Feeding, Respiration and Excretion of the Copepod *Calanus hyperboreus* from Baffin Bay, Including Waters Contaminated by Oil Seeps EDWARD S. GILFILLAN,¹ JOHN H. VANDERMEULEN² and SHERRY HANSON¹

(Received 26 March 1984; accepted in revised form 17 July 1985)

ABSTRACT. Metabolic processes in eastern arctic copepods Calanus hyperboreus were analyzed during the post-bloom period (August-September). Mixed adult and subadult copepods were collected from 12 stations in Baffin Bay (Davis Strait to Lancaster Sound) by trawling from 0-300 m. Measurements were made of clearance rate, 0_2 -consumption and NH₃ excretion. The cruise track included 6 stations in oil-seep contaminated waters of Scott Inlet and Buchan Gulf. Physiological parameters for populations of *C. hyperboreus* from the latter stations were compared with those from non-seep stations.

Mean O_2 consumption rates (0.309-0.907 µl O_2 ·mg dry wt⁻¹·h⁻¹) for all stations were similar to those described for Antarctic calanoid species but were higher than reported from more northern arctic waters. Mean ammonia excretion rates (0.023-0.071 µg N·mg dry wt⁻¹·h⁻¹) were somewhat lower than reported for comparable Antarctic species and were similar to values from other eastern arctic studies. O:N ratios for 11 of the 12 stations occupied ranged between 8.4 and 22.1, indicative of protein-based metabolism. The single exception was a High Arctic station with O:N ratio 43.6. Clearance rates were low to nonexistent for all stations.

Most of the non-feeding values came from the Scott Inlet-Buchan Gulf region of western Baffin Bay. At those stations in this region a strong negative correlation (P < .01) exists between clearance rate and hydrocarbon contamination. This suggests that in the oil-seep region of Baffin Bay feeding may be suppressed in *Calanus hyperboreus* by low concentrations of petroleum hydrocarbons derived from sub-sea seepage.

Key words: zooplankton, Calanus hyperboreus, Arctic, metabolism, oil seep, petroleum, hydrocarbons, oil pollution

RÉSUMÉ. On a analysé les processus métaboliques du copépode *Calanus hyperboreus* de l'est de l'Arctique, durant la période ultérieure à la phase de prolifération du phytoplancton (août-septembre). On a recueilli dans douze stations de la baie de Baffin (du détroit de Davis au détroit de Lancaster) des populations mixtes de copépodes adultes et sub-adultes, en pêchant au chalut entre 0 et 300 m de profondeur. On a mesuré les taux de clairance, de consommation de O_2 et d'excrétion de NH_3 . Le trajet du navire d'exploration passait par six stations situées dans les eaux de l'inlet Scott et du golfe Buchan, contaminées par des suitements de pétrole. On a comparé les paramètres physiologiques des populations de *C. hyperboreus* provenant des stations susmentionnées, à ceux de stations non contaminées.

Les taux moyens de consommation de O_2 (0,309-0,907 μ l $O_2 \cdot mg$ poids sec⁻¹ · h⁻¹) dans toutes les stations étaient semblables à ceux cités à propos d'espèces calanoïdes de l'Antarctique, mais étaient plus élevés que ceux relevés chez des espèces des eaux arctiques plus septentrionales.

Les taux moyens d'excrétion de l'ammoniac $(0,023-0,071 \ \mu g \ N \cdot mg \cdot poids \ sec^{-1} \cdot h^{-1})$ étaient légèrement plus bas que relevés chez des espèces comparables de l'Antarctique, et semblables aux valeurs données par d'autres études sur l'est de l'Arctique. Les rapports O:N de 11 des 12 stations occupées se situaient entre 8,4 et 22,1 ce qui indiquait un métabolisme protidique. La seule exception était une station du Haut-Arctique où l'on a noté un rapport O:N de 43,6. Les taux de clairance étaient faibles à nuls dans toutes les stations.

La plupart des valeurs sur l'absence d'alimentation provenaient de la région de l'inlet Scott et du golfe Buchan, dans l'ouest de la baie de Baffin. Dans toutes les stations de cette région, il existe une forte corrélation négative (P<0,01) entre le taux de clairance et le taux de contamination par les hydrocarbures. Ceci suggère que dans la région de la baie de Baffin où ont lieu des suitements de pétrole, l'alimentation de *Calanus hyperboreus* peut être arrêtée par la présence de faibles concentrations d'hydrocarbures provenant de suitements sous-marins de pétrole.

Mots clés: zooplancton, Calanus hyperboreus, Arctique, métabolisme, suitements de pétrole, pétrole, hydrocarbures, pollution par les hydrocarbures

INTRODUCTION

Calanus hyperboreus is a dominant member of northern marine zooplankton assemblages (Buchanan and Sekerak, 1982) and is found throughout the central (Dawson, 1978) and eastern Canadian Arctic (Huntley *et al.*, 1983). It is also of particular interest because it apparently spends most of the year in deep, cold waters as a result of seasonal vertical migration and well away from its phytoplankton food source (Conover, 1962; Widborg, 1940; Ostvedt, 1955; Ussing, 1938; Rudjakov, 1983; Dawson, 1978). Thus, during the spring phytoplankton blooms, the animals are found in the surface layers (Buchanan and Sekerak, 1982; Huntley *et al.*, 1983; Huntley, 1981). During the remainder of the year the animals reportedly survive on stored fats at a reduced metabolic level (Conover, 1968).

However, except for a single study by Lee (1974) of lipid buildup and decrease in *C. hyperboreus* from the western Arctic, very little was known of the metabolism of this or other arctic copepods. Two recent studies of grazing, respiration and nitrogen excretion (Conover and Cota, 1985) and urea-NH4 requirements (Harrison *et al.*, 1985) have since provided the first data from the High Arctic. In this paper we present data on the feeding (clearance), respiration and nitrogen excretion in *C.* hyperboreus collected in late summer (August-September) at a number of stations from Baffin Bay between Davis Strait and Lancaster Sound. The cruise track also included a number of stations in Scott Inlet and Buchan Gulf, along the western side of Baffin Bay. These waters are influenced by a chronic input of petroleum hydrocarbons from sub-sea oil seeps and, on the basis of a large number of water column samples, have been shown to have anomalously high hydrocarbon concentrations (Levy, 1979, 1981; MacLean *et al.*, 1981).

MATERIALS AND METHODS

Field Collection

Animals were collected by oblique plankton tows (0-300 m) at stations in Davis Strait on cruise 78-026 (25 August - 17 September 1978) (Fig. 1). The cruise track crossed areas of western Davis Strait known to have elevated levels of hydrocarbons in the surface film (Levy, 1978). All possible care was taken to minimize damage to the animals. The cod end of the plankton net contained no vents; animals reaching the cod end

¹Marine Research Laboratory, Bowdoin College, Brunswick, Maine 04011, U.S.A.

²Marine Ecology Laboratory, Department of Fisheries and Oceans, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada B2Y 4A2 ©The Arctic Institute of North America



FIG. 1. Cruise track and location of sampling stations in Baffin Bay for C. *hyperboreus* plankton tows. Inset figures show petroleum hydrocarbon concentration profiles for known seep areas (after Levy, 1979).

were in relatively non-turbulent water. As soon as the net was recovered the contents of the cod end were emptied and diluted into 8-10 l of surface seawater. The animals were then maintained at ambient seawater temperature. Experimental animals were selected with a stainless steel spoon. All physiological determinations were made on adult or stage V C. hyperboreus, averaging 10 mg dry weight per animal. Measurements were made aboard ship within 12 h of capture. Feeding, respiration and N-excretion measurements were made on copepods from the same collection for each station occupied.

Experimental Methodology

Clearance rates, i.e., volume of water swept clear of particles per hour, were determined using a modification of the methods of Gilfillan *et al.* (1977). A glass 1 l bottle was filled with glass fiber (GF-C) filtered seawater. To this an aliquot of *Dunaliella tertiolecta* culture grown in F2 medium (Guillard and Ryther, 1962) prepared with ambient seawater was added so as to yield the approximate density of cells as found in the ambient seawater as determined using a Coulter ZBI particle counter (*ca.* 1×10^3 cells·ml⁻¹). *D. tertiolecta* was used because it was readily cultured in the shipboard laboratory and because cells of 5 to 10 µm have been described as typically the most abundant in these waters (Huntley, 1981).

At the beginning of each experiment five subsamples of water were taken from each bottle to establish initial food levels. The number of food-size particles was determined for each subsample (mean of five replicate counts) using a Coulter Counter, as described above. The bottles were then stoppered and incubated for 12 h in the dark, rotating (0.5 rpm) on a wheel in a 981 water bath to prevent sedimentation of either food or copepods. The water bath was maintained within 0.5°C of ambient water temperatures. Following incubation five subsamples of water were taken for particle determination from each bottle; the copepods were freeze-dried and weighed. Clearance rates were determined in triplicate. Control bottles containing only seawater and food were incubated concurrently.

The volume swept clear of particles was calculated from the following equation, $V_f = V(Ln I - Ln F) / T$, where $V_f =$ volume filtered, V = bottle volume, I = initial particle count, F = final particle count, and T = duration of incubation. Results were expressed as volume swept clear mg dry wt⁻¹·h⁻¹.

Oxygen consumption was determined using a mechanically refrigerated differential respirometer (Gilson) in triplicate. Five copepods were placed in 30 ml glass fiber filtered seawater in each flask. Carbon dioxide was absorbed by a concentrated KOH solution in a side arm. After an initial 1 h equilibration, readings were taken every 30 min for 150 min. Oxygen consumption was determined by regressing change in volume against time. The resulting value was divided by the dry weight of the copepods to yield respiration rate as $\mu l O_2 \cdot mg^{-1} \cdot h^{-1}$.

Ammonia excretion was determined using an Orion specific ion electrode by the method of Garside *et al.* (1977). The method has a detection limit of 0.2 μ M of NH₃, a precision of \pm 0.1 μ M, and is not affected by salt. At each station five groups of ten animals were incubated in 1 l of glass fiber filtered seawater in glass-stoppered 1 l bottles for 12 h. Ammonia concentrations were measured both prior to and following incubation. Results are expressed as μ g N·mg⁻¹·h⁻¹. Control bottles containing only seawater were incubated concurrently.

O:N atomic ratios were calculated by multiplying ratios of O_2 consumption to N-excretion by $1.428 \times {}^{14}\!/_{16}$, where 1.428 is the density of O_2 at 1 atmosphere and 1°C, and the ratio ${}^{14}\!/_{16}$ corrects for differing atomic weights of O_2 and N_2 .

Silicate, phosphate and nitrate concentrations for the stations sampled are reported elsewhere (Irwin *et al.*, 1980; Cruise report 78-026).

An index of petroleum hydrocarbon contamination of the water column, "%-hydrocarbon-anomalies" (Levy, 1979), was calculated from hydrocarbon concentration measurements made concurrently with our physiological measurements (Cruise report 78-026; Levy, 1979). The index represents the percentage of water samples per station from various depths with hydrocarbon concentrations greater than the established background level for Baffin Bay (mean $0.46 \,\mu g \cdot 1^{-1}$, 99.9% confidence limits $0.41-0.52 \,\mu g \cdot 1^{-1}$; Levy, 1979, 1981) as determined analytically (Levy, 1977, 1978, 1979).

All statistical analyses were performed using the Regress II statistical program (Human Systems Dynamics, Northridge LA, 91324).

RESULTS

Clearance rates were generally low for all stations (Table 1), with negligible to no clearance observed at six of the twelve stations occupied. Highest mean clearance rate was measured in Lancaster Sound (0.18 ml·mg dry wt⁻¹·h⁻¹) at station 87. The stations with significant clearance rates, above 0.08 ml·mg dry wt⁻¹·h⁻¹, were near Cape Raper in Davis Strait, Lancaster Sound and the North Water. Stations with zero to negligible clearance rates all were from the Scott Inlet/Buchan Gulf stations.

Oxygen consumption (Table 1) ranged from 0.31 to 0.91 μ l O₂·mg dry wt⁻¹·h⁻¹. There were no obvious patterns of difference in respiration rate between stations. The same range of values was observed at the Scott Inlet-Buchan Gulf stations as at either Cape Raper or the northernmost stations.

Station	Surface temperature (°C)	Feeding rate ¹	Respiration rate ²	Ammonia excretion ³	O:N atomic ratio	% HC anomaly
13	2.0	.0878	.4916	.0526	11.70	+ 80
		(.0851)	(.4758)	(.0279)		
284	1.0	.0000.	.4755	.0708	8.41	+ 56
		(.0000)	(.1123)	(.0106)		
33	1.0	.0749	.5187	.0294	22.07	+ 7
		(.0999)	(.2264)	(.0043)		
40	2.0	.0000	.7906	.0494	20.03	+ 45
		(.0000)	(.0387)	(.0042)		
45	1.0	.0009	.3482	.0440	9.90	+ 22
		(.0012)	(.0583)	(.0217)		
52	1.0	.0000	.3847	.0277	17.38	+ 47
		(.0000)	(.1269)	(.0055)		
60	1.0	.0103	.3873	.0498	9.73	+ 20
		(.0178)	(.3573)	(.0167)		
70	1.0	.0290	.9067	.0260	43.63	+ 36
		(.0251)	(.1090)	(.0073)		
83	1.0	.0809	.3376	.0225	18.09	+ 9
		(.0244)	(.3383)	(.0069)		
87	1.0	.1801	.4804	.0626	9.60	+ 29
		(.1460)	(.0485)	(.0112)		
91	1.0	.1174	.3093	.0237	16.33	+ 92
		(.0550)	(.2688)	(.0070)		
94	1.0	.0018	.4133	.0480	10.77	no
		(.0040)	(.1189)	(.0165)	·	data

TABLE 1. Feeding, respiration and ammonia excretion data for *Calanus hyperboreus* from Davis Strait-Baffin Bay, July-August 1978; data given are arithmetic means (\pm standard deviation)

¹ ml·mg dry wt⁻¹·h⁻¹

² μ l O₂·mg dry wt⁻¹·h⁻¹

³ μg N·mg dry wt⁻¹·h⁻¹

⁴ Stations 28-70 constitute the Scott Inlet/Buchan Gulf oil seep region.

Ammonia excretion (Table 1) ranged from 0.023 to 0.070 μ g N·mg dry wt⁻¹·h⁻¹. There was no discernible difference in nitrogen excretion rates at stations from the Scott Inlet-Buchan Gulf area as compared with other stations in Baffin Bay. Mean values ranged between 0.026 and 0.07 μ g N·mg dry wt⁻¹·h⁻¹ for the former, and from 0.024 to 0.063 μ g N·mg dry wt⁻¹·h⁻¹ for the latter.

The calculated O:N ratios were quite variable. Most values were near or less than 20 (8.4 - 22.1). The single exception was station 70 near Pond Inlet, where an O:N ratio of 43.6 was obtained.

Regression analysis of the metabolic parameters measured showed no significant correlation between %-hydrocarbonanomaly and either clearance, ammonia excretion or respiration when the data from all stations were used (Table 2). However, a highly significant negative correlation (P<.01) was found between clearance rate and %-hydrocarbon-anomaly in the data from the Scott Inlet-Buchan Gulf area. The best fit to the data was obtained using an exponential model, Clearance = 0.947 $e^{(-0.253HC)}$ where HC is %-hydrocarbon-anomaly with coeffi-

TABLE 2. Correlation between metabolism (dependent variable) in C. hyperboreus (clearance, respiration, NH_3 -excretion) and excess hydrocarbon concentrations (independent variable) in Davis Strait and Baffin Bay, summer 1978

Dependent variable	Coefficient of determination	F-value
respiration (O ₂ consumption)	.05	.264
clearance, all stations	.018	.163
clearance, seep stations only	.737	14.005
NH ₃ -excretion	.114	.647
<u>O:N</u>	.005	.028

cient of determination of 0.737 and coefficient of correlation of 0.850 (Fig. 2).



FIG. 2. Relationship between clearance rate for *C. hyperboreus* from Baffin Bay and petroleum hydrocarbon concentrations in the water column (%-hydrocarbon-anomalies). Curve is regression line for stations occupied in the seep zone (solid circles). Open circles denote stations outside of seep zone.

DISCUSSION

The observations detailed above are interesting for two reasons. They contribute to the very few measurements that have been made on a dominant arctic copepod for the months of August and September. But these data also suggest that feeding in this species may be suppressed by very low concentrations of petroleum hydrocarbons, less than 10 μ g·l⁻¹.

TABLE 3. Reported values for N-excretion, respiration and feeding rates for polar copepods

	Season	Temperature	Rate*	Reference
N-EXCRETION				
Antarctic				
Calanus tonsus	austral summer	$10 \pm 2C$	4.6-6.1 μ g-at·g wet wt ⁻¹ ·h ⁻¹	(1,2)
Mixed copepods	Aug/Sept	$-1 \pm 2C$	0.8-1.8 μ g-at·g wet wt ⁻¹ ·h ⁻¹	(2)
Calanus spp.	Jan		$0.1-0.11 \ \mu g N \cdot mg dry \ wt^{-1} \cdot h^{-1}$	(3)
Arctic				
C. hyperboreus	Aug/Sept	1C	0.023-0.071 µgN·mg dry wt ⁻¹ ·h ⁻¹	(this study)
C. hyperboreus	July/Aug	0-1C	0.4-1.8 μ gN·mg dry wt ⁻¹ ·d ⁻¹	(4)
C. hyperboreus	summer	0-1C	$1.30 \pm 0.67 \ \mu$ g-at N·mg dry wt ⁻¹ ·d ⁻¹	(5)
C. finmarchicus & C. glacialis	summer	0-1C	$1.11 \pm 0.37 \ \mu g$ -at N·mg dry wt ⁻¹ ·d ⁻¹	(5)
C. glacialis	July/Aug	0-1C	$1.112 \pm 0.386 \ \mu g N \cdot mg \ dry \ wt^{-1} \cdot d^{-1}$	(4)
Metridium longa	July/Aug	0-1C	$0.618 \pm 0.317 \ \mu g N \cdot mg dry \ wt^{-1} \cdot d^{-1}$	(4)
Metridia sp.	summer	0-1C	$0.62 \pm 0.35 \ \mu$ g-at N·mg dry wt ⁻¹ ·d ⁻¹	(5)
OXYGEN CONSUMPTION				
Antarctic				
Rhincalanus gigas	austral winter	-1.8C	$0.110-0.140 \ \mu lO_2 \cdot mg \ wet \ wt^{-1} \cdot h^{-1}$	(6)
C. tonsus	austral summer	10 + 2C	$0.430-1.080 \ \mu lO_2 \cdot mg \ wet \ wt^{-1} \cdot h^{-1}$	(2)
Mixed copepods	austral summer		$0.120-0.240 \ \mu lO_2 \cdot mg$ wet wt ⁻¹ · h ⁻¹	(2)
Eastern Arctic				
C. hyperboreus	Aug/Sept	-1C	0.309-1.877 µlO ₂ ·mg dry wt ⁻¹ ·h ⁻¹	(this study)
C. hyperboreus	July/Aug	0-1C	5-30 μ lO ₂ ·mg dry wt ⁻¹ ·d ⁻¹	(4)
C. glacialis	July/Aug	0-1C	9-40 μ lO ₂ ·mg dry wt ⁻¹ ·d ⁻¹	(4)
M. longa	July/Aug	0-1C	15-35 μ lO ₂ ·mg dry wt ⁻¹ ·d ⁻¹	(4)
Boreal				
copepods	Jun/Aug	5-10C	$0.13 \cdot 1.19 \ \mu lO_2 \cdot mg$ wet wt ⁻¹ · h ⁻¹	(7)
C. hyperboreus	July/Aug		$0.200-0.990 \mu lO_2 \cdot mg dry wt^{-1} \cdot h^{-1}$	(4)
C. hyperboreus			5-20 μ lO ₂ mg dry wt ⁻¹ d ⁻¹	(8)
mixed copepods	Jan	-1C	$0.8-1.1 \ \mu lO_2 \cdot mg \ dry \ wt^{-1} \cdot h^{-1}$	(3)
O:N				
Antarctic				
Calanus		$-1 \pm 2C$	11-20	(2)
copepods	Jan		9.2-15.2	(3)
calanoid copepods	Dec/Jan		15 ± 3	(9)
Subantarctic				
Calanus		10C	8-16	(2)
Eastern Arctic				
C. hyperboreus	Aug/Sept	1C	8.41-43.63	(this study)
C. hyperboreus	July/Aug	0-1C	13.4-36.9	(4)
C. glacialis	July/Aug	0-1C	28.5 ± 16.6	(4)
M. longa	July/Aug	0-1C	139.0 ± 134.0	(4)
Boreal	g			
C. hyperboreus			16.4-34.6	(9)
FEEDING/CLEARANCE RATE				
C. hyperboreus (young stage)	Jul/Aug		23.56, 24.60 ml·mg dry wt ⁻¹ ·d ⁻¹	(10,4)
C. glacialis (late stage)	Jul/Aug		52.12,54.76 ml·mg dry wt ⁻¹ ·d ⁻¹	(10,4)
C. hyperboreus (adult)	Aug/Sept		0180 ml mg dry wt ⁻¹ h ⁻¹	(this study)
C. hyperboreus (C VI)	Apr/May		1-14 ml·copepod ⁻¹ ·h ⁻¹	(11)
 For conversion from wet weight to dry weight see Discussion. Biggs, 1982. 			(7) Ikeda, 1970.(8) Conover and Corner, 1968.	

(3) Ikeda and Mitchell, 1982. (4) Conover and Cota, 1985.

(5) Harrison et al., 1985.

(6) Rakusa-Suszczewski et al., 1976.

Rates of oxygen consumption observed for C. hyperboreus in this study are nearly identical with those observed by Conover (1968) for the same species in the Gulf of Maine (Table 3). They are also generally comparable with respiration rates obtained for a range of Antarctic copepods (Ikeda and Mitchell, 1982; Rakusa-Suszczewski et al., 1976; Biggs, 1982) when the Antarctic data is converted to a dry weight basis (Table 1 in Rakusa-Suszczewski et al., 1976). They are higher, however, than values obtained for adult female C. hyperboreus from a slightly higher latitude (northern Baffin Bay and Lancaster Sound, Conover and Cota, 1985).

Observed values for nitrogen excretion fall midway between those measured by Conover (1968) working with temperate species and those observed for Antarctic species (Ikeda and Mitchell, 1982; Biggs, 1982). Excretion values observed in this study are internally highly consistent, with low variability (see Table 1). They are also in the same range as excretion values obtained recently with C. hyperboreus from northern Baffin Bay (stage II to adult female, Conover and Cota, 1985; mixed stages, Harrison et al., 1985).

(10) Determined from particle volume and by chlorophyll

(9) El-Sayed et al., 1978.

(11) Huntley, 1981.

changes respectively.

The resultant O:N ratios, with the exception of an anomalously high value for station 70, group around a mean of 14.0 ± 4.7 . This value is in the same range as reported for Antarctic copepods (Ikeda and Hing Fay, 1981:Table 4) and is only slightly lower than reported for more northern Baffin Bay C. hyperboreus for July and August 1980 (Conover and Cota, 1985). These values suggest that for most of the stations reported here, C. hyperboreus in August to September had a largely protein-based metabolism (O:N < 20, Ikeda and Mitchell, 1982). The single exception is the high value for station 70, which is considered more characteristic of catabolism of lipids.

The clearance rates obtained here were about one-tenth of those obtained by Conover and Cota (1985) with C. hyperboreus in their July/August 1980 study. Because our determinations were made approximately one month later in the season, it may be that they reflect the annual decrease in feeding and reduction in metabolism that signals the seasonal descent to deeper, colder waters (Conover, 1968). However, it is also likely that these low clearance rates may result from our use of D. tertiolecta as food in our clearance rate experiments. Although unicellular phytoplankton form a normal part of the diet of these copepods and phytoplankton of the size of D. tertiolecta are abundant in these waters at this time, it is at the small end (5-10 μ m) of the size spectrum for grazing by C. hyperboreus (Huntley, 1981). Conover and Cota (1985:Fig. 2) did observe ingestion by young stages of C. hyperboreus of smaller phytoplankton down to $6 \,\mu m$ at one of their stations (15), but we nonetheless recognize that feeding in our own experiments may not have been optimal.

Despite this potential shortcoming, we did measure clearance rates significantly greater than zero. More interestingly, because of its ecological implications, we observed a significant difference between clearance rates in animals sampled from the oil seep stations and in those from the other Baffin Bay stations that indicate a strong correlation between reduced clearance rates and the occurrence of anomalously high hydrocarbon concentrations in the waters along the east coast of Baffin Island. It is worthwhile noting, in this context, that these particular stations are not apparently different from the rest of Baffin Bay with respect to such characteristics as nutrient levels and water type (Coote and Jones, 1982; Harrison *et al.*, 1985).

Although the concentration of the presumed seep-derived petroleum hydrocarbons in these waters is not very high (< 1.25 μ g·l⁻¹), it is well above background levels for offshore Baffin Bay waters $(0.46 \mu g \cdot l^{-1})$. Also, all stations with such anomalously higher hydrocarbon concentrations were found to be clustered between Scott Inlet and Lancaster Sound (Levy, 1979, 1981). There is ample evidence from a number of experimental studies that concentrations of petroleum hydrocarbons as low as 10-90 μ g·l⁻¹ and under conditions of chronic exposure can affect the composition of planktonic communities (Lee and Takahashi, 1975; Elmgren and Frithsen, 1982; Giesy, 1980). Actual observations on natural zooplanktons from oil spill sites are few, but Samain et al. (1981) have reported on unusual enzyme ratios (amylase:trypsin) in zooplankton populations from the English Channel in waters contaminated with 10-20 µg·l⁻¹ hydrocarbons from the supertanker Amoco Cadiz (Marchand and Caprais, 1981). Also, reductions in clearance rate have been observed in a polluted bay in Greece (Ignatiades and Mimocos, 1977) and in meso-scale experimental studies (Elmgren et al., 1980). This then raises the possibility that feeding by C. hyperboreus in the oil seep stations was depressed by the chronic presence of seep-derived hydrocarbons.

Details on the amount and composition of petroleum hydrocarbons in the water column in the seep area are still preliminary. Observations of surface oil films covering several km² have suggested that at times there was a considerable input of petroleum into the seep area (Levy and MacLean, 1981). Analytical results obtained to date indicate that the Scott Inlet-Buchan Gulf petroleum seepage constitutes a single large system extending to the vicinity of Lancaster Sound (Levy, 1981). In the areas of active seepage, concentrations of hydrocarbons in the surface microlayer were in the range from 3 to over 1700 $\mu g \cdot l^{-1}$, while concentrations within the water column were generally an order of magnitude lower, ranging from 0 to $87.5 \ \mu g \cdot l^{-1}$ total extractable residues. While not remarkably high, all stations from seep areas contained water samples with anomalously high hydrocarbon concentrations. Little is known as yet of the composition of the water column hydrocarbons. Preliminary analyses of the surface microlayer, presumably representative of the source material, have indicated a broad spectrum of saturated hydrocarbons, with an unresolved envelope of saturated and aromatic hydrocarbons (MacLean et al., 1981). Low molecular weight compounds, such as those observed in the unresolved envelope, are precisely those that can elicit the depression in clearance rate observed in C. hyperboreus in the seep area.

Regarding those stations outside of the oil seep areas that also contained high hydrocarbon contamination levels, one likely explanation is that those represent populations and sources of hydrocarbons different than found in the seep zone. The measurements on which the hydrocarbon contamination index, %-hydrocarbon-anomaly, was based gives only quantitative information on hydrocarbon concentrations but contained no qualitative information on their relative composition. As has been suggested by Levy (1979, 1981), it is entirely likely that the hydrocarbons found throughout Baffin Bay originate from a number of different sources, including atmospheric, each with a different composition after weathering and with a different degree of toxicity. Therefore it is not at all surprising that some high %-hydrocarbon-anomaly values were found outside the seep area that were not correlated with reduced clearance rates.

The ecological implication of partial or total inhibition of clearance by a dominant planktonic herbivore by petroleum hydrocarbons in seep areas is reduced secondary productivity. The data in Table 1 suggest that in the immediate area of the seep there may be a significant decrease in the amount of energy transferred from primary producers to the zooplankton. Thus, within the immediate seep area the amount of energy available to higher trophic levels may be largely dependent on the rate of advection of zooplankton. The significance of this reduction in secondary productivity will depend on the concentration of seep-derived hydrocarbons, the residence time of water in the seep area and the total area affected by the seep.

ACKNOWLEDGEMENTS

This work was part of a multidisciplinary study carried out by the Bedford Institute of Oceanography during 1978. We express our gratitude to Captain D. Deer and his officers and crew of CSS *Hudson* and to members of the scientific personnel for their cooperation in this study. We wish to thank R.J. Conover, M. Paranjape and J. Percy for their constructive criticism of the manuscript while it was in preparation. We particularly acknowledge the constructive criticism provided by two anonymous reviewers.

REFERENCES

waters of the southern ocean. I. Ross Sea, Austral summer 1977-1978. Polar Biology 1:55-67.

- BUCHANAN, R.A., and SEKERAK, A.D. 1982. Vertical distribution of zooplankton in eastern Lancaster Sound and western Baffin Bay, July-October 1978. Arctic 35(1):41-55.
- CONOVER, R.J. 1962. Metabolism and growth in *Calanus hyperboreus* in relation to its life cycle. Rapport Processus-Verbaux Conseil International pour l'Exploration de la Mer 153;190-197.
 - _____. 1968. Zooplankton Life in a nutritionally dilute environment. American Zoologist 8:107-118.
- and CORNER, E.D.S. 1968. Respiration and nitrogen excretion by some marine zooplankton in relation to their life cycles. Journal Marine Biological Association of the U.K. 48:49-75.
- CONOVER, R.J., and COTA, G.F. 1985. Balance experiments with arctic zooplankton. In: Gray, J.S., and Christiansen, M.E., eds. Marine Biology of Polar Regions and Effects of Stress on Marine Organisms. New York: J. Wiley & Sons Ltd. 217-236.
- COOTÉ, A.R., and JONES, E.P. 1982. Nutrient distributions and their relationships to water masses in Baffin Bay. Canadian Journal Fisheries and Aquatic Sciences 39(8):1210-1214.
- CRUISE REPORT 78-026. CSS Hudson, Chemical Oceanography, August-September 1978. Halifax, Nova Scotia: Bedford Institute of Oceanography. 47 p.
- DAWSON, J.K. 1978. Vertical distribution of *Calanus hyperboreus* in the central Arctic Ocean. Limnology and Oceanography 23(5):950-957.
- ELMGREN, R., VARGO, G.A., GRASSLE, G.A., GRASSLE, J.F., HEINLE, J.P., LANGLOIS, P.R., and VARGO, S.L. 1980. Trophic interactions in experimental marine ecosystems, perturbed by oil. In: Giesy, J.P., ed. Microcosms in Ecological Research. DOE Symposium Series 781101. Springfield, Virginia: National Technical Information Service. 153-165.
- ELMGREN, R., and FRITHSEN, J.B. 1982. The use of experimental ecosystems for evaluating the environmental impact of pollutants: a comparison of an oil spill in the Baltic Sea and two long-term, low-level addition experiments in mesocosms. In: Grice, G.D., and Reeves, M., eds. Marine Ecosystems — Biological and Chemical Research in Experimental Ecosystems. New York: Springer-Verlag. 153-165.
- EL-SAYED, S.Z., BÍGGS, D.C., STOCKWELL, D., WARNER, R., and MEYERS, M. 1978. Biogeography and metabolism of phytoplankton and zooplankton in the Ross Sea, Antarctica. Antarctic Journal of the U.S. 13:131-122.
- GARSIDE, Ch., HULL, G., and MURAY, S. 1977. Determination of submicromolar concentrations of ammonia in natural waters by a standard addition method using a gas-sensing electrode. Limnology and Oceanography 23(5):1073-1076.
- GIESY, J.P., Jr., ed. 1980. Microcosms in Ecological Research. DOE Symposium Series 781101. Springfield, Virginia: National Technical Information Service. 1110 p.
- GILFILLAN, E.S., MAYO, D.W., PAGE, D.S., DONOVAN, D., and HANSON, S.A. 1977. Effects of varying concentrations of hydrocarbons in sediments on carbon flux in *Mya arenaria*. In: Vernberg, F.S., ed. Physiological Responses of Marine Biota to Pollutants. New York: Academic Press. 299-314.
- GUILLARD, R.R.L., and RYTHER, J.H. 1962. Studies of marine planktonic diatoms. 1. Cyclotella nana Hustedt and Detonula confervacea (Cleve) Gran. Canadian Journal of Microbiology 8:229-239.
- HARRISON, W.G., HEAD, E.J.H., CONOVER, R.J., LONGHURST, A.R., and SAMEOTO, D.D. 1985. The distribution and metabolism of urea in the eastern Canadian Arctic. Deep-Sea Research 32(1):223-242.
- HUNTLEY, M. 1981. Nonselective, nonsaturated feeding by three calanid copepod species in the Labrador Sea. Limnology and Oceanography 26(5):831-842.
- _____, STRONG, K.W., and DENGLER, A.T. 1983. Dynamics and community structure of zooplankton in the Davis Strait and Northern Labrador Sea. Arctic 36(2):143-161.

- IGNATIADES, L., and MIMOCOS, N. 1977. Ecological responses of phytoplankton to chronic oil pollution. Environmental Pollution 13:109-118.
- IKEDA, T. 1970. Relationship between respiration rate and body size in marine plankton animals as a function of the temperature of habitat. Bulletin of Faculty of Fisheries, Hokkaido University 21(2):91-112.
- and HING FAY, E. 1981. The metabolic activity of zooplankton from the Antarctic Ocean. Australian Journal of Marine and Freshwater Research 33:55-70.
- IKEDA, T., and MITCHELL, A.W. 1982. Oxygen uptake, ammonia excretion and phosphate excretion by krill and other antarctic zooplankton in relation to their body size and chemical composition. Marine Biology 71:283-298.
- IRWIN, B., HARRISON, W.G., GALLEGOS, C.L., and PLATT, T. 1980. Phytoplankton productivity experiments and nutrient measurements in the Labrador Sea, Davis Strait, Baffin Bay and Lancaster Sound from 26 August to 14 September 1978. Canadian Data Report, Fisheries and Aquatic Sciences, No. 213. 103 p.
- LEE, R.F. 1974. Lipid composition of the copepod *Calanus hyperboreas* from the Arctic Ocean. Changes with depth and season. Marine Biology 26:313-318.
- and TAKAHASHI, M. 1975. The fate and effect of petroleum in controlled ecosystem enclosures. Rapports Process-Verbaux Réunion Conseils Internationales Exploration Mer 171:150-156.
- LEVY, E.M. 1977. Fluorescence spectrophotometry: principles and practice as related to the determination of dissolved/dispersed petroleum residues in seawater. Bedford Institute of Oceanography Report Series /BI-R-77-7. July 1979. 17 p.
- . 1978. Visual and chemical evidence for a natural seep at Scott Inlet, Baffin Island, District of Franklin. In: Geological Survey of Canada, Paper 78-1B:21-26.
- . 1979. Further chemical evidence for natural seepage on the Baffin Island shelf. Current Research, Part B, Geological Survey of Canada, Paper 79-1B:379-383.
- . 1981. Background levels of petroleum residues in Baffin Bay and the eastern Canadian Arctic: role of natural seepage. In: Petroleum and the Marine Environment. PETROMAR-80. Eurocean. London: Graham & Trotman Ltd. 345-362.
- and MACLEAN, B. 1981. Natural hydrocarbon seepage at Scott Inlet and Buchan Gulf, Baffin Island Shelf: 1980 Update. Scientific and Tech. Notes. In: Current Research, Part A: Geological Survey of Canada, Paper 81-1A:401-403.
- MACLEAN, B., FALCONER, R.K.H., and LEVY, E.M. 1981. Geological, geophysical and chemical evidence for natural seepage of petroleum off the northeast coast of Baffin Island. Bulletin Canadian Petroleum Geology 29(1):75-95.
- MARCHAND, M., and CAPRAIS, M.-P. 1981. Suivi de la pollution de l'AMOCO CADIZ dans l'eau de mer et de les sédiments marins. In: AMOCO CADIZ. Fates and Effects of the Oil Spill. CNEXO-Paris, France. 23-54.
- OSTVEDT, O.J., 1955. Zooplankton investigations from weathership M in the Norwegian Sea, 1948-49. Hvalrad. Skr. 40:1-93.
- RAKUSA-SUSZCZEWSKI, S., McWHINNIE, M.A., and CAHOON, M.O. 1976. Respiration of the antarctic copepod, *Rhincalanus gigas*. Limnology and Oceanography 21:763-765.
- RUDJAKOV, J.A. 1983. The vertical distribution of *Calanus hyperboreus* (Copepoda) in the Arctic Basin. Okeanologeia 23(2):332-339.
- SAMAIN, J.F., MOAL, J., LE COZ, J.R., DANIEL, J.Y., and COUM, A. 1981. Impact de l'AMOCO CADIZ sur l'écophysiologie du zooplancton: une nouvelle possibilité de surveillance écologique. In: AMOCO CADIZ. Fates and Effects of the Oil Spill. CNEXO-Paris, France. 481-498.
- USSING, H.H. 1938. The biology of some important plankton animals in the fjords of East Greenland. Medd. om Gronland 100:1-108.
- WIDBORG, K.F. 1940. The production of zooplankton in Oslo-fjord in 1933-1934. Hvalrad. Skr. 21. 85 p.