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Energy Distribution in an Arctic Coastal Macrozooplankton Community

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ABSTRACT. The proportion of caloric energy associated with each of the macrozooplankton populations at two stations in upper Frobisher Bay was determined at intervals during three consecutive open-water seasons. In the upper 50 m of the water column three species (the ctenophore *Mertensia ovum*, the chaetognath *Sagitta elegans*, and the hyperiid amphipod *Parathemisto libellula*) consistently accounted for 90% of the caloric content of the macrozooplankton community. The ctenophore dominated the samples and accounted for 60-95% of the total calories. In deeper water (>70 m) euphausiids, primarily *Thysanoessa inermis*, accounted for most of the macrozooplankton calories. Ctenophores do not appear to be major prey of arctic marine vertebrates. Thus, in Frobisher Bay surface waters a large proportion of the available energy ends up in an apparent trophic dead end of low specific caloricity. The ctenophores' precise role in this northern marine ecosystem is as yet unclear.

Key words: macrozooplankton, Frobisher Bay, caloric content, *Mertensia ovum*, ctenophores, *Sagitta elegans, Parathemisto libellula, Thysanoessa inermis*

RÉSUMÉ. La production d'énergie calorique associée à chacune des populations de macrozooplancton à deux stations dans le nord de la baie Frobisher fut déterminée à certaines intervalles au cours de trois saisons d'eau libre consécutives. Dans les 50 m supérieurs de la colonne d'eau, trois espèces (le cténophore *Mertensia ovum*, le chaetognathe *Sagitta elegans* et l'amphipode "hypérique" *Parathemisto libellula*) formaient de façon consistante 90% du contenu calorique de la communauté de macrozooplancton. A la tête des échantillons figurait le cténophore qui comptait pour entre 60 et 95% des calories totales. Dans les eaux plus profondes (>70 m), les euphausiacés, et surtout le *Thysanoessa inermis*, fournissaient la majeure partie des calories en macrozooplancton. Les cténophores ne semblent pas être des proies importantes des vertébrés marins arctiques. Une proportion élevée de l'énergie disponible dans les eaux de surface de la baie Frobisher semble donc être perdue dans la discontinuation de la chaîne alimentaire en raison de la caloricité spécifique peu élevée des proies. Le rôle précis des cténophores dans l'écosystème marin du nord demeure toujours indéterminé.

Mots clés: macrozooplancton, baie Frobisher, contenu calorique, *Mertensia ovum*, cténophores, *Sagitta elegans, Parathemisto libellula, Thysanoessa inermis*

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INTRODUCTION

In the marine environment carnivorous macrozooplankton (includes macroplankton >1 mm and megaloplankton >1 cm as defined by Baker *et al.*, 1966) are an important trophic link between herbivorous microzooplankton (<1 mm) and marine fish, birds, and mammals. Although much has been learned about the ecology of the more common macrozooplankton species in arctic waters (Dunbar, 1940, 1941, 1946, 1957, 1962; Grainger, 1971b), little quantitative information is available about their role in secondary production.

An important first step in studying energy flow in ecosystems is to identify the major energy compartments. The earlier studies, based largely on numbers of individuals in preserved collections, suggested that hyperiid amphipods and chaetognaths are the dominant carnivorous macrozooplankton in the coastal waters of southern Baffin Island. However, ctenophores and coelenterates are also abundant in this area, but because of difficulties in collection and preservation their role has never been properly evaluated. The great range in size and organic composition of macroplankton organisms precludes the use of numbers of individuals or wet or dry biomass as suitable methods for comparing energetic importance. It is more meaningful to compare the proportion of energy present in the different populations. In this study we compare the relative caloric contents of the different macrozooplankton groups during three open-water seasons at two stations in upper Frobisher Bay.

MATERIALS AND METHODS

Macrozooplankton were collected by oblique tows (Sands, 1978) from near-bottom to the surface with a 1-m ring net (1 mm mesh) at two stations (Fig. 1) in upper Frobisher Bay during the open-water seasons of 1979, 1980, and 1981. Station 5 on the eastern side of the bay is approximately 55 m deep and tows were made from 50 m. Station 51, located on the western side of the bay in a narrow trench, is more than 200 m deep and tows were made from 175 m. Temperature and salinity data for the two stations can be found in Grainger (1971a) and Percy and Fife (1985).

Four replicate oblique tows were taken at each station. The contents of one was preserved in buffered formalin (5%) for species identification and enumeration (Table 1), after first counting and removing cydippid ctenophores. The contents of the other three were transported to the laboratory in large jugs of seawater in insulated boxes. Ctenophores were removed and transported in separate containers.

The three live samples were pooled and sorted into the 11 taxonomic groups listed in Table 1. The biomass and energy content of herbivorous calanoid copepods in the samples were measured, but they are considered microzooplankton, and the results are not included in the community energy analysis. Samples were rinsed with 3% ammonium formate and drained on plankton netting over low vacuum (except for ctenophores and coelenterates which were carefully drained in a scoop), weighed, frozen, and lyophilized.

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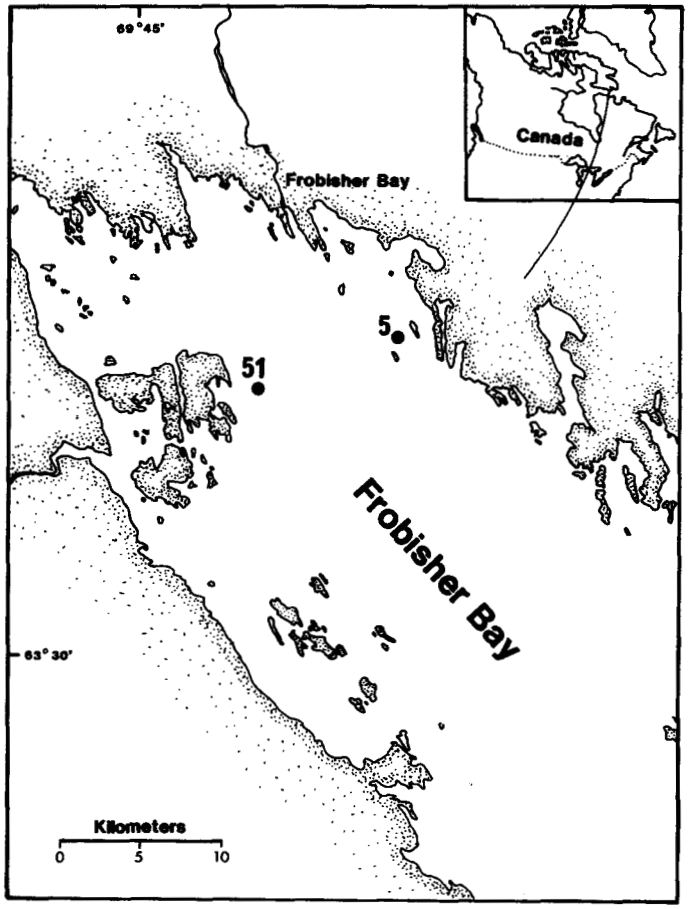

FIG. 1. Locations of stations 5 and 51 in upper Frobisher Bay.

TABLE 1. Macrozooplankton species and total numbers of individuals present in formalin-preserved oblique tow samples from stations 5 and 51

Taxonomic Group	Species	Total Number 5	51	Σ
Coelenterata	*Aeginopsis laurenti*	1	1	2
	Aglantha digitale	11	12	23
	Sarsia tubulosa	5	1	6
	Sarsia princeps	3	1	4
	Bougainvillia superciliaris	31	21	52
	Euphysa flammea	7	1	8
	Hybocodon prolifer	23	4	27
	Halitholus cirratus	3	2	5
	Halitholus pauper	7	2	9
	Halitholus sp.	2	0	2
	Catablema vesicarium	3	3	6
Ctenophora	*Mertensia ovum*	341	269	610
	Beroe cucumis	189	5	194
Polychaeta	*Autolytus* sp.	12	10	22
	unidentified	0	4	4
Pteropoda	*Spiratella helicina*	125	6	131
	Clione limacina	1	2	3
Gammaridea	*Onisimus glacialis*	7	5	12
	Onisimus litoralis	0	1	1
	Apherusa glacialis	0	5	5
	Pardalisca cuspidata	0	1	1
Hyperiidea	*Parathemisto libellula*	71	141	212
	Parathemisto abyssorum	0	1	1
	Hyperia galba	1	1	2
Euphausiacea	*Thysanoessa inermis*	3	108	111
	Thysanoessa raschii	0	16	16
	unidentified larvae	25	5	30
Decapoda	unidentified larvae	151	12	163
Chaetognatha	*Sagitta elegans*	352	402	754
	Eukrohnia hamata	7	6	13
Copelata	*Oikopleura vanhoeffeni*	2	10	12
Fish	unidentified larvae	5	0	5

For analysis the samples were brought to constant weight at 60°C and weighed. They were then finely ground and formed into pellets of 10-20 mg dry weight. Caloric content was determined with a Phillipson microbomb calorimeter (Phillipson, 1964). Benzoic acid (20-40%) was added to tissues with high ash content (ctenophores and coelenterates) to ensure complete ignition.

The biomass of each taxonomic group in a sample was determined in terms of both wet and dry weight, and the percentage contribution of each group calculated. From the dry weight and the weight-specific caloric value of each group, the caloric content was calculated and expressed as a percentage of the summed energy content of all the groups in the sample. Only the caloric data are considered here. Biomass estimates and detailed data for all collections are available in a data report (Percy and Fife, 1983). In all, 15 sets of oblique tows were obtained from station 5 and 8 sets from station 51.

RESULTS AND DISCUSSION

The weight-specific caloric contents of the principal groups of macrozooplankton present in Frobisher Bay are shown in Figure 2. Three distinct energy levels are apparent. A seasonal high-energy group with >6 calories·mg^{-1} includes euphausiids and calanoid copepods that accumulate lipids during the

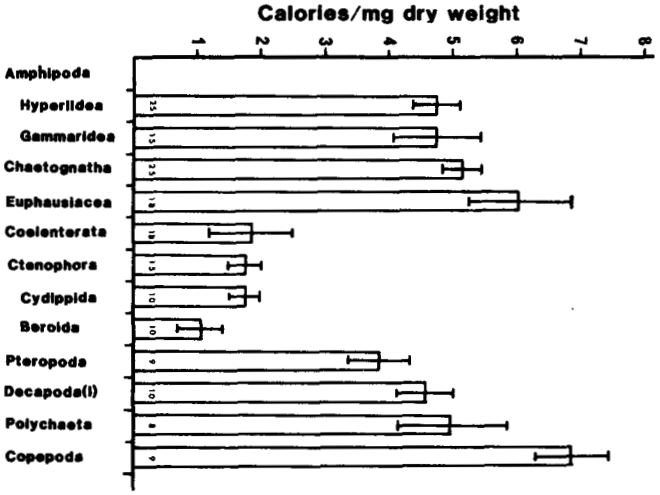

FIG. 2. Caloric content of principal macrozooplankton groups during the open-water season. Vertical lines represent standard deviations and numbers within bars indicate the number of discrete samples (each sample value is the mean of 3-5 replicate subsamples).

summer. A medium-energy group with 4-5 calories·mg^{-1} consists of amphipods, chaetognaths, pteropods, decapods, and polychaetes. A low-energy group composed of gelatinous ctenophores and coelenterates has <2 calories·mg^{-1}.

Cydippid ctenophores dominated samples from station 5 in terms of both weight and caloric content. They consistently accounted for 60-95% of the total macrozooplankton calories (Fig. 3). Chaetognaths and hyperiid amphipods were the only other groups that regularly accounted for a large part of the energy. The chaetognaths were usually dominant, but occasionally the amphipods were, particularly early in the summer. Dunbar (1941) noted that in Baffin Island coastal waters hyperiid amphipod abundance is greatest early in the open-water season. Together, these three groups consistently accounted for >90% of the macrozooplankton caloric energy at station 5 during the summer (Fig. 3).

A single exception occurred in late August 1980 when the pteropod *Spiratella* (=*Limacina*) *helicina* dominated the plankton community in the upper bay for about a week. Up to 284 animals·100 m^{-3} were present in the surface waters. Dunbar (1941) and others have also noted the sporadic and usually brief occurrence of large numbers of these organisms in eastern Arctic coastal waters, usually in late summer. Their caloric content ranges from 3.7 to 4.2 calories·mg^{-1} (Percy and Fife, 1981) and during their brief appearance they accounted for >90% of the caloric energy of the macrozooplankton community. In all other collections pteropods (predominantly *Clione limacina*) accounted for <4% of the total energy. Decapod larvae were only present early in the summer and never accounted for >10% of the energy content of the sample. Gammarid amphipods, coelenterates and polychaetes never exceeded 4%, 3%, and 1% respectively of the total energy content.

Euphausiids were rare at station 5. In contrast, at the deeper station 51 they formed a major component of the macrozooplankton community, frequently outstripping the ctenophores in energetic significance (Fig. 4). Because the euphausiids are energy-rich they may account for much of the energy content of a sample even when they constitute only a small fraction of the wet biomass. In some samples they accounted for almost 90% of the energy content but represented only 20% of the wet weight. Chaetognaths and hyperiid amphipods usually accounted for up to 28% and 21% respectively of the total energy. Gammarid amphipods tended to include more species and be more abundant at the deep station (up to 9% of the energy) than at the shallow one (<4% of the energy). Few decapod larvae were encountered at station 51.

The upper bay is well mixed tidally and the water column is relatively homogeneous (Percy and Fife, 1985). With the exception of the upper few metres the temperature does not exceed 1°C and the salinity remains above 32‰ throughout the summer. At the shallow station the temperature of the whole water column usually rises above 0°C by mid-August. However, at the deeper station subzero water is present throughout the open-water season at depths below about 70 m. Zooplankton collections obtained by horizontal net tows at discrete depths at station 51 clearly show that through the open-water season the euphausiid populations reside in the subzero water at depths >70 m during the day (Percy and Fife, 1985).

These results demonstrate that four groups of organisms account for much of the caloric energy in the macrozooplankton community in upper Frobisher Bay. Each group consists almost entirely of a single species (Table 1). The hyperiid amphipods are overwhelmingly *Parathemisto libellula*, the euphausiids predominantly *Thysanoessa inermis*, and the chaetognaths essentially all *Sagitta elegans*. The bulk of the ctenophores are *Mertensia ovum*. Another ctenophore *Beroe cucumis*, although abundant, were mostly small and contributed little (<8%) in the way of biomass and energy con-

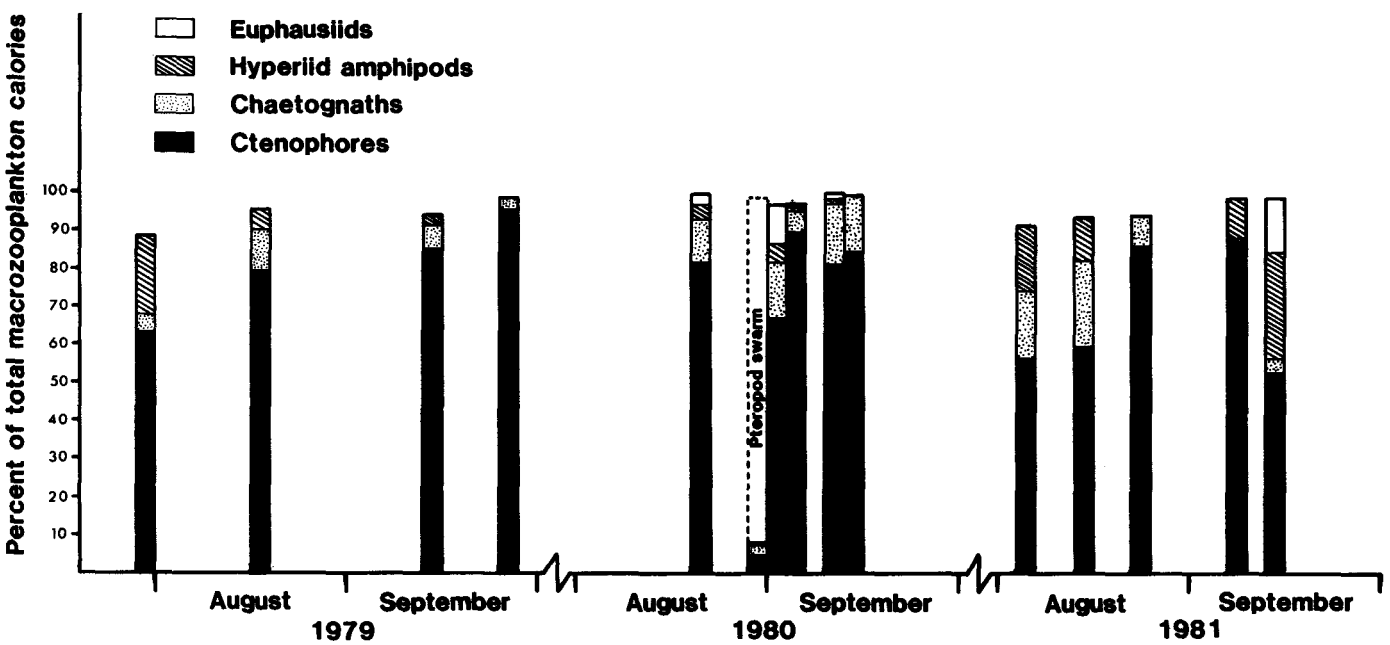

FIG. 3. Relative distribution of caloric energy among the dominant macrozooplankton groups at station 5.

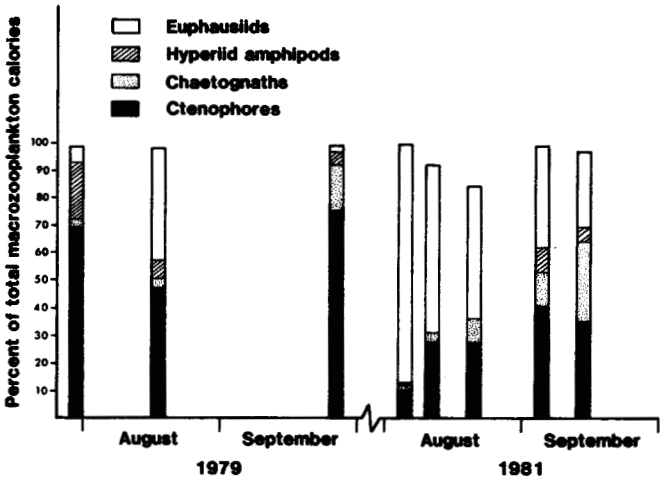

FIG. 4. Relative distribution of caloric energy among the dominant macrozooplankton groups at station 51.

tent. Estimating the proportion of available energy actually being utilized by each of these species will be a more complex undertaking, requiring comprehensive information not only about fluctuations in biomass, but also about rates of energy consumption and transformation. These questions are now being addressed in studies on the individual species.

The results also show that the ctenophore *Mertensia ovum* consistently dominates the shallow-water macrozooplankton community of Frobisher Bay. Furthermore, adult ctenophores remain abundant at station 5 throughout the winter season, while the numbers of most other macrozooplankton species decline sharply (Percy, unpublished). This ctenophore dominance may be peculiar to the bay itself and not necessarily characteristic of southern Baffin coastal waters generally. At Brevoort Island, on the open coast east of Frobisher Bay, ctenophores accounted for only a small fraction of the macrozooplankton caloric content; most was associated with mysids and hydromedusae (Percy and Fife, 1980). It is not yet clear whether the bay traps and preferentially concentrates the ctenophores in some manner or whether a localized stable population is able to flourish in spite of intense tidal flushing. Similar persistent localized aggregations of hydromedusae have been reported in Barents Sea fjords (Zelickman *et al.*, 1969). The authors attribute the phenomenon to a "mutually conditioned aggregation" involving an unspecified interaction among individuals.

The trophic role of *Mertensia ovum* in the Frobisher Bay ecosystem is unclear. There is no evidence that any of the marine vertebrate predators common to these waters consume large numbers of ctenophores. It thus appears that a large amount of energy is being channelled into a trophic dead end of very low specific energy. Reeve and Walters (1978) and others have argued that the ctenophores may play an important role in the marine ecosystem by restraining herbivorous microzooplankton populations from depleting phytoplankton populations. At the same time the ctenophores liberate nutrients that stimulate phytoplankton growth. Deason and Smayda (1982) have observed cycles in natural plankton assemblages that support this hypothesis. Reeve and Walters (1978) suggest that ctenophores thus help to retain in the water column nutrients that might otherwise be lost to the benthos as dead copepod biomass. Whether such recycling is important in the Frobisher Bay ecosystem can only be determined by further study of the rate of energy flow through the ctenophore and other populations.

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