Distribution of and Feeding by the Copepod *Pseudocalanus* Under Fast Ice During the Arctic Spring

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The arctic copepod *Pseudocalanus* can be highly aggregated in the first few centimeters under landfast ice during spring in concentrations up to 10^6 per cubic meter. Chlorophyll-derived pigments in the water, the abundance of animals, and their gut pigment index show fluctuations that may be tidally related. Short-term grazing experiments performed at −1.7°C, in which ice algae was used as food, yielded feeding rates comparable to the highest known for the genus. Arctic *Pseudocalanus* seem to feed opportunistically near the ice-water interface, either directly on the attached epontic (under ice) algae or as it erodes from the ice.

LANDFAST SEA ICE INHIBITS PRIMARY production in the water column in the Canadian Arctic Archipelago for 8 months of the year. In such environments algae appear in the sea ice at freeze-up, showing slow but measurable increases in abundance during winter, followed by rapid proliferation at the ice-water interface when light returns in early spring. Maximum concentrations equivalent to 7.2×10^7 cells or 300 μg of chlorophyll per liter have been recorded in May at the bottom of the ice in the Canadian Arctic (*1*).

In such environments many species of herbivorous zooplankton require two or more years to complete their life cycles (*2*). The common arctic form *Pseudocalanus* sp. (*3*) usually produces a single brood with reproduction taking place just before or after breakup of the ice during the vernal pulse of phytoplankton. Development is relatively rapid during open-water season with most individuals reaching copepodid stages 3 to 5 by November. Near Igloolik in Foxe Basin (69°20.5′N, 81°43.5′W), where sampling was carried out from September 1955 to September 1956, *Pseudocalanus* was the numerically dominant zooplankton organism at all seasons (*4*). From October to August the environment was covered with ice. Adult males and females were present only from April to September, while development of copepodid stages 3 to 5 apparently continued over the winter, adults appearing in April and May. From October until mid-May there was virtually no phytoplankton in the water (*5*). How then were the overwintering copepodids nourished as they developed into sexually mature adults during late winter and early spring?

Between 23 March and 6 June 1983, a series of vertical plankton samples were collected through a hole in the ice of Resolute Passage (74°40′N, 94°54′W), Northwest Territories, Canada, which showed that, of the copepods present, only *Pseudocalanus* sp. was developing. During this period the chlorophyll concentration in the water column was between 0.01 and 0.2 μg liter^{-1}, which did not appear adequate to sustain the observed growth.

In the spring of 1984 we returned to Resolute Passage with a newly designed under-ice pumping system that could be lowered through a 25-cm hole but could sample the ice-water interface away from the physical and hydraulic disturbance of the hole. It could also profile the upper 2.5 m of the water column. The pump itself was submersible and capable of delivering 30 liter min^{-1}. Instead of the expected ice-related animals and plants, we caught primarily *Pseudocalanus* (at copepodid stages 3 to 6) in concentrations up to 10^6 m^{-3}. Despite considerable variability, the largest catches of copepods were usually taken in the 10 cm immediately under the ice, but no similar augmentation of plant pigments was found.

We also collected water and animals just under the ice on several occasions at 3-hour intervals over a 24-hour period. Sub-ice concentrations of plant pigments (Fig. 1A) and the abundance of zooplankton (Fig. 1B) seemed to undergo a pattern of change, but with somewhat different periodicity. The gut chlorophyll index (*6*) also suggests some pattern in the feeding behavior of the zooplankton (Fig. 1C). We have constructed a model of current speed and direction (Fig. 1D) and tidal range (Fig. 1E) based on observations made near our station at the same season in 1982 (*7*). At this season the tides are rather asymmetrical so that slack water occurs about 2 hours after high tide; similarly, the maximum westerly current, here about 40 cm sec^{-1}, occurs about 2 hours after low tide. Maximum chlorophyll and total pigment concentrations occur near high tide after a period of strong currents, while minimum pigment is found after a period of weak currents (Fig. 1, A and D) (*8*). If the behavior of hungry zooplankton dictates that they migrate toward the ice and their presumed food supply at every opportunity, their concentration in the upper water might be expected to correspond closely with slack water, which seems to have been the case on 20 May at about 1900 and on 21 May at 0800. A third peak, however, on 21 May, at about 0130, did not fit such a pattern (Fig. 1, B and D). On the other hand, gut pigment concentration (Fig. 1C) follows the total pigment and chlorophyll concentrations in the water (Fig. 1A) better than the zooplankton abundance near the ice (Fig. 1B). At the same time, fluctuations in phaeopigments are about 180° out of phase. We have found that the bottom few

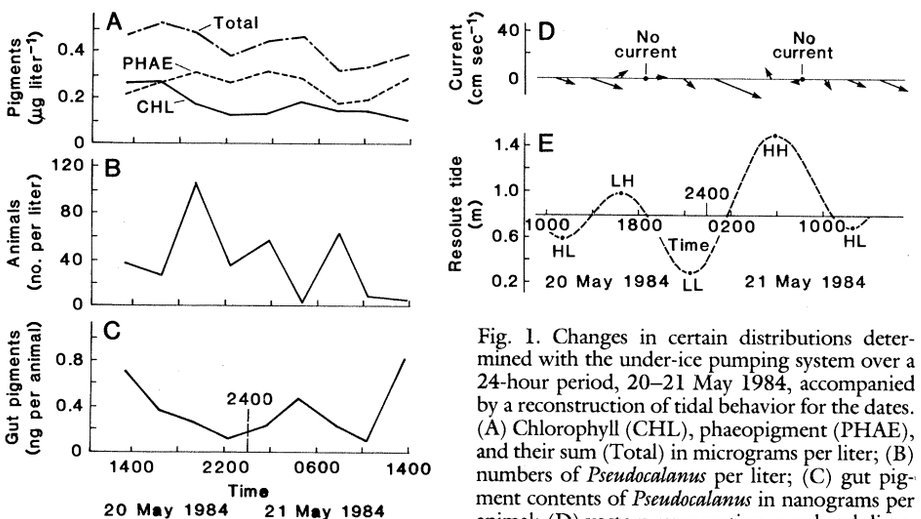

Fig. 1. Changes in certain distributions determined with the under-ice pumping system over a 24-hour period, 20–21 May 1984, accompanied by a reconstruction of tidal behavior for the dates. (A) Chlorophyll (CHL), phaeopigment (PHAE), and their sum (Total) in micrograms per liter; (B) numbers of *Pseudocalanus* per liter; (C) gut pigment contents of *Pseudocalanus* in nanograms per animal; (D) vectors representing speed and direction of current, in which length is proportional to the ordinate scale that extends from south (0) to north (40); (E) times of high and low tide with the tidal range in meters. Abbreviations for the tides are as follows: HL, higher low; LH, lower high; LL, lower low; HH, higher high.

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centimeters of an ice core, with its epontic algae, contain only small amounts of phaeopigments, in agreement with other observations in the Canadian Arctic (*9*). Most chlorophyll is converted to phaeophorbide during passage through a copepod's gut (*10*). Therefore, we believe that the phaeopigment concentrations in the water column near the ice probably reflect fecal production by grazers during heavy feeding, which here tends to be greatest between 2000 and 0500, the period of minimum light intensity. Ambient light and food concentration have recently been shown to affect the in situ feeding behavior of arctic *Calanus* species (*11*).

We are uncertain whether *Pseudocalanus* can actually remove cells from the under-ice surface, but they grazed on ice algae melted from the interface with remarkable facility. In a preliminary experiment (*12*), we used an initial concentration of 3.9 μg of chlorophyll per liter of ice algae and found that *Pseudocalanus* incorporated pigment at a constant rate for 1.6 hours, reaching a concentration of 1.63 ± 0.31 ng of gut pigment per animal. In another experiment (experiment 1, Table 1), filtration rates based on the amount of chlorophyll consumed were between 0.66 and 1.09 ml per animal per hour, while parallel cell count experiments yielded rates of 2.50 to 4.64. Perhaps a significant fraction of pigment was contained in forms too small to be identified in preserved samples, or cells were destroyed but their contents leached into the medium without being ingested; either could contribute to such a discrepancy. We also examined the effect of increasing concentrations of ice algae, over a range from 2.15 (experiment 2, Table 1) to about 35 μg of pigment per liter, on the feeding of *Pseudocalanus*. The results showed that the gut pigment index saturated at about 9 μg of chlorophyll per liter in about 1.3 hours, although we were unable to determine a filtration rate in that period of time at the higher pigment concentrations. At saturation, gut pigment concentration was about 3 ng per animal.

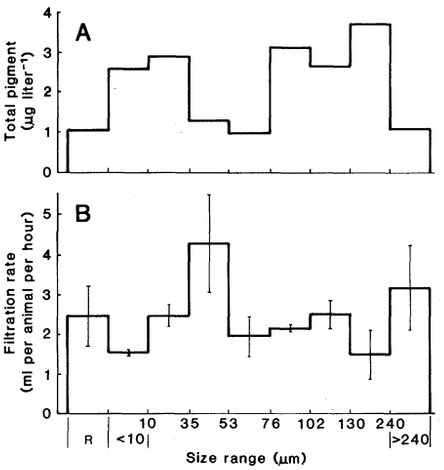

Fig. 2. (A) Experimental concentrations of different sizes (in micrograms) of sea-ice algae in total chlorophyll-derived pigment per liter and in untreated seawater, R. (B) Filtration rates in milliliters swept clear per animal per hour for *Pseudocalanus* feeding on different size fractions of melted sea-ice algae or on untreated seawater from just beneath the ice. Error bars represent 1 SD.

In a final experiment (experiment 3, Table 1) we fractionated melted ice algae into eight categories of sizes with Nitex screens and compared each with ambient seawater as a nutritional source for *Pseudocalanus*. As we had no means of determining pigment concentration in the field before setting up the experiment, the actual concentration given the copepods varied by a factor of nearly 4 (Fig. 2A). However, we could not demonstrate any statistical trends between either the size of particles or their concentration and the rate of filtration (Fig. 2B). The diversity of sea-ice algal communities is often great, but a number of important species form colonies containing variable numbers of cells. Hence no striking differences existed in the species composition of the several sizes of fractions tested, but apparently the entire assemblage was available to *Pseudocalanus*.

To better understand the performance of these arctic populations, we compared the highest filtration rates for each of our experiments with the highest rates for *Pseudocalanus* from the literature (Table 1). On a weight-specific basis, the fastest grazers (from Fig. 2) at −1.7°C filtered 20.9 liters per milligram (dry weight) per day compared with an average of 20.76 at 12.5°C for another species of *Pseudocalanus* feeding on low concentrations of cultured *Thalassiosira rotula* (*13*). Ice algae apparently can provide several times the largest ration afforded by either cultured or natural algal assemblages (Table 1).

The principal difference between our experiments and others in Table 1 is their duration. If arctic *Pseudocalanus* really fed at rates we observed for 1 to 2 hours over the full 24-hour period, their growth rates should also have been high, which was not the case. Therefore we believe that these *Pseudocalanus* are adapted for opportunistic feeding on or near the under-ice surface. When ice algae are added to filtered seawater containing unfed *Pseudocalanus*, green pigment is observable within 1 minute in the gut, which becomes virtually full within 5 minutes. Near Resolute, tidal currents up to 50 cm sec^{-1} occur (*7*); this speed is 100 times the swimming speed of feeding *Pseudocalanus* (*14*). Although the copepod should be able to feed most successfully at slack water, providing food were available, strong currents erode the maximum amount of ice algae (Fig. 1, A and D). Hence, feeding conditions probably become opti-

Table 1. Comparison of near maximum filtration rates for *Pseudocalanus* from Resolute Passage and their estimated ration, with some earlier measurements of high feeding rates for the genus. Abbreviations: *n*, number of replications; C, carbon; Chl, chlorophyll.

Food	C or Chl concentration (μg $liter^{-1}$)	Temperature (°C)	Experiment length (hour)	Filtration rate		Estimated ration (% body weight per day)	Source
				Milliliters per animal per day ± 1 SD	Milliliters per milligram of dry weight per day ± 1 SD		
Skeletonema costatum plus small flagellates	760 (C)	5–7				45*	(*15*)
Mostly dinoflagellates	1.83 (Chl)	12–15	16–24	≈25	≈1,185	23	(*16*)
Thalassiosira rotula	25 (C)	12.5	24	207.6	20,760†	63	(*13*)
Ice algae (experiment 1)	8.14 (Chl)	−1.7	1–1.2	19.5 ± 4.1 $n = 5$	2,628 ± 1,000	148‡	This report
Ice algae (experiment 2)	2.15 (Chl)	−1.7	1.1	42.2 ± 11.8 $n = 3$	10,830 ± 3,004	227‡	This report
Ice algae (experiment 3)	1.25 (Chl)	−1.7	1.6	103.0 ± 29.5 $n = 3$	15,835 ± 4,540	141‡	This report

*Some *Oithona* sp. were also present in this experiment. †Based on ash-free dry weight. ‡Assuming a carbon:chlorophyll ratio of 50 and that carbon is 45% of dry weight for *Pseudocalanus*.

mal, perhaps for only a brief period each tidal cycle, as currents are decreasing on the approach to slack water. To cope, these *Pseudocalanus* have acquired the capacity to gorge whenever food is available.

How often the individual *Pseudocalanus* is in a favorable position to feed must still be determined. Although zooplankton concentrations near the ice may be large, the same species occurs throughout the water column. Whether animals at depth, through daily, seasonal, or ontogenetic migration, or through strong tidal mixing, can reach the vicinity of the epontic primary production is problematic. However, this potential source of nutrition can apparently extend the period of growth for some members of the calanoid copepod community.

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12. Animals were dipped with a beaker or plastic bucket from a sampling hole cut in the ice and were usually not concentrated further. Polycarbonate 500- or 1000-ml bottles containing from 100 to 1400 animals and an appropriate amount of well-mixed ice algae were used in experiments, and replicate bottles without animals served as controls. The bottles were incubated at ambient temperature (≈−1.7°C) for 5 minutes to 1.75 hours. Changes in chlorophyll, phaeopigment, and, in a few cases, cell concentration were determined for each experimental and control bottle. Experimental animals were preserved at the end for counting and determination of stage distribution and dry weight.
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17. We thank P. Hunter, C. Fraser, G. Enright, B. Milbury, and P. Lawrence, who participated in the analysis of data reported here, and G. Harding and E. Head who read and commented on the text. This work was facilitated by the cooperation of the Polar Continental Shelf Project (Energy Mines and Resources, Canada).

26 November 1985; accepted 21 March 1986

Shape Analysis of the Histone Octamer in Solution

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The conformation of the histone octamer is shown to depend upon the specific salt used to solubilize it. In 2*M* sodium chloride the octamer is similar in size and shape to the histone component of crystallized core nucleosomes. In contrast, in 3.5*M* ammonium sulfate the octamer is elongated, resembling an ellipsoid with approximate dimensions of 114 by 62 by 62 angstroms. These results indicate that the elongated conformation seen in the 3.3 angstroms electron density map of the histone octamer crystallized in ammonium sulfate is due to the particular salt conditions used.

THE FUNDAMENTAL SIZE, SHAPE, and DNA superhelical parameters of core nucleosomes, deduced from x-ray crystallographic studies (*1, 2*), are the cornerstones of virtually all theories concerning the manner in which DNA is packaged into chromatin. These attributes also provide the basis for studying, at the nucleosomal level, regulatory mechanisms whereby DNA accessibility is controlled during transcription and other functions.

Recently, a 3.3 Å resolution map of the histone octamer was reported by Burlingame *et al.* (*3*). The histone octamer structure they presented differed surprisingly in shape from that of the histone octamer in core nucleosomes as determined by the crystallographic studies, by neutron scattering (*4, 5*), and by electron microscopy (*6, 7*). Burlingame *et al.* suggested the alternative structure for the nucleosome based upon their placement of DNA, by inspection, on the octamer structure. The result was a particle significantly larger than a core nucleosome, and so different with respect to DNA superhelical parameters as to challenge many preceding ideas about chromatin structure.

Burlingame *et al.* addressed the discrepancy between the two types of structures by proposing that core nucleosomes are artifacts generated by removing H1 and linker DNA from chromatin, and concluded that crystallographic studies of core particles generate maps of structures that do not represent the native chromatin subunit. Klug *et al.* (*8*) raised the possibility that the crystallographic methods used in (*3*) were incorrect, and therefore the octamer described in (*3*) does not exist in solution. Uberbacher and Bunick suggested that the extended configuration of the crystallized octamer is attributable to the absence of DNA and the high concentration of ammonium sulfate in which the histones were crystallized (*9*).

Since small-angle neutron scattering (SANS) affords the opportunity to make direct measurements of the size and shape of biomolecules as they exist in solution, we performed a SANS study of the histone octamer in conditions similar to those employed by Burlingame *et al.* in order to answer three questions: Does the extended octamer exist in solution? If so, does its conformation reflect a salt effect? Finally, if it exists in solution, what is its relation to nucleosomes and to chromatosomes (nucleosomes retaining H1 and part of the linker DNA)?

Histone octamer, prepared as in (*10*), was examined by SANS in two sets of conditions: first, in 2*M* NaCl at *p*H 7.5; second, in 3.5*M* ammonium sulfate through a *p*H range of 5.8 to 7.5, a salt condition very similar to that used to crystallize the histone octamer (*3*). Octamer samples were prepared in H_2O to avoid any question that D_2O might affect conformation.

Neutron scattering measurements were performed on the 30-m small-angle neutron scattering instrument at the National Center for Small-Angle Scattering Research, Oak Ridge National Laboratory. The scattered neutrons were detected by a two-dimensional position-sensitive ^3He detector with 1-cm^2 elements (64 by 64). The sample detector distance was set to 3.0 m, which gave a usable K (scattering vector) range of from 0.012 to 0.15 $Å^{-1}$. All samples were maintained at 4°C throughout preparation and data collection. At least four independent measurements were made on each type of sample and buffer. A concentration series for each type of sample demonstrated the absence of concentration-dependent effects, such as aggregation or interparticle interference. This finding was further confirmed by the fact that different samples showed consistent ratios of forward scattering [$I(0)$] to concentration (c), and produced Guinier plots with no deviation from linearity in the

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