocha speculum	×					×			
Licmophora spp.	×					×	×		
Chloromeson sp.	×					×	×		
Chaetoceros schimperianum	×							×	×
Nitzschia lineata	×	×						×	×
Amphiprora spp.			×	×		×			
Charcotia actinochilus						×			
Dinophyceae	×				×	×			
Coscinodiscus oppositus					×				
Nitzschia sublineata	×	×						?	?
Corethron criophillum			×	×					
Rhizosolenia inermis			×	×					
Phaeocystis antarctica	×	×						?	?
Gyrosigma attenuatum			×	×					
Chlamydomonas sp. 89	×				×			?	?
Chaetoceros sp. 32			×	×	×				
Anabaena sp. 74	×				×			?	?
Nitzschia closterium					×				?
Thalassiosira sp. 65					×				
Nitzschia rhombica	×				×			?	?
Biddulphia striata			×	×					

TABLE V. ESTIMATIONS OF RELATIVE AMOUNTS OF FOOD TYPES IN GUTS OF *Pontogeneia antarctica* ON VARIOUS SAMPLING DATES

Date 1973	*Percentage of material in total fresh samples*		
	Algal	*Crustacean*	*Other (mainly detrital)*
13 May	85	5	10
31 May	40	0	60
27 June	75	5	20
24 July	90	0	10
20 August	85	10	5
13 September	95	0	5
5 October	85	10	5
15 October	100	0	0
29 October	100	0	0
26 November	100	0	0
Mean percentage	85	3	12

TABLE VI. A COMPARISON BETWEEN THE PERCENTAGE FULLNESS OF GUTS OF OVIGEROUS AND NON-OVIGEROUS FEMALE *Pontogeneia antarctica* OF THE SAME SIZE GROUP

Percentage fullness	*Numbers in feeding class*		*Percentage non-ovigerous*	*Percentage ovigerous*
	Non-ovigerous	*Ovigerous*		
0	0	58	0	39·0
1	2	18	6·5	12·1
2	3	28	9·7	18·8
3	4	24	12·9	16·1
4	6	14	19·2	9·4
5	3	5	9·7	3·3
6	4	2	12·9	1·3
7	5	0	16·1	0
8	2	0	6·5	0
9	2	0	6·5	0
10	0	0	0	0
TOTAL	31	149	100·0	100·0

juvenile and hatchling amphipods, may be adaptations to reduce cannibalism by this facultatively carnivorous species.

CONCLUSIONS

Contrary to the observations of Barnard (1959), sea ice affords a very attractive habitat for animals capable of survival at low temperatures. During the period in the year when planktonic

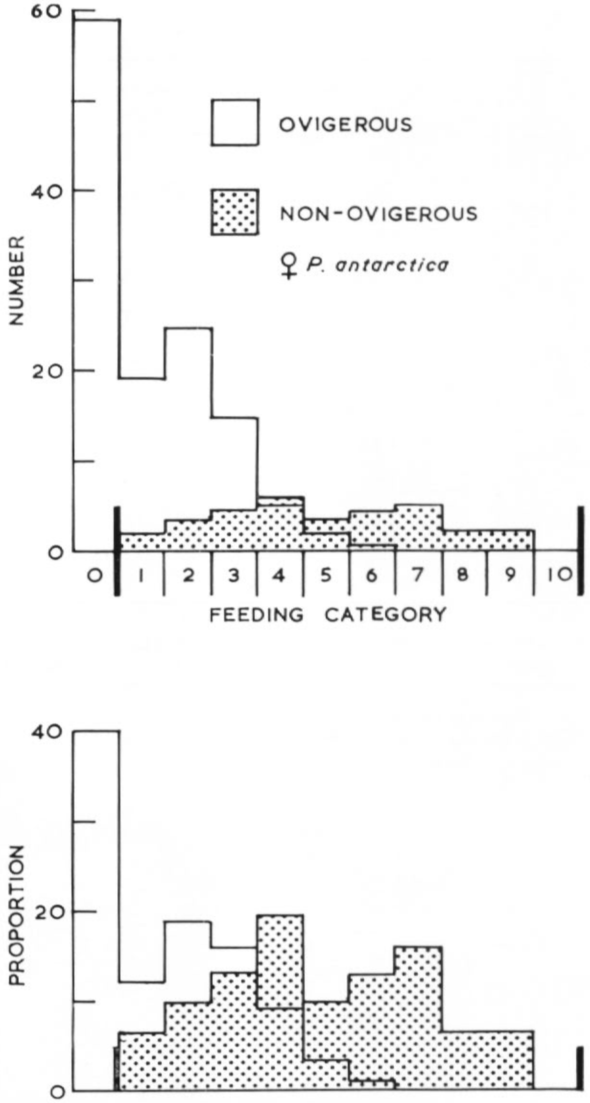

Fig. 2. The data in Table VI represented in histogram form.

and benthic primary productivity has slowed or ceased, micro-algal primary productivity within the sea-ice layer is increasing. At Signy Island, the amphipod *Pontogeneia antarctica* shows several behavioural adaptations to utilize this source of food which is present during most winters.

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