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Exploitation of arctic sea ice by epibenthic copepods

E. H. Grainger

Arctic Biological Station, 555 St. Pierre Blvd., Ste. Anne de Bellevue, Quebec, Canada H9X 3R4

ABSTRACT: The harpacticoid *Tisbe furcata* and the cyclopoid *Cyclopina schneideri* are the dominant ice meiofaunal copepods in Frobisher Bay, Canadian Arctic. Maximum concentrations of *T furcata* in the lower 5 cm of the ice exceed 250 000 m^{-3}, of *C. schneideri* 125 000 m^{-3}, and by late winter the 2 species are 10^3 to 10^4 more concentrated in the ice than in the water column below. In contrast, the 2 species appear during the ice-free season to be relatively minor components of the nearshore system, living mainly in the epibenthic phytal habitat. Their feeding style is well suited to phytal living, as it is to ice dwelling, but they are less well equipped to feed in the water column. Ascending in mid-winter from relatively poor epibenthic feeding conditions, they encounter the rich food supply developing at that time in the lower levels of the ice, where algal concentations are at least 10^3 times higher than in the water column below. In this environment the ice copepods flourish. As the ice melts, the surviving ice copepods disperse, some apparently returning to their near-bottom habitat.

INTRODUCTION

The harpacticoid copepod *Tisbe furcata* (Baird) and the cyclopoid copepod *Cyclopina schneideri* (Scott) have long been considered as minor components of the arctic marine fauna. In the North American Arctic, both species have been encountered occasionally, usually in small numbers on or close to the sea bottom or less often higher in the water column (Shih et al. 1971).

In contrast to the usually small numbers encountered elsewhere, large numbers of both species have been shown to occupy the lower few centimetres of annual sea ice in the Arctic (Cross 1982, Kern & Carey 1983, Horner & Murphy 1985, Grainger & Mohammed 1986, Cross & Martin 1987, Grainger 1988). *Tisbe furcata* is also reported from the Antarctic ice (Gruzov et al. 1967, Andriashev 1968).

As part of a study of the ice fauna carried out between 1980 and 1985 in Frobisher Bay (Canadian eastern Arctic), the 2 species were shown to be the numerically dominant copepods in the ice, accounting for more than 95 % of all copepods collected between February and late May. Both were found as minor constituents, at no time comprising more than 4 % of copepods, in the plankton during the year. Both moved into the lower levels of the sea ice during the winter and there developed especially dense populations, more concentrated by more than 2 orders of magnitude than any found outside the ice. With the disappearance of the annual ice cover in early summer, both apparently descended into deeper water where they remained for the most part until the following ice season.

The objective of this paper is to show how, in the presence of a suitable sea ice cover, these 2 comparatively minor elements of the open-water demersal or shallow-water planktonic fauna of the Arctic expand their habitat, enter the lower levels of the sea ice, and in the presence of the abundant food supply developed there become dominant members of the temporary winter-spring sea ice fauna.

METHODS

The study area is located at the head of Frobisher Bay, on the southeast coast of Baffin Island. The main collecting site, about 40 m deep, is ice-covered from November until July, during which time the ice reaches a maximum thickness of close to 2 m. The sea ice melts from late May or early June into July, then clears, leaving open water which persists until November (Grainger 1975). The algal bloom is already

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present in the lower levels of the ice in February and remains until it is lost by melting into the water column below in early summer. The ice fauna develops in the same levels of the ice and also remains until the ice begins to melt. The sea bottom in the study area supports a dense growth of *Laminaria* spp. and other macrophytes.

Using an ice corer of 7.6 cm diameter, 24 cores taken from the lower 5 cm of the ice in February, March, April and May included *Tisbe furcata* and *Cyclopina schneideri* as part of the ice biota. Samples at the ice-water interface and in the ca 5 cm of water just beneath the ice were obtained from an under-ice sampler which scraped the lower surface of the ice and from a submersible pump.

The under-ice sampler (Grainger & Hsiao 1982) includes a collector box with a rectangular opening 15.2 cm wide and 3.0 cm deep. The collector is moved along the lower surface of the ice with the opening forward. It is controlled from the top of the ice by a vertical component which penetrates the ice hole and a horizontal arm which guides the collector along a circular path with an adjustable radius (183 cm maximum). A single sweep of one full circle scrapes an ice surface of 1.75 m^2 and samples 0.05 m^3 of water.

The submersible pump, a commercial 'Little Giant', was used to make 21 collections just below the surface of the ice and about 25 cm above the sea bottom (see below). Pumping rates were measured in each field situation and varied from 3.9 to 9.3 l min^{-1}. Pumping times ranged from 2 to 15 min. All ice-related samples were taken during daylight hours.

In the water column, 28 vertical plankton tows using nets of 30 cm ring diameter and 73 µm mesh made from about 1 m above the sea bottom to the surface yielded one or both of these species. The nets collected only during the ascent. No meter was used, but the relatively small quantity of plankton filtered during single hauls not exceeding 50 m in length precluded clogging of the meshes. Catching efficiency was therefore close to 100 %

Sixteen pump samples were collected 25 cm above the sea bottom at about 40 m depth in May and in August, using the submersible pump. All were taken amongst *Laminaria* and other macrophytes which grew densely in the area where the ice studies were conducted.

The benthic meiofauna in the area was examined with the aid of 10 core samples taken to a depth of 12 cm into the substrate. These were collected in summer and winter. In addition, a large number of Petersen type grab hauls taken on the site through all seasons over a period of 10 years were examined for meiobenthic copepods.

RESULTS

Numbers of *Tisbe furcata* in the sea ice of upper Frobisher Bay increased from 5987 m^{-3} in February to 250 988 m^{-3} in May (Fig. 1). The opposite trend was evident in the water column below the ice, where numbers fell from 55 m^{-3} in February to near 0 in May. The species persisted in small concentrations in the water column through June and July.

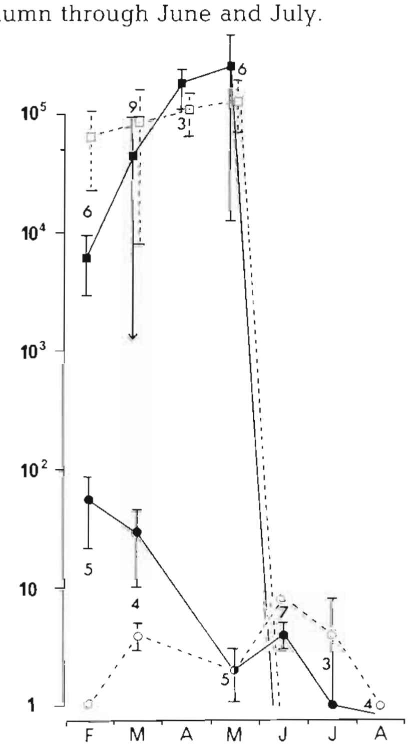

Fig. 1. Numbers (m^{-3}) of *Tisbe furcata* in the ice (■) and in the water column (●), and of *Cyclopina schneideri* in the ice (□) and in the water column (○) between February and August in Frobisher Bay, Canada. Vertical lines represent ± 1 standard deviation. Numbers of collections used to determine each mean are shown in the figure

Adults of both sexes dominated in the ice in February (Fig. 2). Egg-bearing females were present in March, and there was evidence of a new generation of early copepodid stages in the ice, and only in the ice, in May. During the same period, the small numbers found at the ice-water interface were mainly older copepodids, but the slightly larger numbers occurring in the water column below the ice were younger individuals which gradually diminished over winter.

As the ice melted in June only small numbers of animals of all kinds were collected in the water column. Early summer collections from near the bottom are lacking, but material taken in August shows that a substantial population of *Tisbe furcata* of around 4500 m^{-3}, consisting mainly of young copepodid stages

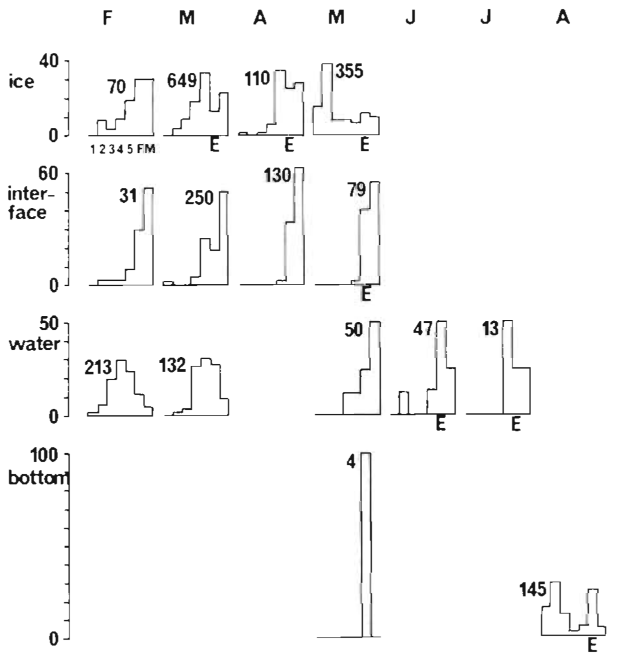

Fig. 2. *Tisbe furcata*. Relative frequency of developmental stages (C-1 to C-5, adult females and males) in the ice, at the ice-water interface, in the water column and just off the sea bottom between February and August in Frobisher Bay. E: females bearing eggs. Numbers of specimens used to construct each histogram are shown in the figure

and egg-bearing females, existed just above the bottom, amongst thickly growing macrophytes, at that time.

During summer, vertical net hauls made from about 1 m above the bottom to the surface took only small numbers of mostly adult *Tisbe furcata* (Fig. 2). During the same period, coring and grab sampling of the bottom collected a variety of harpacticoids, but at no time did they include *T. furcata*, which has not yet been found as a component of the benthic infauna in Frobisher Bay but only as a demersal copepod close to, but not on or in, the substrate.

Cyclopina schneideri was confined largely to the ice during this study. Unlike *Tisbe furcata, C. schneideri* showed a fairly steady concentration of copepodids in the ice, varying only from about 64 700 to 128 400 m^{-3} (Fig. 1). No clear trend was discernible in the water column below the ice, where numbers were consistently low.

Copepodid stages 1 and 2 dominated in the ice in February and March, C-3 in April and C-4 in May (Fig. 3). Stage C-5 increased in number between April and May and both adult males and females with eggs appeared in May. There were only small differences between stage frequencies at the ice-water interface and in the ice above, except for the presence at the interface of females in February, March and April, not found at the time in the ice. Numbers were extremely small in the water column. They were small in May just above the bottom, but grew to more than 1800 m^{-3} by August, by which time C-1 and adult females predominated.

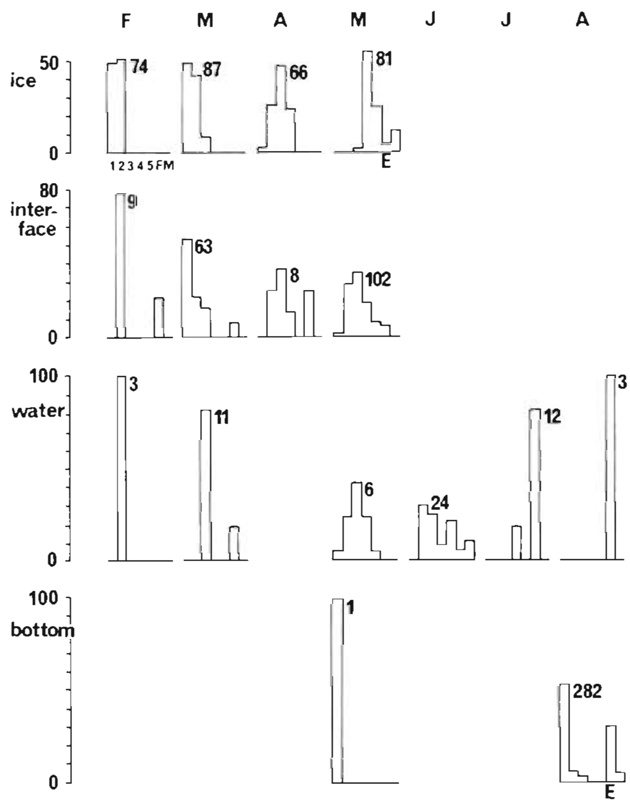

Fig. 3. *Cyclopina schneiderei*. Relative frequency of developmental stages (C-1 to C-5, adult females and males) in the ice, at the ice-water interface, in the water column and just off the sea bottom between February and August in Frobisher Bay. E: females bearing eggs. Numbers of specimens used to construct each histogram are shown in the figure

A sequence of development from C-1 to egg-bearing adults took place in the ice between February and May. A new generation then appeared in the water column as the ice disappeared. Evidence of this was seen in the water column in June, and of continued breeding just above the bottom in August.

DISCUSSION

Tisbe furcata was described by Lang (1948) as being mainly benthic. Although shown as long as 70 yr ago to occur planktonically in arctic waters (Willey 1920), it was included only relatively recently (Hauspie & Polk 1973) among 'some harpacticoid species, until now considered benthic [which] became pelagic at times'. These authors concluded that the copepodids could swim, and that the nauplii could not.

Tisbe furcata was included by Hicks (1980) among the phytal species, and found associated with a number of macrophytes. Several authors since have emphasized the phytal affinities of *T. furcata* (Hicks 1986, Walters & Bell 1986, Bell et al. 1987, Hicks 1988).

The ability of both *Tisbe furcata* and *Cyclopina schneideri*, as well as other copepods, to undergo vertical migrations has been shown (Alldredge & King 1980, Walters & Bell 1986, Bell et al. 1988, Walters 1988). Food was shown to be a stimulus to movement by Decho (1986), who observed meiobenthic copepods moving upward to feed on diatoms in the water column. According to Hicks (1988), the great majority of meiobenthic copepods occurring in the water column are truly phytal species.

Suspension feeding is generally little practised among most of the harpacticoids and, with a few exceptions, the cyclopoids. Mouth parts in *Tisbe* and *Cyclopina* spp. are suited to grasping and holding prey rather than to straining out small organisms. *T. furcata*, along with the other harpacticoids which live in the ice, has been shown by Hicks & Coull (1983) to feed from surfaces and to be a food crusher fitted with prehensile appendages to grasp its prey. It is not well adapted, therefore, to feeding in the water column, but it is especially equipped to remove food from surfaces such as those found in the various cryptic places of the phytal, and in the tight spaces of the lower surface of the sea ice.

A plant cell concentration of 2 to 3 orders of magnitude higher in the ice than in the water column below it makes the lower few centimetres of the ice an attractive source of nourishment for herbivores able to gain access to it and feed within it (Grainger & Hsiao 1990). These abilities exist in both *Tisbe furcata* and *Cyclopina schneideri*. Ice algae of the genera *Nitzschia*, *Navicula* and *Chlamydomonas* have each been found in more than half the *T furcata* shown to have fed in the ice in Frobisher Bay (Grainger & Hsiao 1990). Species of the same 3 genera dominated the food of *Cyclopina* spp. in the same study, and they were among the most abundant food taxa living in the ice.

Tisbe furcata and *Cyclopina schneideri* in their winter movement to the ice entered a rich feeding habitat at a time when algal production in the ice was probably substantially greater than on the sea bottom or in the water column (Matheke & Horner 1974, Horner & Schrader 1982). Ice populations remained high as long as the ice algae continued abundant, that is until the decline of ice algae early in June (Fig. 4). During this time, phytoplankton numbers at 10 m and near the bottom grew, as did the rate of sedimentation to the sea bottom. Despite phytoplankton growth early in the open-water season (July), *T. furcata* and *C. schneideri* did not increase in numbers in the water column (thus differing from the major calanoid copepods of the water column, which began their summer population growth at that time). Instead, their numbers declined in the water column, as they apparently descended to near the bottom. There they appear to have reached fairly large concentrations during the period when organic sediments were falling to the bottom at their maximum rate for the year (Fig. 4).

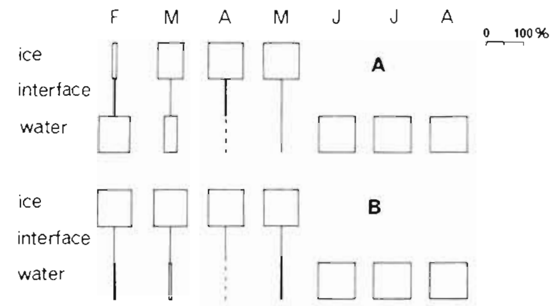

Fig. 4. *Tisbe furcata* and *Cyclopina schneideri*. Relative numbers in the ice, at the ice-water interface and in the water column between February and August in Frobisher Bay

These 2 ice-dwelling copepods show different strategies in their exploitation of the ice habitat. *Tisbe furcata* appeared to enter the ice over a prolonged period, lasting from February until at least April, during which time the ratio of water dwellers to ice occupants gradually shifted (Fig. 5). The ice-occupancy phase ended with the production of a new generation. *Cyclopina schneideri* consisted of only young copepodids in the ice in early winter. There was comparatively little migration from the water below during the rest of the winter, in the course of which development in the ice appeared to reach maturity. Different stages of development, and hence different size groups of the 2 taxa (both of which are approximately the same size in comparable stages), were predominant in the ice at any one time. Thus, although they have closely similar diets, the size range of food particles may have been partitioned by the taxa when both occurred together in the ice.

The period of copepod occupancy of the ice began as long as 5 mo before the spring-summer phytoplankton bloom in Frobisher Bay. Access to a food-rich habitat this long before phytoplankton becomes abundant in the water column represents a significant 'head start' for the seasonal growth cycle of the copepods in the ice. While water-dwelling holoplanktonic copepods are still undergoing winter decline in numbers and planktonic food is falling to its lowest concentration of the year, copepods in the ice are moving rapidly towards their maximum annual population levels. Both ice species

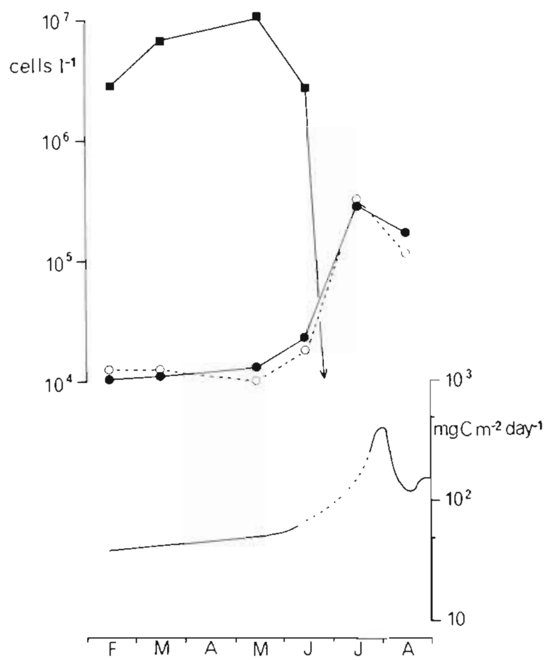

Fig. 5. Counts of ice algae (■) and of phytoplankton at 10 m (●) and 1 to 2 m above the bottom (○) as cells l^{-1}, and sedimentation rates as mg m^{-2} d^{-1} between February and August in Frobisher Bay. From data in Grainger & Hsiao (1982), Hsiao & Pinkewycz (1983), and Atkinson & Wacasey (1987)

are able to expand significantly their habitat, their numbers and their ecological importance by exploiting the highly favourable seasonal environment provided by the ice.

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