

The Sea Ice Fauna of Frobisher Bay, Arctic Canada

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ABSTRACT. The fauna of the lower few centimetres of the sea ice in Frobisher Bay, Arctic Canada, consists mainly of meroplanktonic young of benthic adults and holoplanktonic representatives of generally benthic groups. The major arctic zooplankton species are not included. The ice fauna comprises nematodes, harpacticoid copepods, polychaete larvae, ciliates, various benthic larvae, young gammaridean amphipods, and others. Some species occur in the ice as young animals only, others in all stages of development. Adaptation to the ice is shown best by the copepods, some of which occur there in all stages from egg to adult. The most abundant ice inhabitants reach high concentrations in the ice (nematodes more than 100 000, *Cyclopina* nearly 10 000·m⁻²). Others appear to show only accidental presence in the ice, and are found in small numbers only, often at times when great numbers of the same species are present in the water below the ice. Probable feeding of the ice fauna and the food chain linking the ice flora to vertebrate predators are discussed.

Key words: arctic waters, sea ice, ice fauna, food chain, zooplankton

RÉSUMÉ. La faune présente dans les quelques centimètres inférieurs de la glace marine de la baie de Frobisher, est constituée principalement de juvéniles méroplanctoniques dont les formes adultes appartiennent au benthos et de représentants holoplanctoniques de groupes généralement benthiques. Nous n'y retrouvons point les principales espèces du zooplancton arctique. La faune de la glace comprend des nématodes, des copépodes harpacticoides, des larves de polychètes, des ciliés, différentes larves benthiques, des amphipodes gammarides juvéniles et bien d'autres. Certaines espèces ne se retrouvent dans la glace qu'à l'état juvénile, tandis que d'autres sont représentées par des animaux ayant atteint des stades variés de développement. Les copépodes représentent le groupe s'étant le mieux adapté à la vie dans la glace; certains d'entre eux s'y retrouvent à tous les stades de leur développement, de l'oeuf jusqu'à la forme adulte. Les habitants de la glace les plus abondants y atteignent des concentrations élevées (les nématodes plus de 100 000, *Cyclopina* près de 10 000·m⁻²). D'autres semblent n'apparaître dans la glace qu'accidentellement et en nombre réduit, souvent lorsqu'un grand nombre d'individus de la même espèce évoluent dans les eaux sous-jacentes. Le mode de nutrition probable de la faune de la glace de même que les liens unissant celle-ci aux prédateurs vertébrés au travers de la chaîne alimentaire sont discutés.

Mots clés: eaux de l'arctique, glace marine, faune de la glace, chaîne alimentaire, zooplancton

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INTRODUCTION

Considerable interest in plants found in sea ice, both arctic and antarctic, was shown throughout the second half of the nineteenth century, but it was not until Nansen (1906) observed ciliates on the surface of ice in the Arctic Ocean that animals were also recognized as sea ice inhabitants. Nansen concluded that the protozoans were of marine origin, frozen into the ice in autumn.

In his 1906 work, Nansen referred to an earlier observation of his made in 1882 in East Greenland waters. There he had noticed that ice 30-60 cm thick was frequently coloured reddish-brown on the underside. It was called "seal-ice" by the sealers because the seals seemed to prefer it. Nansen recognized the coloured material as diatoms, and suggested the existence of a trophic link between the under-ice diatoms, crustaceans which he stated would be expected to be attracted by the diatoms, and seals, which would feed on the crustaceans. This may have been the first serious statement on the ice-based food chain which, almost exactly 100 years later, we are still far from understanding clearly.

Nearly half a century passed before Usachev's (1949) account of protozoans in ice in the Kara Sea appeared. He found several ciliates, including *Euplotes candata* Meunier, *E. truncata* Meunier, *Proboscidium armatum* Meunier, *Cephalotrichium tonsuratum* Meunier, *Amphorella vitrea* (Brandt) and *Diffugia* sp.

This was followed by a series of reports on the larger and

more readily visible amphipods found associated with the lower surface of the ice. MacGinitie (1955) observed large numbers of *Apherusa glacialis* on the underside of ice floes on the north coast of Alaska. Barnard (1959) reported *Gammaracanthus loricatus* as possibly associated with the sea ice and *Onisimus* (as *Pseudalibrotus*) *nanseni* and *Gammarus wilkitzkii* as positively associated with the ice of the central Arctic Ocean. Horner (1972) found *Onisimus* (as *Pseudalibrotus*) *litoralis*, *Gammaracanthus loricatus*, and *Gammarus wilkitzkii* on the lower surface of the ice on the north Alaska coast.

Amphipods (*Apherusa glacialis* and *Gammarus setosus*) of the "cryopelagic biocoenosis" in the Soviet Arctic were discussed by Golikov and Scarlato (1973). Green and Steele (1975) observed *Gammarus setosus* and *Gammaracanthus loricatus* on the lower surface of the ice in Resolute Bay, and Welch and Kalff (1975) described unidentified amphipods from the same bay.

Some highly detailed information was supplied by Buchanan *et al.* (1977) on under-ice amphipods from Bridport Inlet, Melville Island. Three species of *Onisimus* (*O. litoralis*, *O. glacialis*, and *O. nanseni*) along with *Gammarus setosus* and *Gammaracanthus loricatus* were discussed in relation to the ice surface. Mention was made also of the amphipods *Gammarus wilkitzkii* and *Apherusa glacialis*.

Several amphipods and copepods and a single mysid were shown in loose association with the lower surface of the ice of the Arctic Ocean by Mel'nikov and Kulikov (1980). Several of

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the species above, with the addition of *Apherusa megalops* and *Weyprechtia pinguis*, were found just under the February ice on the north Alaskan coast by Griffiths and Dillinger (1981). A number of familiar amphipods along with previously unreported *Ischyrocerus anguipes*, *Eusirus holmi*, and *Parathemisto libellula* and the mysid *Mysis polaris* were listed by Cross (1982a) from beneath the ice in Pond Inlet, north Baffin Island. Many of the same amphipods, with the addition of *Pontogeneia inermis*, were taken at Cape Hatt, north Baffin Island, by Cross (1982b).

Horner and Alexander (1972) seem to be the first to have looked for the smaller multi-cellular animals within arctic sea ice (Andriashev (1968) had already done so in the Antarctic, and had shown the presence of young polychaetes, calanoid, cyclopoid, and harpacticoid copepods and amphipods). They produced from the north Alaskan coast the most interesting and diversified list of ice animals to date, including ciliates, mainly hypotrichs of the genera *Euplotes* and *Stylonchia*, unidentified heliozoans, nematodes, polychaetes, turbellarians, and a single small, unnamed copepod. More recently, Cross (1982a) reported a number of invertebrate animals from the bottom layer of ice in Pond Inlet, north Baffin Island, and Carey and Montagna (1982) and Kern and Carey (1983) described an invertebrate ice fauna from north Alaska. These included such small ice-dwelling animals as nematodes, rotifers, polychaete larvae, and crustaceans.

Considerable knowledge of the ice flora has already been assembled (Horner, 1977; Hsiao, 1980), and indications given of the potential importance of the ice plants as a food source for plankton and fishes. Fairly extensive information has been gathered on the larger animals associated mainly with the bottom of the ice. Knowledge of the smaller animals living within the ice has remained rudimentary, however, regarding their identity and number, their possible mobility and relationships with the fauna in the water beneath the ice, their food and predators, their origin, and their fate when the ice melts in spring.

Our study was carried out in Frobisher Bay, in the eastern Canadian Arctic, at a nearshore site (63°42.8'N, 68°30.8'W) between 40 and 50 m deep (Fig. 1). Physical and chemical properties of the ice and water below were measured at the times of ice sampling (Grainger and Hsiao, 1982; Lovrity, 1982; and unpublished data of the Arctic Biological Station). Collections considered here were made during the winter-spring periods of 1981 and 1982.

METHODS

Ice fauna was collected in two ways. The first method involved digging holes 60-90 cm in diameter, going from the surface down to about 15 cm from the bottom of the ice. The remaining ice was carefully extracted from the holes and retrieved with as little disturbance to the lower surface as possible. Alternatively, we used a SIPRE ice corer, which delivers a core 7.2 cm in diameter. Generally only single samples were taken. Visual (diver) examination from below of the penetration of the lower surface from above and the lifting

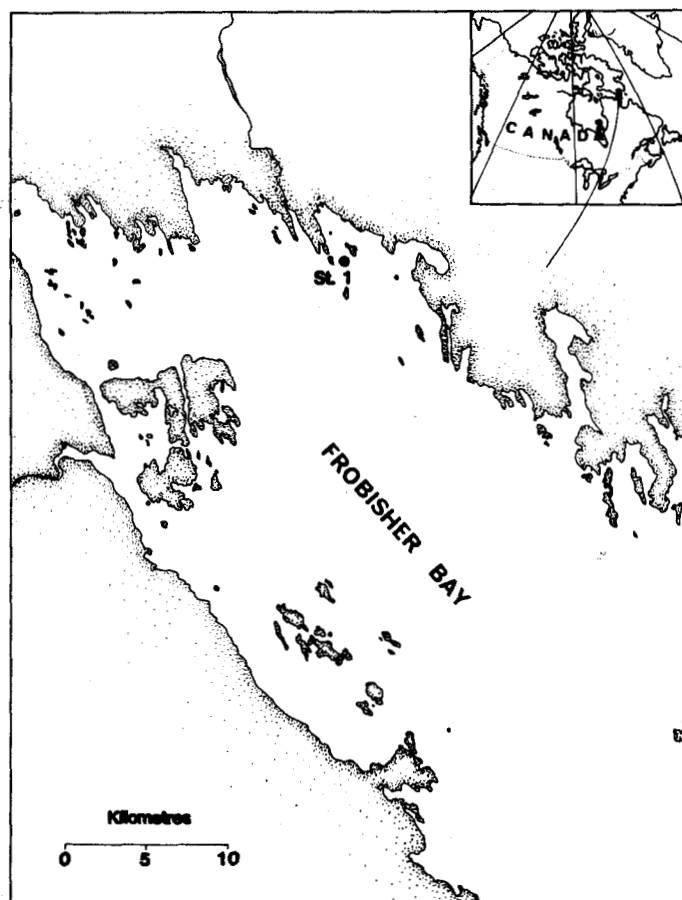


FIG. 1. Origin of sea ice collections (St. 1) in upper Frobisher Bay, Baffin Island.

of ice in both procedures showed little loss of material from within the lower surface of the ice.

Following collection, the ice samples were melted and excess water drained through nylon mesh (73 μ m for the first collection of 1981, then 10 μ m for the remaining samples of both years). All organisms retained were identified and counted. The change to a finer mesh was made to reduce possible loss of the smaller organisms such as nematodes and ciliates. Such loss through the larger mesh appeared in fact to be extremely small.

For comparison with ice samples, zooplankton was collected from the water beneath the ice, using 73- μ m mesh nets hauled vertically. Additionally, water was pumped from a few centimetres below the ice, and the zooplankton taken was retained on a 73- μ m mesh. We also used a hand-operated ice-bottom sampler.

RESULTS

The sea ice sampled ranged in thickness from 80 to 159 cm during the collection periods, the snow cover from negligible to about 50 cm. Salinity was variable in the water immediately under the ice (7.5-33.6%), and water temperature was consistently low (-1.8 to -0.1°C).

The Frobisher Bay sea-ice fauna collected in 1981 and 1982

is listed in Tables 1 and 2. Table 1 includes numbers of the ice-inhabiting species collected in the plankton under the ice. Nematodes were the most numerous individuals in the ice (up to more than 100 000 in the lower 3 cm of ice under 1 m²), and they were consistently more abundant in the ice than in the water samples. Mollusc larvae were consistently less numerous in the ice than in the water samples, peaking in May

in the ice but continuing through the spring to increase in numbers in the water. Numbers of *Cyclopina* declined progressively in the ice collections from the first to the last sampling date. Numbers in the water samples were low initially, then grew rapidly in June. *Tisbe* in the water, outnumbering those collected in the ice for most of the period, declined until May, then increased slightly while numbers fell in the ice. Copepod

TABLE 1. Sea ice fauna, Frobisher Bay, 1981. Numbers·m⁻² (in the lower 3 cm of ice and in 40-50 m of water)

Ice thickness (cm)	14 Feb 81 123		24 Mar 81 142		1 May 81 145		27 May 81 148		19 Jun 81 137	
	Ice	Water	Ice	Water	Ice	Water	Ice	Water	Ice	Water
Ciliates	0	0	0	713	720	158	14	0	40	0
Other protozoans	520	0	0	0	0	0	0	42	0	0
Nematodes	10560	185	30320	57	20700	70	108800	168	16000	1080
Polychaete larvae	460	1927	110	2542	8040	1584	28	504	0	16800
Rotifers	40	0	240	0	400	114	14	13	460	320
Pelecypod larvae	0	0	0	0	1680	6248	400	12726	20	39760
Gastropod larvae	0	115	0	1148	0	339	14	0	0	1160
<i>Balanus</i> larvae	0	0	0	0	0	154	0	421	20	19440
<i>Acartia longiremis</i> (Lilljeborg)	5	4633	0	4633	IBS*	4444	IBS*	840	0	0
<i>Cyclopina</i> sp.	2175	0	1770	114	800	114	98	39	0	332
VIM	5	0	0	0	0	0	0	0	0	32
VIF	15	0	40	57	680	0	28	0	0	16
V	5	0	0	0	0	0	14	13	0	72
IV	5	0	10	0	0	0	14	0	0	28
III	70	0	150	57	120	114	28	13	0	84
II	1790	0	720	0	0	0	14	0	0	100
I	285	0	850	0	0	0	0	13	0	0
<i>Ectinosoma</i> sp.	0	29	10	0	0	13	0	0	0	76
<i>Harpacticus superflexus</i> Willey	20	12	50	0	IBS*	0	84	13	20	76
VIM	0	0	0	0	0	0	14	0	0	16
VIF	20	12	10	0	0	0	14	13	0	44
V	0	0	0	0	0	0	42	0	0	16
IV	0	0	0	0	0	0	0	0	0	0
III	0	0	0	0	0	0	0	0	0	0
II	0	0	40	0	0	0	14	0	0	0
I	0	0	0	0	0	0	0	0	20	0
<i>Monstrilla</i> sp. VIF	5	0	0	0	0	0	0	0	0	0
<i>Pseudocalanus</i> sp.	0	54530	IBS*	43091	0	24200	IBS*	6846	0	17360
<i>Tisbe furcata</i> (Baird)	255	2108	310	1746	120	537	70	68	0	260
VIM	100	312	80	0	0	128	14	42	0	72
VIF	70	312	50	57	0	57	0	0	0	144
V	25	451	70	1066	0	313	56	13	0	16
IV	20	451	80	451	0	0	0	0	0	0
III	10	283	30	115	0	26	0	0	0	0
II	30	242	0	57	120	13	0	13	0	28
I	0	57	0	0	0	0	0	0	0	0
Copepodite casts	120 ¹	185 ¹	70 ¹	283 ¹	380 ¹	2992	2002 ²	391	20 ³	232 ⁴
Copepod nauplii (entire)	90920	697	26080	1025	4200	1936	800	1302	800	8440
(casts)	2440	0	0	57	0	229	98	0	1600	0
Eggs (mainly copepods)	7040	4305	2720	1886	7880	792	0	3696	60	15080
<i>Onisimus</i> sp.	60	0	110	0	120	0	IBS*	0	0	0
Tunicate larvae	0	451	40	0	0	0	14	25	0	0

*IBS = ice bottom sampler collections, non-quantitative

¹Mainly *Tisbe*

²*H. superflexus* (1862), *Tisbe* (98), *Cyclopina* sp. (42)

³All *H. superflexus*

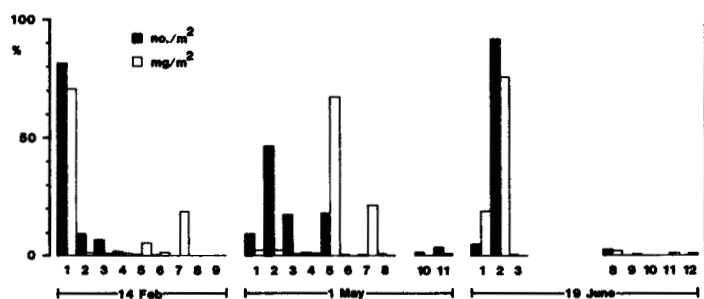
⁴Mainly *Harpacticus*

TABLE 2. Sea ice fauna, Frobisher Bay, 1982. Numbers·m⁻² (in the lower 3 cm)

Ice thickness (cm)	3 Feb 82 80	24 Mar 82 141	13 May 82 159
Ciliates	585	9	164
Other protozoans	68	28	0
Nematodes	8282	1962	14606
Polychaete larvae	0	3460	82
Rotifers	68	1637	2694
Gastropod larvae	0	9	0
<i>Cyclopina</i> sp.	3680	9364	82
VIM	15	0	0
VIF	66	130	18
V	15	0	0
IV	9	28	0
III	0	446	0
II	1460	3422	0
I	2115	5338	64
<i>Ectinosoma</i> sp.	2	660	9
<i>Harpacticus superflexus</i> Willey	3	381	18
VIF	3	0	9
V	0	0	9
II	0	9	0
I	0	372	0
<i>Monstrilla</i> sp.	9	0	0
<i>Pseudocalanus</i> sp.	2	0	0
<i>Tisbe furcata</i> (Baird)	31	1182	0
VIM	15	140	0
VIF	7	270	0
V	2	223	0
IV	7	316	0
III	0	177	0
II	0	56	0
Copepodite casts	34	205	130
Copepod nauplii	48156	7886	8891
Eggs (mainly copepod)	3305	6919	410
<i>Onisimus</i> sp.	19	140	9
Acarina (mites)	0	0	18
Tunicate larvae	46	9	0

TABLE 3. Sea ice fauna, Frobisher Bay, Station 1, 1981. Mg·m⁻² (wet) in the lower 3 cm

	14 Feb	24 Mar	1 May	27 May	19 Jun
Protozoans	0	0	0.1	+	+
Nematodes	10.6	30.3	20.7	108.8	16.0
Polychaete larvae	36.8	8.8	643.2	2.2	0
Rotifers	+	0.2	0.4	+	0.5
Mollusc larvae	0	0	8.4	2.8	0.1
<i>Balanus</i> larvae	0	0	0	0	0.4
<i>Acartia longiremis</i> (Lilljeborg)	0.3	0	0	0	0
<i>Cyclopina</i> sp.	9.0	7.3	15.0	1.2	0
<i>Ectinosoma</i> sp.	0	0.3	0	0	0
<i>Harpacticus superflexus</i> Willey	1.1	0.9	0	2.9	0.1
<i>Monstrilla</i> sp.	+	0	0	0	0
<i>Pseudocalanus</i> sp.	0	0	0	0	0
<i>Tisbe furcata</i> (Baird)	8.8	7.6	0.5	2.0	0
Copepod nauplii	454.6	130.4	21.0	4.0	4.0
Eggs	7.0	2.7	7.9	+	+
<i>Onisimus</i> sp.	120.0	220.0	240.0	0	0
Tunicate larvae	0	2.0	0	0.7	0
	648.2	410.5	957.2	124.6	21.2

+ = fewer than 0.1 mg·m⁻²FIG. 2. Seasonal changes in number and wet weight of the sea ice fauna of Frobisher Bay in 1981. 1, copepod nauplii; 2, nematodes; 3, eggs; 4, *Cyclopina*; 5, polychaetes; 6, *Tisbe*; 7, *Onisimus*; 8, rotifers; 9, *Harpacticus*; 10, ciliates; 11, mollusc larvae; 12, cirriped larvae.

nauplii (all species combined) were especially numerous in the ice samples in February, after which time they declined through the rest of the season while numbers generally rose in the water collections.

Differences, some fairly large, are apparent between the two years sampled. Nematodes were more numerous in the collections from March and May of 1981 than in 1982, and mollusc larvae were also more abundant in the 1981 material. Rotifers and young stages of *Cyclopina* were more numerous in the ice samples in 1982 than in 1981. Total numbers taken in 1981 were roughly double those caught in 1982.

Wet weights of major species and groups in the ice fauna are given in Table 3 for the 1981 collections, and comparisons of wet weights and counts for three of the collections in 1981 are shown in Figure 2. In February, numbers were accounted for mainly by copepod nauplii and nematodes, and weights by the copepod nauplii and individually large but relatively few *Onisimus* and polychaete larvae. Nematodes, polychaetes, and eggs were the most numerous in early May, at a time when polychaetes dominated the biomass and, along with *Onisimus*,

accounted for most of the biomass measured. In June, nematodes were strongly dominant, both numerically and in biomass, followed in both categories by copepod nauplii.

An indication of comparative population levels of ice inhabitants in the ice and in the water below the ice was shown in Table 1. Table 4 examines the relationship from the point of view of major species in the plankton. The most abundant member of the zooplankton in February, March, and early May was *Pseudocalanus* sp., predominantly as stages C-III to C-V. *Pseudocalanus* and the second most plentiful planktonic copepod, *Acartia longiremis*, were both found very rarely in the ice. The two most abundant cyclopoid copepods in plankton, *Oncaea borealis* and *Oithona similis*, were not found at all in the Frobisher ice in 1981 or 1982. Some groups were abundant in both locations, including copepod nauplii, eggs, and various benthic larvae. The most frequently occurring under-ice harpacticoid copepod, *Tisbe furcata*, was also the most numerous in the ice. Some were noticeably more numerous in the ice than in the water, including nematodes, rotifers, *Cyclopina* sp., *Harpacticus superflexus*, and young of the

TABLE 4. Major planktonic forms taken in the water under the ice in Frobisher Bay, 1981

Species	Species
<i>Pseudocalanus</i> sp. (*)	<i>Ectinosoma neglectum</i> G.O. Sars*
<i>Acartia longiremis</i> (Lilljeborg) (*)	<i>Microsetella norvegica</i> (Boeck)
Copepod eggs*	<i>Danielssenia typica</i> Boeck
<i>Tisbe furcata</i> (Baird)*	<i>Parathemisto libellula</i> (Lich.)
Polychaete larvae*	<i>Harpacticus superflexus</i> Willey*
<i>Oncaea borealis</i> G.O. Sars	Ciliates*
Copepod nauplii*	<i>Cyclopina schneideri</i> Scott*
<i>Oithona similis</i> Claus	<i>Mertensia ovum</i> (Fabricius)
Tunicate larvae*	Pelecypod larvae*
Nematodes*	<i>Balanus nauplii</i> *
<i>Metridia longa</i> (Lubbock)	Rotifers*
Gastropod larvae*	<i>Zaus abbreviatus</i> G.O. Sars
<i>Oncaea minuta</i> Giesbrecht	<i>Sarsia tubulosa</i> (M. Sars)
<i>Fritillaria borealis</i> Lohmann	<i>Dactylopodia signata</i> (Willey)

Found in the Frobisher sea ice; () very few in the Frobisher ice

amphipod *Onisimus* sp. (older representatives of which were present under the ice but not taken in any of the collections on the five dates discussed here). Finally, some species collected in the plankton were not found in the ice at all. They included the copepod *Metridia longa*, the amphipod *Parathemisto libellula*, and the ctenophore *Mertensia ovum*, along with the copepods *Calanus glacialis* and *C. hyperboreus* (both absent from plankton hauls on the five dates under discussion, but common at other times in upper Frobisher Bay).

DISCUSSION

The ice cover in Frobisher Bay usually becomes stable by early December. Initially rapid growth gradually slows as the winter progresses, and maximum ice thickness occurs in late May or early June (Grainger, 1971). Breakup normally occurs a few weeks after ice growth stops. Ice covers the inner bay for close to eight months each year and clears away completely during the intervening summers. Each winter produces an entirely new ice cover; consequently no ice older than about eight months was sampled at any time. In Frobisher, therefore, the sea-ice biota is completely renewed annually, differing in that way from what is found, for instance, in the multi-year ice of the Arctic Ocean (Mel'nikov, 1980).

It is convenient to separate the animals which we associate with the sea ice into two groups. One comprises the smaller organisms (sometimes referred to as the meiofauna) which are the numerically dominant group within the ice. Most are < 1 mm in maximum linear dimension, with a few up to 2-3 mm. The second group includes larger animals found linked in various degrees to the ice, totally or partly enveloped in it, or free in the water but in close physical association with the ice. Fully grown, most of these are > 10 mm. Young animals of the same species are of course smaller, and some of them may be included in the first group.

The large animals (mainly amphipods) were not included in the material collected for this paper. The smaller animals (Table 5) comprise a larger number of more diverse taxa than the larger animals. All clearly occur within the ice, where

TABLE 5. The meiofauna of the ice fauna of the Arctic

Protozoans	Copepods — Harpacticoida
Ciliates	<i>Dactylopodia signata</i> (Willey)*
Helizoans*	<i>Ectinosoma finmarchicum</i> (Scott)
Nematodes (<i>Theristus</i> sp.)	<i>Ectinosoma neglectum</i> G.O. Sars
Turbellarians*	<i>Harpacticus superflexus</i> Willey
Polychaetes	<i>H. uniremis</i> Kroyer
Rotifers (<i>Encentrum</i> sp. and <i>Proales</i> sp.)	<i>Pseudobradya</i> sp.*
Pelecypods (larvae)	<i>Tisbe furcata</i> (Baird)
Gastropods (larvae)	Copepods — Monstrilloida
Cirripedes	<i>Monstrilla</i> sp.
<i>Balanus</i> sp. larvae	Copepod eggs
Copepods — Calanoida	Amphipods
<i>Acartia longiremis</i> (Lilljeborg)	<i>Onisimus glacialis</i> (G.O. Sars)
<i>Calanus</i> sp.	<i>O. litoralis</i> (Kroyer)
<i>Pseudocalanus</i> sp.	Acarina
Copepods — Cyclopoida	Tunicates — larvae
<i>Cyclopina gracilis</i> Claus	
<i>C. schneideri</i> Scott	
<i>Oithona similis</i> Claus*	
<i>Oncaea borealis</i> G.O. Sars*	

*Not taken in the ice in Frobisher Bay; recorded elsewhere in the ice by Horner and Alexander (1972), Cross (1982a), Carey and Montagna (1982), Kern and Carey (1983).

some appear to undergo a major part of their life cycle. All are known to be planktonic during at least part of their lives, and are found in the plankton of ice-free as well as ice-covered water. Although they are at least temporarily pelagic, it is perhaps significant that most are included in taxa normally characterized by a bottom-living habit. Members of the group may be classed generally as feeders on small plants, bacteria and detrital particles.

Different species evidently spend different periods of their life cycles in the ice. The harpacticoid and cyclopoid copepods appear to be especially well adapted to existence within the ice, where some were found throughout their development cycles. These include *Cyclopina*, *Tisbe*, and *Harpacticus*, found in the ice in all stages, including adults of both sexes. Some females of *Cyclopina* and *Tisbe* were carrying eggs. In contrast, many of the larvae of benthic species, such as molluscs and barnacles, were present in the ice only during a small part of the animals' life cycles.

Most protozoans, adult worms, rotifers, adult molluscs and barnacles, harpacticoid copepods, gammaridean amphipods, mites, and adult tunicates are benthic rather than planktonic animals. These are the major animal groups inhabiting the sea ice. They are represented in the ice, however, not by holobenthic species but either by meroplanktonic young of primarily benthic adults or by holoplanktonic representatives of generally benthic groups. It is perhaps significant that the sea ice fauna is totally distinct from the dominant arctic zooplankton group, including the calanoid copepods *Pseudocalanus*, *Calanus*, and *Metridia*, the amphipod *Parathemisto*, the chaetognath *Sagitta*, the holoplanktonic medusa *Aglantha*, the ctenophore *Mertensia*, and the larvacean *Oikopleura*. These are circumpolar species found virtually everywhere in true arctic waters, but either very rare or unknown in the ice.

Herbivorous feeding by the small animal inhabitants of the ice has been mentioned in the literature (Nansen, 1906;

TABLE 6. Representative food and predators of some of the species found in the arctic sea ice

Species	Food	Predators	References
Ciliates	bacteria, detritus, diatoms, dinoflagellates	various zooplankton, including copepods	Beers & Stewart (1967), Burkovsky (1976), Beklemishev (1954)
Heliozoans	bacteria, diatoms, protozoans, rotifers, nematodes		Barnes (1968)
Nematodes	bacteria, diatoms, dinoflagellates, detritus, small metazoans	larger nematodes	Boaden (1964), Clasby <i>et al.</i> (1976), McIntyre (1969)
Turbellarians	rotifers, nematodes, annelids, cladocerans, copepods	larger turbellarians	Hyman (1951)
Polychaete larvae	diatoms	medusae, copepods	Barry (1974), Fraser (1970), Lebour (1922, 1923)
Mollusc larvae	diatoms	ctenophores, medusae	Barry (1974), Fraser (1970), Lebour (1922)
Rotifers	bacteria, protozoans, plant cells, detritus	larger rotifers	Barnes (1968), Boaden (1964)
Cirripede larvae	plant cells	medusae, ctenophores, copepods, amphipods, chaetognaths, fishes	Barry (1974), Fraser (1970), Grainger <i>et al.</i> (1980), Lebour (1923), Raymont (1963), Thorson (1946)
Copepods			
<i>Acartia longiremis</i>	plant cells, bacteria, small crustaceans, chaetognaths	copepods, ctenophores, fishes	Davis (1977), Lebour (1922, 1923), Ponomarenko (1967), Sorokin <i>et al.</i> (1970)
<i>Harpacticus superflexus</i> and <i>H. uniremis</i>	diatoms, bacteria	fishes	Brown and Sibert (1977), Grainger <i>et al.</i> (1980)
<i>Tisbe furcata</i>	plant cells, bacteria, fish larvae	fishes	Brown and Sibert (1977), Grainger <i>et al.</i> (1980), Berghe and Bergmans (1981)
nauplii	plant cells	ctenophores, medusae, copepods, amphipods, mysids, chaetognaths, fishes	Barry (1974), Dunbar (1946), Grainger <i>et al.</i> (1980), Lebour (1922, 1923), Petipa <i>et al.</i> (1970)
Amphipods			
<i>Onisimus glacialis</i>	diatoms	fishes, birds, seals	Bradstreet and Cross (1982), Dunbar (1941), McLaren (1958)

Andriashev, 1968; Horner and Alexander, 1972; Whitaker, 1977). Bradstreet and Cross (1982) have provided by far the best information on the subject to date. No detailed studies have been done on most of the ice animals, however, and we have only rudimentary knowledge of the feeding habits of most of the ice dwellers.

All the most abundantly represented animal groups in the ice for which information on feeding habits is available are shown to feed on plant cells; some groups also feed on bacteria, ciliates, and other nanoplankton and microplankton (Table 6). Tunicate larvae are non-feeders, and we lack information on the feeding of the less common ice-inhabiting copepods.

Several species found in the plankton under the ice are small enough to inhabit the ice but seem to do so either only rarely or not at all. One of these is *Oncaea borealis*, which was not found in the Frobisher Bay ice during this study but is known from the ice elsewhere; it is a mixed feeder depending to a degree, although by no means entirely, on animal food. *Oithona similis* is another. Gauld (1966) suggested that *Oithona* feeds herbivorously only on large plant cells, and Petipa *et al.* (1970) reported that it preys on small animals at least during its late copepodite stages. *Acartia longiremis*, rare in the Frobisher ice, is a plant feeder in its young stages but a mixed feeder when older, according to Petipa *et al.* (1970). *Pseudocalanus* is also a rare occupant of the Frobisher Bay ice, but its diet would appear to be suited to ice feeding.

The role of the arctic cod (*Boreogadus saida*) as a trophic link between invertebrates and higher vertebrates was indicated some time ago by Andriashev (1954). The same author (Andriashev, 1968) described a food chain based in the antarctic sea ice extending from ice diatoms through ice-dwelling crustaceans to the broadhead fish (*Trematomus*), and suggested that in the Arctic, *Boreogadus saida* occupied a niche similar to *Trematomus* in the Antarctic.

There is evidence that the arctic cod does show some dependence on the ice biota, and that it is a link in an ice-based food chain. It feeds on ice-related copepods and amphipods (Bradstreet and Cross, 1982), and is eaten in turn by the sea-run arctic charr, birds, and seals (McAllister, 1975). At least some of the ice-related amphipods (*Gammarus*, *Onisimus* and *Apherusa*) feed on the species of algae which are found in the ice, and *Gammarus*, at least, appears to feed on crustaceans as well (Bradstreet and Cross, 1982). These amphipods too are the prey of birds and seals (Bradstreet and Cross, 1982). Specific feeding studies have not yet been done on the major copepods or larvae in the ice, but known food habits of the same species in other habitats, or of related species, indicate that all probably feed on plants and other small organic particles in the ice.

There can be no question that a considerable food supply exists in the lower part of the sea ice in Frobisher Bay, available to a large and diversified community of animals for at least five months of the year. This represents a concentration of prey substantially greater than anything to be found in the diminishing zooplankton stock below the ice in late winter and spring until the time of emergence of the new summer generation.

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