Energy Flow through the Marine Ecosystem of the Lancaster Sound Region, Arctic Canada

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ABSTRACT. This paper synthesizes the trophic dynamics of a Canadian arctic marine ecosystem in so far as it is known, using new data on primary production, zooplankton, the bivalve *Mya truncata*, and arctic cod (*Boreogadus saida*), as well as literature values for marine mammals and seabirds. The 98 000 km^2 region has a high rate of primary production relative to other parts of arctic Canada. About 60 g C·m^{-2} are fixed annually, of which approximately 90% is contributed by phytoplankton, 10% by ice algae, and 1% by kelp. Phytoplankton production is twofold higher along the south coast of Cornwallis Island than elsewhere in Barrow Strait. Four copepod species, of which *Pseudocalanus acuspes* is the most important energetically, graze about one-third of the phytoplankton production. Bivalves maintain high biomass but low energy flow, acting as sedimenting agents. Arctic cod is a major component, with 125 000 tonnes being consumed by marine mammals and 23 000 tonnes by seabirds annually. Our hydroacoustic estimate for mean arctic cod density, 0.0022 fish·m^{-2}, is probably too low, partly because we have been unable to quantify dense aggregations of schooling fish. The ecological efficiency of ringed seal is near maximum, with 5% of ringed seal ingestion going to bears and man as seal flesh. The data on total kill and prey consumption in whales and birds is incomplete because they migrate out of the Lancaster Sound region in winter. The food chain is very long, with bears occupying the fifth trophic level; this is reflected by high biomagnification factors for persistent lipophilic pollutants such as PCBs. There are major data gaps for some zooplankton and most of the benthos, as well as for winter populations and energetics. This trophic analysis is therefore incomplete and efficiencies for entire trophic levels cannot be calculated.

Key words: seals, whales, seabirds, benthos, zooplankton, phytoplankton, primary production, secondary production, harvest, yield

RÉSUMÉ. Cet article résume la dynamique trophique de l'écosystème marin dans le Canada arctique dans la mesure où il est connu, en utilisant de nouvelles données sur la production primaire, le zooplancton, le bivalve *Mya truncata*, et la morue polaire (*Boreogadus saida*), ainsi que les valeurs trouvées dans la documentation sur les mammifères et les oiseaux marins. Cette région d'une superficie de 98 000 km^2 possède un taux élevé de production primaire par rapport à d'autres parties du Canada arctique. Environ 60 g C·m^{-2} sont fixés annuellement, dont environ 90 p. cent par le phytoplancton, 10 p. cent par les algues glaciaires et 1 p. cent par les laminaires. La production de phytoplancton est deux fois plus élevée le long de la côte méridionale de l'île Cornwallis qu'ailleurs dans le détroit de Barrow. Quatre espèces de copépodes, dont la *Pseudocalanus acuspes* est la plus importante du point de vue énergétique, utilisent environ un tiers de la production de phytoplancton pour se nourrir. Les bivalves contribuent de façon importante à la biomasse mais peu au flux énergétique, étant des agents de sédimentation. La morue arctique est une composante importante, étant consommée au taux annuel de 125 000 tonnes par les mammifères marins et de 23 000 tonnes par les oiseaux marins. Notre estimation hydroacoustique pour la densité moyenne de la morue arctique, 0,0022 poissons·m^{-2}, est probablement trop faible, en partie parce que nous avons été incapables de quantifier les regroupements denses des poissons se rassemblant en bancs. L'efficacité écologique du phoque annelé est proche de son maximum, 5 p. cent de l'ingestion de cet animal allant à l'ours et à l'homme sous forme de chair de phoque. Les données sur le nombre d'animaux tués et sur la consommation de proies chez les baleines et les oiseaux sont incomplètes en raison de leur migration hivernale à l'extérieur du détroit de Lancaster. La chaîne alimentaire est très longue, les ours occupant le cinquième niveau trophique; cela se traduit par des facteurs de bioamplification élevés en ce qui concerne les polluants lipophiles persistants tels que les BPC. Il existe des lacunes dans les données pour certains éléments du zooplancton et pour la plupart du benthos, ainsi que pour les populations et l'énergétique hivernales. Cette analyse trophique est donc incomplète et il n'est pas possible de calculer l'efficacité pour l'ensemble des niveaux trophiques.

Mots clés: phoques, baleines, oiseaux marins, benthos, zooplancton, phytoplancton, production primaire, production secondaire, prélèvement, rendement

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INTRODUCTION

Our overall objective in this paper is to quantify the trophic dynamics of the Lancaster Sound region (LSR) marine ecosystem (Fig. 1). The LSR is important because it is used intensively by many marine mammal and seabird populations in the eastern Arctic, and it supports several Inuit communities. It is also of industrial importance because it forms the eastern part of the Northwest Passage, includes two heavy metal mines, and is a potential source of hydrocarbons. For these reasons, and because regular aircraft and ship service to Resolute provides easy access to the area, the LSR has been better studied than other parts of the Canadian Arctic, although in an absolute sense it still remains a poorly understood ecosystem.

We expect that a model of the ecosystem energy flow will help define the food supplies of marine mammals and seabirds and will form a basis for assessing marine mammal exploitation.

Also, pollutants originating far to the south are occurring in arctic carnivores in significant concentrations (Muir et al., 1988; Norstrom et al., 1988), and the dynamics of these contaminants can only be understood in the context of the food web and energy flow. Some idea of the trophic dynamics of a system — "who eats whom and how many" — is also essential to an understanding of the biology of that system. For these reasons we have pieced together what is currently known about the trophic dynamics of the LSR marine ecosystem.

Description of the Study Area

The LSR is considered herein to constitute about 98 000 km^2 of sea surface (Fig. 1; Table 1). Ocean currents are dominated by southward and eastward flow out of the Polar Basin into Baffin Bay via Barrow Strait, McDougall Sound, Wellington Channel, and Lancaster Sound (summarized from Fissel et

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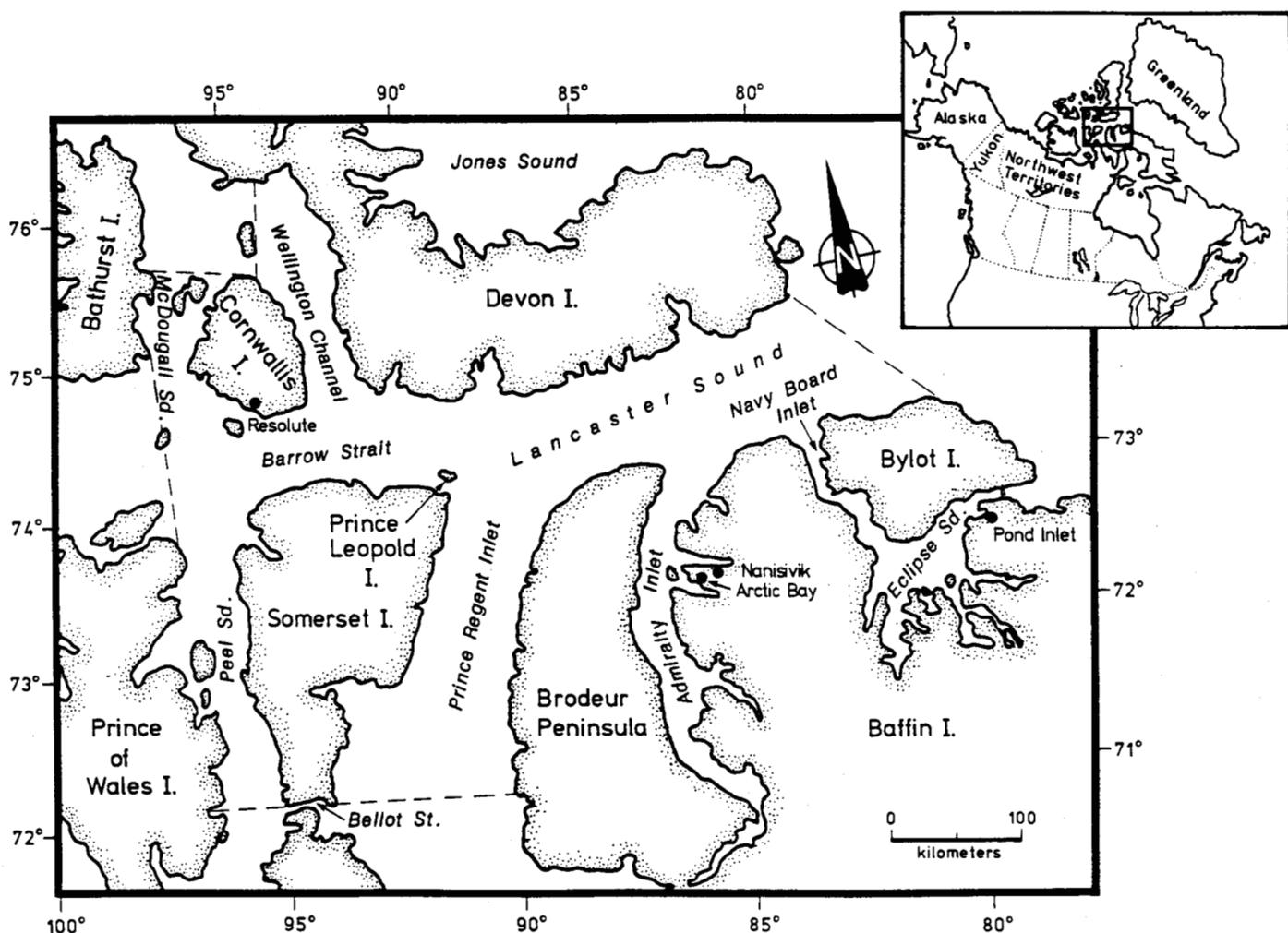
FIG. 1. Place-names in the Lancaster Sound region (LSR), arctic Canada. The LSR is defined by the dashed lines for the purposes of this paper.

al., 1982; Gorman, 1988; Leblond, 1980; Marko, 1978; Prinsenberg and Bennett, 1987). Narrow counter currents are found going northward on the east side of channels oriented north-south and going westward on the north side of Parry Channel along the south coasts of Devon and Cornwallis islands (Leblond, 1980). The counter-clockwise current in north Baffin Bay gives rise to large eddies at the mouth of Lancaster Sound (Fissel et al., 1982) (Fig. 2). The western end of Barrow Strait is a relatively shallow sill of 150 m depth, with deeper water in the surrounding channels and particularly eastward toward Baffin Bay (Fig. 2). The sill constricts the

eastward flow, resulting in turbulence and complex water movements in the downstream portion of Barrow Strait, where water masses enter from Wellington Channel and Peel Sound (Prinsenberg and Bennett, 1987). Eastward current speeds

TABLE 1. Areas of water bodies in the Lancaster Sound region

Water body	Area (km²)
Barrow Strait (BS)	17 338
Lancaster Sound (LS)	26 335
Peel Sound (PS)	9 600
Prince Regent Inlet (PRI)	19 103
Wellington Channel (WC)	7 593
McDougall Sound (McS)	4 327
Admiralty Inlet (AI)	8 557
Eclipse Sound (ES)	3 514
Navy Board Inlet (NBI)	1 331
Total Lancaster Sound Region (LSR)	97 698
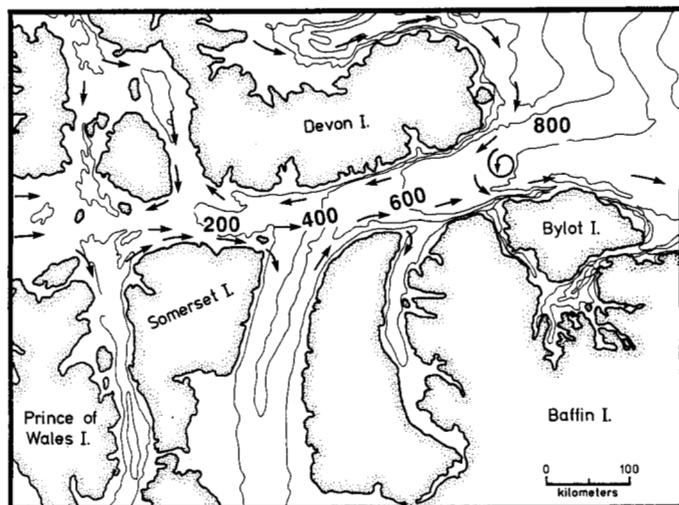
FIG. 2. Water depths (m) (after Fissel et al., 1984) and major currents (Leblond, 1980) in the Lancaster Sound region.

adjacent to the northeast coast of Somerset Island are typically 30 nautical miles (55 km) per day (Fig. 2). Surface current velocities are probably lower in winter months (Fissel et al., 1981).

Freeze-up begins in mid-September in the bays and narrow channels and proceeds seaward, with the strong currents delaying ice consolidation in a well-established sequence from north to south and west to east (Gorman, 1988; Fig. 3). First-year ice dominates throughout, reaching 1.3-1.6 m thick at Arctic Bay and 1.6-1.8 m thick at Resolute by May (Marko, 1982). Ice keels and ridges are generally abundant due to high currents and numerous early winter storms. The North Water polynya of north Baffin Bay (Stirling and Cleator, 1981) extends into Lancaster Sound as a flaw lead with variable amounts of ice-free water. Depending upon the winter, the final consolidation in February or early March may leave a flaw lead as far west as Resolute, or the ice may become fast as far east as Bylot Island (Fig. 3). The ice breaks away sequentially from the eastern edge in spring, with breakup occurring at Resolute about 20 July. Birds and mammals follow the ice edge westward from Baffin Bay (e.g., McLaren, 1982; Sergeant and Hay, 1978). Ice continues to move into the LSR from the west, northwest, and southwest in August and September, at which time both first-year and multiyear ice passes through. At no time is the area completely ice free (Fig. 4).

There are four predominately Inuit communities in the area (with 1989 populations): Pond Inlet (909), Arctic Bay (554), Nanisivik (319), and Resolute Bay (164), including the outpost camp at Creswell Bay on Somerset Island (Fig. 1), consisting of a single extended family.

METHODS

Ecosystem Energy Flow Model

We have chosen the trophic dynamics model (Lindeman, 1942; Odum, 1968) as the framework within which to organize our observations. The trophic model compartmentalizes biotic energy flow into primary production and the subsequent utilization of that energy by a series of consumers. When species A is ingested by species B, which is in turn eaten by species C, three trophic levels are present. Of the consumed animal, some is not digested (assimilated) but will be excreted and is therefore still available at the original trophic level. The rest is digested and used to perform work (metabolism) and to add bodily mass (growth), and it is growth that constitutes the input to the next trophic level.

This is a deceptively simple presentation of what is, in reality, a complex scheme for exactly detailing the hundreds of species present in any large natural ecosystem. For example, few heterotrophs feed exclusively on one trophic level, requiring the energy flow through each species to be partitioned among the trophic levels within which it operates (Burns, 1989). Nonetheless the trophic paradigm remains a useful framework for ecosystem investigation and the subsequent analysis of energy pathways. Although we speak of energy, solar radiation is the only energy flux directly measured; the rest are computed from the flows of materials (biomass, O_2, C, etc.) combined with data on the energy density of tissues.

Plants constitute the first trophic level, transforming solar energy into chemical potential energy, using inorganic nutrients (N, P, Si, CO_2 and possibly Fe are the most important to consider in polar waters) to synthesize organic matter (carbohydrates, lipids, proteins), releasing O_2 in the process. While the flux of any component can be used to estimate rates, the accumulation of biomass, the uptake of CO_2, and the evolution of O_2 are most commonly employed and give good agreement among each other (e.g., Irwin, 1991).

The general approach we have used for animals is to determine one or more of the components of the energy budget for an individual: $I = G + R + E$, where $I = $ ingestion, $G = $ growth, $R = $ respiratory heat loss, and $E = $ excretory and egestion losses. The unknown energetics parameters can then be calculated, often using known growth and assimilation (digestion) efficiencies and assigning Ingestion a value of 100, where: Assimilation Efficiency (AE) $= \frac{G+R}{I}$ (this can also be determined directly by measurement of I and E); Gross Growth Efficiency (GGE) $= \frac{G}{I}$; Net Growth Efficiency (NGE) $= \frac{G}{G+R}$, or $\frac{G}{Assimilated\ Energy}$. This energy budget corresponds to the "universal" model of ecological energy flow of Odum (1968). It
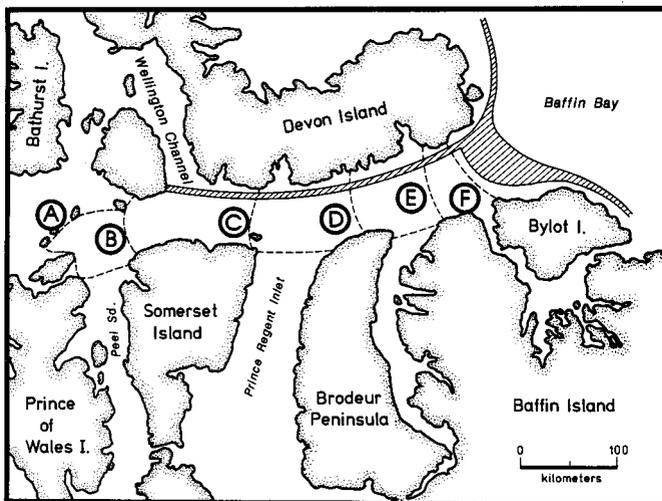
FIG. 3. Position of ice edge in Lancaster Sound-Barrow Strait in winter (after Gorman, 1988). About 50% of the time the final consolidation in February-March occurs at "C" (Gorman, 1988). The hatched area represents the flaw lead and polynya, an extension of the North Water polynya in north Baffin Bay (Stirling and Cleator, 1981).
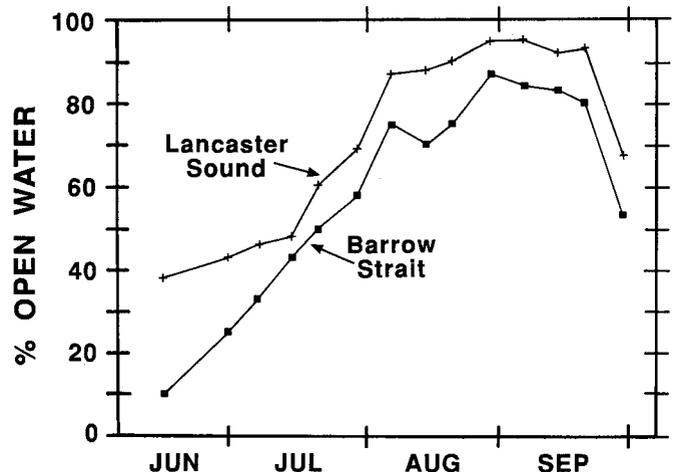
FIG. 4. Percent open water in Barrow Strait and Lancaster Sound, 6 yr mean (1982-87) compiled from weekly ice charts (Atmospheric Environment Service, Ice Forecasting Central, Ottawa).

can be further divided (e.g., urinary energy, heat of fermentation, etc.) (Lavigne et al., 1982), but we have not done so in this paper. Energy budget components were combined with information on abundance to derive population energy flow. All data are reported per m^2 of sea surface per year, then applied to whatever geographic area is appropriate. For higher vertebrates that aggregate, this means division of the total biomass by the area they occupy for a given length of time. We have used the following conversion factors: 4.1868 joules = 1 kilocalorie; 1 g C = 47.7 J (Platt and Irwin, 1973); 1 g O_2 = 14.24 J, or 1 L O_2 = 20.5 J (Conover, 1978; Brett and Groves, 1979); dw = dry weight; ww = wet weight. To be consistent with current usage, all energy values are reported as joules, although most of the ecological energetics literature has used kilocalories until recently. Minor discrepancies due to rounding errors should be disregarded.

Primary Producers

Phytoplankton: We have used the standard short-term incorporation of ^{14}C-labelled inorganic carbon into phytoplankton cells as the measure of photosynthesis. A total of 80 experimental photosynthesis-irradiance (P/I) curves were used to generate the photosynthetic parameters alpha and PBM (Fee et al., 1987; Bergmann et al., 1991), which were then combined with light at metre depth intervals to give half-hourly totals of production throughout the year using the programs of Fee (1990). Surface light data recorded by the RF1 pyranometer at Resolute (Department of Environment, Atmospheric Environment Service) was converted to quanta according to a relationship we derived empirically from comparisons with a Licor model 185 sensor, where: E = 2.154 (watts) + 44.45; n = 155; r^2 = 0.99. Light at depth was calculated from an empirically derived relationship between chlorophyll concentration and light extinction, where: b = 0.017 (chl) + 0.092; n = 54 (range 0.2-20 mg·m^{-3}), r^2 = 0.83, according to Beer's Law, which predicts the intensity (I) of light at depth z as: $I_z = I_o e^{-bz}$. We determined that 0.9-1.4 m thick first-year ice overlain by 0-0.3 m of water in July allowed between 1 and 5% of surface light to penetrate the water column, with less than 1% penetrating below 5 m. We therefore assumed light to be zero (= no phytoplankton production) beneath summer ice cover, and multiplied production rates by the average percent open water (Fig. 4) to obtain area-wide rates. Chlorophyll data were collected weekly at 2, 5, 10, 20, 30, 40, 50, 60, 80, and 100 m about 5 km south of Resolute Bay and during various cruises throughout the LSR.

Ice algae: Briefly, we developed a model that predicted the biomass of ice algae as a function of overlying snow cover and cumulative surface light for much of the Arctic (Welch and Bergmann, 1989; Welch et al., 1991). ^{14}C P/I curves gave photosynthetic parameters that predicted carbon uptake per unit biomass as a function of light. These two data sets were combined with surface light in half-hour intervals and a model of light transmission through snow and ice to generate daily photosynthesis using a modification of Fee's (1990) program (Bergmann et al., 1991).

Kelp: The benthic macrophyte community of Barrow Strait is dominated by the kelps Laminaria longicruris, L. solidungula, Agarum cribosum, and Alaria sp., which grow from a basal meristem where the frond joins the stipe. In October a constriction is formed that delineates subsequent frond growth,

which is virtually complete by the following August (Chapman and Lindley, 1980). We determined the relationships between stipe length and annual frond dimensions and weights. In August we then randomly sampled 54 quadrats of 0.5 m^2 area at 5, 8, 10, and 15 m depths over 100% kelp cover, removing and measuring all stipes to calculate stipe and frond biomass and annual growth. These were then combined with data on percent kelp cover by depth, obtained from video photography of the 5, 10, and 15 m depth strata within 10 km of Resolute, to obtain synoptic estimates of annual kelp production. We used 12.6 J·g^{-1} dw (Cummins and Wuycheck, 1971, average value for Laminaria spp.).

Herbivorous zooplankton: The biomass and life stages of the copepods Calanus hyperboreus, C. glacialis, and Pseudocalanus acuspes were monitored weekly with a 0.5 m^2 vertical tow net (mesh opening 240 m) about 5 km south of Resolute Bay. A total of 14 vertical series (in April, May, June, August, December) were analyzed for 1984, and 35 vertical series (April–September, January) were analyzed for 1986. On each date the daily respiration rate was calculated from the mean dry wt for each species in that sample as: log R = 1.166 – 0.355 log W, where R = μL O_2·mg^{-1} dw·d^{-1}, and W = dry wt (mg) (Conover and Cota, 1985, for mixed copepods in Wellington Channel). Mean monthly rates were calculated from daily rates and summed for the year. We have assumed an assimilation efficiency equal to 0.60 and net growth efficiency equal to 0.60 (Conover, 1978:Table 5-27; C. hyperboreus eating diatoms).

Gelatinous zooplankton: The ctenophore Mertensia ovum constituted 71.5% numerically of the gelatinous zooplankton at Resolute for the years 1985-86 (Siferd, 1990). Mertensia averaged 3.13 mm = 1.17 mg dw summer, 0.63 mg dw winter; mean annual density was 402·m^{-2} and biomass was 0.362 g dw·m^{-2}. Respiration = 1.313 L O_2 summer + 0.353 L O_2 winter = 1.67 L O_2 or 34.3 kJ·m^{-2}·yr^{-1}. AE = 0.74 for other ctenophores (Reeves and Walter, 1978); GGE in three studies was 2-7%, 3 and 11%, and 9% based upon carbon (Reeves and Walter, 1978); we used 8%.

We assumed that the energy flow through the other 28.5% of the gelatinous zooplankton at Resolute (including the ctenophore Beroe cucumis, 5.1%; the hydromedusae Aeginopsis laurentii, 12.1%; and Aglantha digitale, 8.8% (Siferd, 1990)) is proportional to that of Mertensia ovum on a numerical basis.

Parathemisto spp.: Longhurst et al. (1984) reported a mean of 170·m^{-2} in Barrow Strait/Lancaster Sound. Hop (unpubl.) found dry weights ranging from 1.5 to 68 mg, with 4 mg approximating medium-large animals. Respiration is estimated from Percy (1980) for O. affinis at 0°C, where μL O_2·h^{-1} = 0.285 mg dw$^{0.994}$. We have used AE = 0.85 and GGE = 0.37 (summarized from Conover, 1978:Tables 5-21 and 5-27 for carnivorous marine invertebrates).

Chaetognaths: Abundance in Barrow Strait/Lancaster Sound = 1393·m^{-2} (Sameoto, 1987; Longhurst et al., 1984); mean wet wt = 9.3 mg wt (Sameoto, 1987:Table 2); dry:wet wt = 0.083 for Sagitta elegans in Nova Scotia (Sameoto, 1973); respiration 8.2 μL O_2·animal^{-1}·d^{-1} for S. elegans (Sameoto, 1972); AE = 0.85 and NGE = 0.37 (see Parathemisto above).

Ice-associated (sympagic) amphipods: Weyprechtia pinguis and Onisimus litoralis dominate the biomass of Barrow Strait in alternate years (Pike and Welch, 1990). Mean dry wt = 0.109 g·m^{-2} at 0-50 m depth (Pike and Welch, 1990:Table 5);

mean dry wt = 0.010 g·m^{-2} at 50-100 m depth (calculated from Fig. 11 in Pike and Welch, 1990); mean = 0.0050 g·m^{-2} for all of Barrow Strait/Lancaster Sound.

Respiration rate = 1 mg O_2·g^{-1} dw·h^{-1} at 0°C (Lewis, 1987: Table 10, for *W. pinguis*) = 0.0108 g O_2·m^{-2} for 3 months beneath the ice, times 4 = 0.0432 g O_2·m^{-2}·yr^{-1}. AE = 0.70; NGE = 0.34 (Lewis, 1987). *O. affinis* = 15.1 J·g^{-1} dw (calculated from Percy, 1979:Fig. 2).

Benthos: Abundance estimates for the bivalves *Mya truncata*, *Serripes groenlandicus*, and *Hiatella arctica* were obtained by counting siphons in 2000 color photographs taken at 5, 10, 15, 20, 30, 40, 50, 60, 70, and 80 m depth on numerous transects throughout Barrow Strait and Wellington Channel. Brittle stars and sea urchins were also counted at the same time but not classified further. Respiration and filtration rates for *M. truncata* were measured in natural seawater at 0°C pumped from Resolute Bay, using natural phytoplankton chlorophyll to monitor particle disappearance.

A relationship was established between siphon diameter and body size for *Mya truncata* from measurements on photos of individual siphons compared with the size of the same animal removed after photography. This relationship was then used to obtain a size distribution for *Mya* counted and measured in the survey. The size distribution seen in survey photos was approximately normal, indicating that we were unable to count small clams. We have calculated a mean soft body weight of 2.81 g dw·clam^{-1} from the photos, applied against the abundance curve in Figure 5, using the density at 80 m for the 80-100 m stratum, and assuming 5·m^{-2} for 100-200 m, for an overall mean of 10.7 individuals·m^{-2} or 30.1 g dw·m^{-2} in Barrow Strait. The size distribution was integrated with our size-respiration and size-filtration curves to calculate those parameters.

Because the true age distribution for our sample was unknown, we were unable to compute growth directly. However, we have calculated growth for *Mya truncata* at Cape Hatt, north Baffin Island (Cross and Thomson, 1987). For that population: length (mm) = 5.102 + 2.335 (age) − 0.0253 (age)^2 (R.H. Green, University of Western Ontario, London, unpubl. ms.). For the same population we found a log decrease in abundance with increasing size, 5-44 mm size classes inclusive, where $\log_{10}Y = 2.8003 - 0.0222X$, where X = length (mm) and
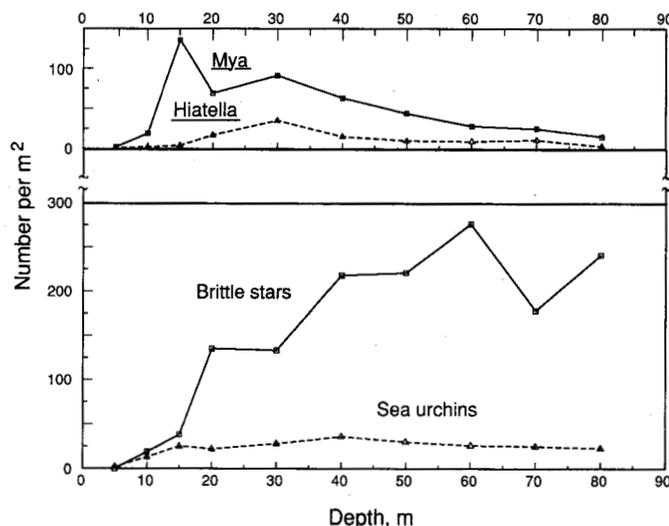
FIG. 5. Surface density of *Mya truncata*, *Hiatella arctica*, sea urchins, and brittle stars in Barrow Strait, from photographic counts.

Y = abundance, r^2 = 0.97, N = 3397 (calculated from Cross and Thomson, 1987:Fig. 4; using reference bay 7, and experimental bays 9-11 pre-spill). Using our own data where dry wt (g) = (age) (0.0958), we have calculated the mean annual growth for Cape Hatt *Mya* as 0.0954 g dw per individual, times 10.7·m^{-2} = 1.02 g·m^{-2}·yr^{-1} growth when applied to Barrow Strait. We used AE = 0.60 (Bayne et al., 1989; for *Mytilus edulis* under low suspended sediment conditions). Wet and dry weights and energy densities are given in Welch and Martin-Bergmann (1990).

Arctic cod (Boreogadus saida)*:* We used several methods to estimate the abundance of arctic cod that were either "dispersed" (i.e., scattered individuals) or in dense schools. Two of these incorporated fisheries acoustics data obtained from a system based on BioSonics dual-beam (200 kHz) equipment (Crawford and Jorgenson, 1990). The transducer was towed at a depth of 2 m behind a 6.7 m boat and acoustic echoes were recorded on a graphic chart recorder (echogram) or in digital form on a magnetic tape for later analysis in the laboratory.

When fish were scattered, we counted marks on echograms and derived the number·m^{-2} according to the nominal volume of the acoustic beam (Crawford and Jorgenson, 1990). When fish were in schools, precluding the discernment of individuals, abundance was estimated with echo integration following standard fisheries acoustics procedures (Johannesson and Mitson, 1983). Data editing was facilitated with graphical techniques (Crawford and Fox, 1992). Biomass was calculated assuming mean fish size of 28 g, derived from pooled samples obtained with a bottom trawl and a gill net during the fisheries acoustic surveys.

We made visual estimates of the sizes of shallow water arctic cod schools and estimated the sizes of schools in deeper (10-30 m) water with an ordinary boat-mounted depth sounder. These data were transformed to biomass estimates (Welch, Crawford, and Hop, unpubl. data). Respiration rates were measured on arctic cod shipped from Resolute to the Vancouver Aquarium. Respiration rate at 2°C = 75 mg O_2·kg^{-1}·h^{-1}; NGE = 0.35; AE = 0.80 (Hop, unpubl. data).

Mammals: Parameter values were obtained from personal communications and literature sources for narwhal (*Monodon monoceros*), beluga (*Delphinapterus leucas*), walrus (*Odobenus rosmarus*), harp seal (*Phoca groenlandica*), bearded seal (*Erignathus barbatus*), killer whale (*Orcinus orca*), ringed seal (*Phoca hispida*), and polar bear (*Ursus maritimus*).

Data for harp seals, ringed seals, and whales show that the basal metabolic rate (BMR) for pinnipeds and cetaceans is at or slightly below the rates predicted for terrestrial carnivores by the standard equation BMR (kcal) = 70 W$^{0.75}$ (Kleiber, 1975), where weight = kg, and that doubling the BMR is a close approximation of average daily metabolic requirement (ADMR) for harp and ringed seals (Gallivan, 1977; Parsons, 1977; Lavigne et al., 1982, 1986; Stewart and Lavigne, 1984; Innes et al., 1987). Digestibility of common fish foods is about 90%, with a further 10% required for urinary and specific dynamic action losses, so division by 0.8 is generally appropriate (Lavigne et al., 1982). Our estimate of daily ingestion for all marine mammals was therefore ADMR/0.8.

For all marine mammals we have used 19.3 J [4.6 kcal]·g^{-1} live weight. Worthy (1982) found 4.585 kcal·g^{-1} live weight for an adult male harp seal with 40% blubber content. Stirling and McEwen (1975) found a mean of 4.66 kcal·g^{-1} live weight for five young ringed seals ranging from 21.1 to 45.7 kg, mean

41% fat content. Measurements for blubber content converge on 40% live weight for arctic seals and whales (Sergeant and Brodie, 1969; Mansfield *et al.*, 1975; Sergeant and Hay, 1978; Lavigne *et al.*, 1982), and walrus (Fay, 1982).

Birds: Values for parameters were obtained from literature sources for thick-billed murres (*Uria lomvia*), black guillemots (*Cepphus grylle*), northern fulmars (*Fulmarus glacialis*), and black-legged kittiwakes (*Rissa tridactyla*). Daily field metabolic rates for seabirds (Nagy, 1987) are: $\log Y = 0.94 + 0.704 \log W$, where $Y = kJ \cdot d^{-1}$ and W = weight in grams. Ingestion assumes 0.8 digestibility (Furness, 1978:Table 1). Our calculated ingestion rate of 1204 kJ for a 900 g bird is similar to the 1375 $kJ \cdot d^{-1}$ maintenance determined experimentally for slightly larger (967 g) birds (Brekke, 1989).

RESULTS AND DISCUSSION

Phytoplankton Production

Phytoplankton chlorophyll was always highest along the south shore of Cornwallis Island, decreasing rapidly south to Somerset Island and more gradually eastward into Lancaster Sound (Fig. 6). The weekly or biweekly mean chlorophyll (0-30 m integrated) was therefore estimated by dividing Barrow Strait into two or three horizontal strata, calculating production for each stratum separately, and adding them to get the total annual production.

We used the mean alpha and PBM for 1984-86, the 1984-87 mean chlorophyll, and the 1985 light to generate an average phytoplankton production of 54 g $C \cdot m^{-2} \cdot yr^{-1}$ for Barrow Strait (Table 2). We have little chlorophyll data for waters outside Barrow Strait and the south coast of Devon Island. Assuming that phytoplankton biomass in Lancaster Sound is similar to that in eastern Barrow Strait, we have estimated a mean open water chlorophyll of 60 mg·chl·m^{-2} (0-30 m integrated) for Lancaster Sound. This is similar to Borstad and Gower's (1984) estimate of 69 mg·chl·m^{-2} (0-35 m integrated) for Lancaster Sound, obtained by remote sensing as ground truthed by ship. Using 1985 light and percentage of open water from Figure 4, we calculated an annual production of 56 g $C \cdot m^{-2} \cdot yr^{-1}$
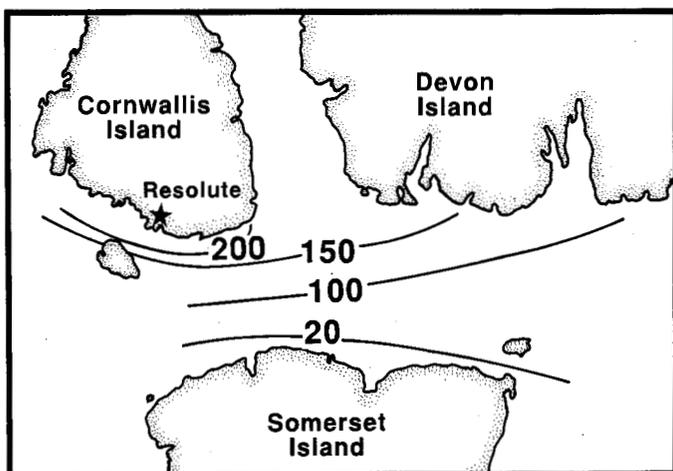
FIG. 6. Typical chlorophyll (mg chl·m^{-2}) distribution during open water in Barrow Strait, integrated over 0-30 m depth. This is based upon data from various cruises during July-September 1984-89 and represents a summary of the specific chlorophyll distributions used to calculate synoptic biomass and photosynthesis.

TABLE 2. Annual phytoplankton production in the Barrow Strait area

Location	Carbon fixed g $C \cdot m^{-2} \cdot yr^{-1}$
Barrow Strait, mean	54
Lancaster Sound, mean	56
Barrow Strait, 1985	47
Barrow Strait, 1986	104
Resolute, 1984	118
Resolute, 1985	108
Resolute, 1986	157

in Lancaster Sound. This is slightly higher than the 54 g $C \cdot m^{-2} \cdot yr^{-1}$ for Barrow Strait, despite the lower average chlorophyll, because there is less ice and therefore more light penetration. We therefore used an average of 55 g $C \cdot m^{-2} \cdot yr^{-1}$ in the energy flow model.

In 1985, late summer (August) chlorophyll was abnormally low (Fig. 7) and early summer ice was average in Barrow Strait. In 1986 the flaw lead extended west to Resolute ("A" in Fig. 3), resulting in considerable photosynthesis in June, and late summer chlorophyll was normal (Fig. 7). Using year-specific P/I parameters, chlorophyll, light, and ice cover, we calculated 47 g $C \cdot m^{-2}$ photosynthesis in 1985 compared with 104 g $C \cdot m^{-2}$ in 1986. We expect that these two values represent the extreme year-to-year variation for phytoplankton photosynthesis in Barrow Strait, as well as the probable range in error for our estimate of 55 g $C \cdot m^{-2} \cdot yr^{-1}$. Annual phytoplankton production is about twice as high in Resolute Passage compared to the average for Barrow Strait (Table 2), probably resulting from nutrient injection into the surface waters by the westerly coastal counter-current (Fig. 2).

Ice Algal Production

Because snow cover controls ice algal production in the Lancaster Sound region (Welch and Bergmann, 1989), synoptic estimation of production requires knowledge of snow-depth distribution, which is not yet available from remote sensing techniques. Therefore we have used our own estimates of snow cover based upon measurements made in Barrow Strait and Wellington Channel in 1984-86 (Welch and Bergmann, 1989) and used 5.0 g $C \cdot m^{-2} \cdot yr^{-1}$ for annual ice algal carbon fixation in the Lancaster Sound region (Table 3; Bergmann *et*
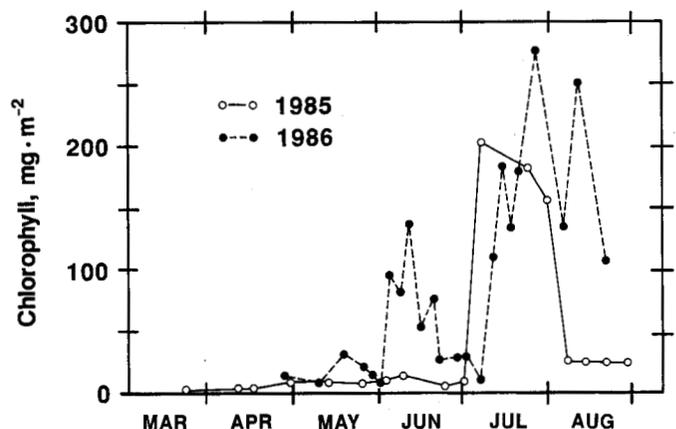
FIG. 7. Seasonal 0-30 m phytoplankton chlorophyll at a standard oceanographic station over 100 m depth offshore from Resolute in Barrow Strait.

TABLE 3. Annual ice algal production integrated for four mean snow depths, Resolute area (from Bergmann et al., 1991)

Snow depth (cm)	Carbon fixed $(g \cdot m^{-2} \cdot yr^{-1})$	
	1985	1986
4.8	2.10	5.90
10.1	1.48	4.20
17.4	0.58	1.90
21.4	0.31	1.10

al., 1991). This estimate is probably within a factor of two of the actual value. It should be noted that the annual variation in surface irradiance at Resolute is not a major factor influencing the calculation of annual production, since the standard deviations for mean monthly irradiance only range from 2 to 12%, increasing during the summer open water period.

Kelp Production

Annual kelp production exceeded 200 g dw·m^{-2}, about 1.3 kg ww·m^{-2}·yr^{-1} at 5 m depth and 15% dry:wet weight (Welch et al., unpubl. data) (Fig. 8). However, integrated over the entire Barrow Strait/Lancaster Sound area, the average is only 1.7 g dw·m^{-2}·yr^{-1}, because the LSR has generally steep submarine slopes, with most of the bottom area below the euphotic zone.

Total Primary Production

Ice algae fix only about 10%, and kelp 1%, of the total primary production (Fig. 9). Phytoplankton production is somewhat higher than previous estimates for the Canadian Arctic (Subba Rao and Platt, 1984), although recent work in Jones Sound suggests that similar rates of photosynthesis occur there (Platt et al., 1987). Welch and Kalff (1975) reported a benthic respiration rate of 120 g O$_2$·m^{-2}·yr^{-1}, the equivalent of about 40 g C·m^{-2}·yr^{-1}, in Resolute Bay. The addition of planktonic respiration would raise that estimate, which adds support to the relatively high rates of primary production we have found in Barrow Strait.

Ice-Associated Amphipods

Ice amphipods are energetically insignificant when averaged over the entire area of Barrow Strait (Table 4; Fig. 9).
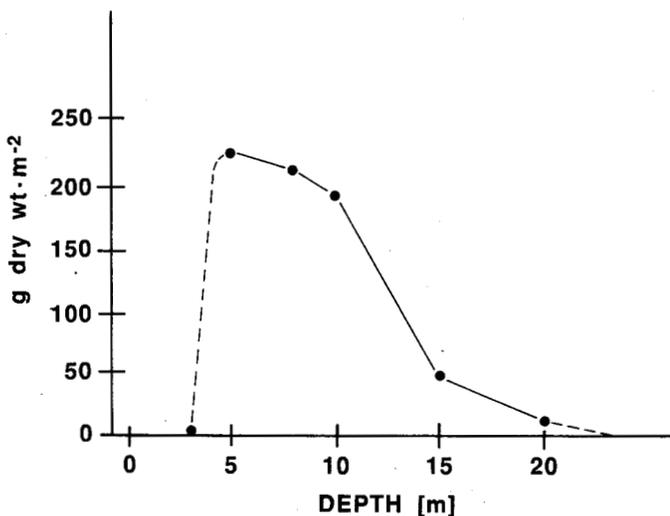
FIG. 8. Kelp biomass as a function of depth in Barrow Strait near Resolute.

Although the density of amphipods is often hundreds per m^2 beneath the ice near shore in spring, abundance drops exponentially with increasing water depth and is near zero over water deeper than 50 m (Pike and Welch, 1990).

The amphipod species found in the Lancaster Sound region, including Apherusa glacialis, Onisimus glacialis, O. litoralis, and Weyprechtia pinguis, are known to inhabit areas that are primarily covered by first-year ice (Carey, 1985). These species are associated with the ice in winter but are members of the benthos or plankton at other times of the year (Gulliksen and Lønne, 1989). The faunal composition is different for the permanent multi-year ice of the Polar Basin, where species such as Gammarus wilkitzkii remain associated with ice year-round (Gulliksen and Lønne, 1989). There, the trophic importance of sympagic amphipods distant from shore is likely much greater than in the first-year ice of the LSR, because their mean density is higher.

Zooplankton

Four species account for nearly all the energy flow through the herbivorous copepods. Pseudocalanus acuspes is metabolically most important, followed by Calanus hyperboreus, C. glacialis, and Metridia longa (Table 5). In 1984 there was an extraordinarily large population of Pseudocalanus acuspes in Barrow Strait. The 1986 copepod populations appear to have been more typical, according to what we have seen, in 1983-91 (Conover, unpubl. data), and therefore we have used the 1986 data in the trophic model (Fig. 9). Together, the copepods eat about one-third of the phytoplankton production. The annual biomass of large Calanus fluctuates only twofold, whereas the biomass of Pseudocalanus can fluctuate tenfold (Conover, unpubl. data). Together with amphipods, large Calanus constitute the bulk of arctic cod diet (Bradstreet et al., 1986), so the large fluctuations in Pseudocalanus may have little influence on the herbivore – arctic cod – higher vertebrate food chain.
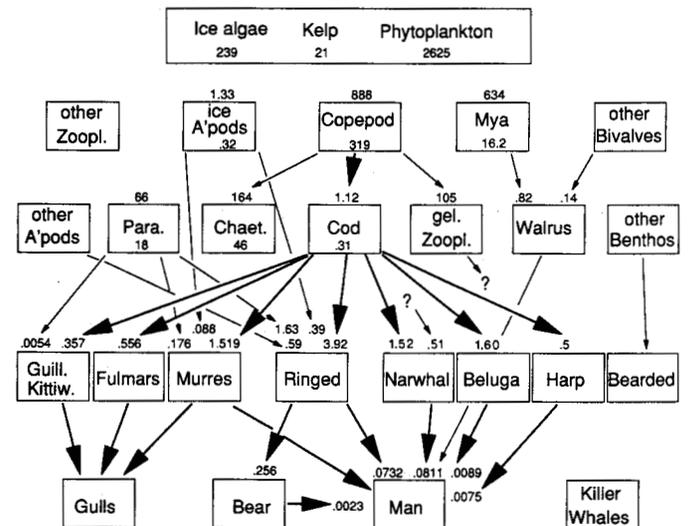
FIG. 9. Energy flow (kJ·m^{-2}·yr^{-1}) through parts of the marine food web, Lancaster Sound region (graphic summary of Tables 4, 6 and 7). Numbers at the tops of the boxes are ingestion; numbers inside the boxes are calculated growth; numbers for man are kill rates. Heavy arrows highlight energy flow mediated by arctic cod.

TABLE 4. Energy flow through middle trophic components in the Lancaster Sound region[1]

Component	Water body	Abundance No. (m^{-2})	Abundance biomass (g·m^{-2})	Ingestion (kJ)	Growth (kJ)	Respiration g O$_2$	Respiration (kJ)	Egestion (kJ)
Ice amphipods	BS		0.005 dw	1.33	0.317	0.0432	(0.615)	0.399
Herbivorous copepods, 1984	BS		2.178 dw	5079	1828	85.6	(1219)	2032
Herbivorous copepods, 1986	BS		0.693 dw	888	319	15.0	(213)	355
Parathemisto spp.	BS/LS	170	0.68 dw	66	18	—	(35)	13
Chaetognaths	BS/LS	1393	1.0 dw	164	46	—	(86)	33
Arctic cod	BS		0.062 ww	1.115	0.312	0.0407	(0.580)	0.223
Mertensia ovum	BS		0.572 dw	51.5	4.1	1.87	(34.0)	13.4
Other gelatinous zooplankton	BS					20.5		
Mya truncata, all depths	BS	10.7	30 dw	634	1.02 g dw (16.2)	25.6	(364)	254
Mya truncata, 0-100 m	BS	40.8	115 dw	2411	3.89 g dw (61.6)	97.3	(1385)	964

[1]Data are given in terms of the units originally measured, with the energy equivalent in kilojoules in parentheses. Data given only in kJ are calculated from the original measurements. All data units are m^{-2}·yr^{-1} for the water bodies listed. Growth is approximately the amount available to the next trophic level (reproductive products, moults, etc., are not considered). BS = Barrow Strait, LS = Lancaster Sound.

Benthos

Abundance of the bivalve *Mya truncata* peaks at 15 m in Barrow Strait and decreases exponentially down to 80 m (Fig. 5). *Mya* is an energetically important component of the system, respiring 25 g O$_2$·m^{-2}·yr^{-1} (Table 4). The production: biomass (P:B) ratio calculated from Table 4 is on the order of 0.03, although this is low by some unknown amount because growth was underestimated and gonadal products were not considered. Robertson (1979) computed correlations between lifespan and P:B ratios for marine benthos, from which we have calculated an expected P:B of only 0.18 for a bivalve with a maximum lifespan of 55 years (the oldest specimen we have aged). *M. truncata* are therefore maintaining a high biomass and growing relatively little.

Bivalves are not only important energetically in the ecosystem; much of the phytoplankton filtered out of the water column may be deposited undigested on the bottom, where it then enters the deposit feeder trophic loop (e.g., eaten by *Macoma calcarea*). The biomass of filter-feeding clams is highest between 10 and 30 m depth (Fig. 5), where phytoplankton productivity and biomass are highest in mid-summer. We found a mean of about 1 mg O$_2$ respired per L of water filtered over the range of clam sizes tested. The filtration rate for *M. truncata* averages 70 L·m^{-2}·d^{-1} or 26 m^3·m^{-2}·yr^{-1} for the 0-200 m zone. At its peak density of 136·m^{-2} at 15 m depth, *Mya* respires 0.9 g O$_2$·m^{-2}·d^{-1} and filters 0.9 m^3·m^{-2}·d^{-1}, thereby filtering the equivalent of the entire water column from 0 to 15 m depth every 2-3 weeks. We have observed extensive accumulation of green pseudofeces around *Mya truncata* siphons when chlorophyll concentrations are high, indicating that much of the phytoplankton filtered out of the water column is deposited undigested on the bottom. *Mya, Serripes, Hiatella,* and other filter-feeding bivalves are thus acting as sedimenting agents, concentrating organic matter at relatively shallow depths and influencing energy flow patterns, much as has been shown for the mussel *Modiolus demissus* in salt marshes (Kuenzler, 1961). We predict therefore that bottom respiration rates will be highest in the 10-30 m range and decrease with increasing depth in the LSR.

The major gaps in Figure 9 are at intermediate trophic levels for most benthic species and all zooplankters except copepods and gelatinous predators. The figures for chaetognaths and *Parathemisto* are little better than guesses, and there are no data for larvaceans and pteropods, seasonally important members of arctic plankton. In the benthos, we have counted some of the more obvious groups in the camera surveys done for clams. The bivalve *Hiatella arctica* is a major benthic component (Fig. 5). The large bivalve *Serripes groenlandicus* averages only 1.7·m^{-2} throughout Barrow Strait, yet reaches high biomass in some areas (unpubl. data). The bivalve *Macoma calcarea,* which we are unable to count in the photos, is probably the most abundant clam in Resolute Bay (Welch, unpubl. data); if its energy flow equalled that of *Mya,* bivalve ingestion might surpass that of the zooplankton (Fig. 9). Sea urchins are another abundant benthic species (Fig. 5), and brittle stars are particularly important numerically in deep water (Fig. 5). Other noticeable benthos includes pycnogonids (5·m^{-2}), sea cucumbers (3-4·m^{-2}), terebellid polychaetes (1-2·m^{-2}), and anemones (1-2·m^{-2}). Note that the observed herbivore consumption in Figure 9 is only about 50% of plant production, because much of the herbivore energetics is not included.

The paucity of winter data is also a serious gap in the model. For annual species such as the ctenophore *Mertensia ovum,* high summer biomass peaks cannot be extrapolated throughout the year (Siferd, 1990). Species that live two years or longer, and thus may be quantified adequately in summer, may undergo changes in energetics parameters throughout the year. The winter respiration metabolism of *M. ovum* is 30% less than in summer (Percy, 1988). *Calanus hyperboreus* in the Gulf of Maine reduce their weight-specific respiration rate by half in

TABLE 5. Annual composition of copepod populations at Resolute

Species	Year	Mean adult dw (mg)	% total copepod biomass	% total copepod respiration
Pseudocalanus acuspes	1984	0.017	71	88
" "	1986		32	57
Calanus hyperboreus	1984	3.8	13	4
" "	1986		35	17
Calanus glacialis	1984	0.8	12	6
" "	1986		21	17
Metridia longa	1984	0.3	4	2
" "	1986		12	9

winter (Conover and Corner, 1968), as do *C. finmarchicus* in the Greenland Sea (Hirche, 1983). Welch and Kalff (1975) found that total benthic respiration in Resolute Bay doubled in August compared with rates in May and June. This is not surprising given the extremely pulsed nature of the primary production input. It suggests that the respiration of long-lived benthic species such as *Mya* may also fluctuate, as would that of microfauna, changing seasonally with changing particulate input to the bottom.

Higher Trophic Levels

The most detailed and reliable trophic information for the Lancaster Sound region tends to be at the top and bottom of the food web (Fig. 9; Tables 6 and 7). Population data for bears and ringed seals are relatively good as a result of tagging, aerial survey, and breeding habitat survey efforts during the past two decades (e.g., Kingsley *et al.*, 1985; Smith *et al.*, 1985; Stirling *et al.*, 1975; Hammill, 1987). More uncertainty is associated with narwhal, beluga, harp seal, and walrus data, because detailed knowledge of food habits, feeding ranges, and populations is mostly lacking. Birds that nest in large colonies, such as thick-billed murres, northern fulmars, and black-legged kittiwakes, have been relatively well studied (e.g., Gaston and Nettleship, 1981). Information on more widely dispersed species, such as black guillemots and glaucous gulls (*Larus hyperboreus*), is sparse or nonexistent. One problem with migratory birds and mammals is that yield and ingestion are often decoupled in space and time, with feeding and growth occurring at a given place and time of year, and with mortality occurring elsewhere at another time. For example, most of the current mortality for thick-billed murres is caused by hunting in Greenland and off Newfoundland (Evans and Kampp, 1991; Elliott *et al.*, 1991). Likewise, narwhal and beluga that feed in the Lancaster Sound region in summer may be harvested in Greenland waters at other times of the year. Determining the rates of ingestion and types of prey taken throughout the year for some of these species, particularly the whales, is not feasible.

Ecological efficiency (EE 5-0 of Kozlovsky, 1968) is equal to the energy passed to trophic level n + 1 divided by ingestion at trophic level n. The ecological efficiency of ringed seals, the yield to bear and man divided by ringed seal ingestions, is 5% (Fig. 9). This is similar to the average gross growth efficiency (G/I) of 4.8% for exploited harp seal populations modeled by Lavigne *et al.* (1985), suggesting that the ringed seal population of the Lancaster Sound region is being utilized by its two main predators at close to its maximum possible yield. An alternative possibility is that there is a net influx of ringed seals into the LSR from outside the region, although we consider this to be unlikely because polar bears are common throughout adjacent areas.

The impact by a species on the ecosystem may be greater than its apparent energy flow would suggest. For example, the energy flow through glaucous gulls in the LSR must be tiny on a square metre basis (Fig. 9), yet the impact of gulls as predators on eggs and young of colonial seabirds is undoubtedly great (Gaston and Nettleship, 1981). Another example is walrus, which eat less than half the *Mya truncata* biomass they kill (Welch and Martin-Bergmann, 1990), enriching the scavenger food chain (Oliver *et al.*, 1985) by about 0.3 g clam biomass·m^{-2}·yr^{-1} (Table 6).

Arctic Cod

Within the LSR, arctic cod occurred in two types of distributions. Fish were generally found throughout the year at all locations in a dispersed state. In addition, aggregations (schools) often appeared in nearshore waters in summer. Hydroacoustic estimates of the abundance of dispersed cod in 1985 suggested adult arctic cod were more abundant to the east of Cornwallis Island (Fig. 10) but fish density there was low (0.002-0.004·m^{-2}). Assuming a mean size of 28 g per fish, mean "dispersed" biomass was 0.062 g·m^{-2} for areas 1-4 (Table 4), for a total of 6000 tonnes extrapolated to the entire LSR.

Much larger amounts of arctic cod occur in schools. For example, schools in Allen Bay (the next embayment west of Resolute Bay; Fig. 1) on 31 August 1989 contained on the order of 75 000 tonnes of biomass. We have found similar aggregations somewhere along the south coasts of Cornwallis and Devon islands in most years (Welch, Crawford, and Hop, unpubl. data).

About 148 000 tonnes of arctic cod are consumed annually by the seabirds and mammals in the LSR (Table 8), about 25 times our abundance estimates for "dispersed" arctic cod. It is unlikely that the estimate of demand by birds and mammals is that much in error. It is more probable that our hydroacoustical surveys did not account for most of the arctic cod biomass and that the missing biomass was held in schools. Such aggregations are difficult to quantify because they occur sporadically in space and time, separated by hundreds of kilometres of coastline. It is also possible that schools exist near the bottom in deep water, where they are difficult or impossible to "see" hydroacoustically. The persistent diving by a radio-tagged beluga to a depth of 350 m in a basin in Barrow Strait (Martin and Smith, 1992) could have been feeding behavior directed at schooling arctic cod.

Given the net current flow eastward through the LSR, arctic cod may also be transported from regions to the north and west; if this is true, the consumption of arctic cod by mammals and birds may have been computed for too small an area. This may also be true for other carnivores feeding on zooplankton transported from the north and west. Some trophic components of the LSR thus may be energy-subsidized by allochthonous organic matter moving into the system.

This analysis corroborates earlier assumptions that arctic cod play a major role in the arctic marine ecosystem (summarized in Davis *et al.*, 1980), both as a consumer and as an agent that concentrates mg-sized particles into energy packets large enough to be eaten efficiently by seals, whales, and birds. Major feeding bouts occur when schools of arctic cod are exploited. We observed a pod of about 500 beluga feeding on dense schools of arctic cod in and near Gascoyne Inlet, 20-23 August 1985, during which time the area covered by the arctic cod schools declined greatly. The whales appeared to enter and feed in Gascoyne Inlet, leave, and return some hours later. At 17 kg cod ingested·animal^{-1}·d^{-1} for maintenance, on the order of 34 tonnes of arctic cod were eaten in that 4 d period, in addition to the consumption of fish by thousands of northern fulmars and hundreds of harp seals. It is difficult to imagine such large whale concentrations finding maintenance rations in the form of dispersed arctic cod at the densities we have observed hydroacoustically (Fig. 10).

In addition to the intra-annual cycle of energy flow caused by pulsed primary production and subsequent respiration,

TABLE 6. Energy flow through marine mammals in the Lancaster Sound region[1]

A	B Distribution, water bodies	C Area (km²)	D Residence time (d)	E Abundance	F Size (kg)	G Prey composition	%	H Ingestion·m⁻²·yr⁻¹ kJ	g ww	I Yield·yr⁻¹ number	tonnes	g ww·m⁻²	kJ·m⁻²	% body wt eaten daily
Narwhal	BS, LS, AI, ES, NB, PS, PRI	85 778	75	20 000	854	Arctic cod	75	1.519	0.279	358	306	0.0036	0.0688	2.5
						halibut	25	0.506	0.093					
Beluga	BS, LS, PRI, WC, PS	79 968	90	12 000	880	Arctic cod	100	1.599	0.294	58	37.1	0.00046	0.0089	2.5
Walrus	—	[30 000]	[365]	[1 000]	512	*Mya*	85	[0.86]	[0.329]	20	10.2	—		5.7
						Serripes	15	[0.142]	[0.052]					
Harp seal	LS, BS, AI, PS, PRI, WC	88 525	75	[25 000]	106	Arctic cod	100	[0.511]	[0.094]	326	34.6	0.0004	0.0075	4.2
Bearded seal	Entire LSR 97 697	—	—	250		various		—	—	180	45	0.00046		—
Killer whale	ES, AI	—	—	[20]	1 900	Narwhal, other?		—	—	0	0	0		0.6
Ringed seal	Entire LSR 97 697	365	161 200	36.3 (1.65·m⁻²)		Arctic cod	60	3.915	0.719	(Man) 7500	375	0.0038	0.0737	
						Parathemisto	25	1.633	0.354	(Bear) —	1300	0.0133	0.2558	
						sympagic amphipods	6	0.389	0.085					
						benthic amphipods	9	0.586	0.127					
Total								6.523	1.285		1675	0.0171		5.9
Polar bear	Entire LSR 97 697	365	1 758	200 (0.018·km⁻²)		Ringed seal	100	0.256	0.0133	38	11.4	0.00012	0.0022	1.0

[1]Numbers in brackets are crude estimates. See Table 1 for abbreviations of water bodies. Data sources are listed below after each species and column heading.

Narwhal. D. Sergeant and Hay, 1978. **E.** Davis *et al.*, 1978a; Smith *et al.*, 1985; Strong, 1988. **F.** Mean size in the population was calculated using 0.90 annual survival to age 25; males are 235, 290, 338 cm for the first 3 yr, asymptoting at 470 cm at age 20; females are 247, 290, 332 cm for the first 3 yr, asymptoting at 420 cm at age 20; weight (kg) = 0.0003231 L (cm) exp. 2.48038 (Hay, 1984; Weaver and Walker, 1988). **G.** Narwhal from the deeper eastern part of the LSR eat Greenland halibut (*Reinhardtius hippoglossoides*) and squid in addition to arctic cod (51% arctic cod, 37% halibut at Pond Inlet, N = 73; Finley and Gibb, 1982). Narwhal feed almost exclusively on arctic cod in Creswell Bay in August (Finley and Johnston, 1977; A. Atagotaaluk, Pond Inlet, pers. comm. 1991) and Resolute (Welch, unpubl. data). Arctic cod are undoubtedly the main food of narwhal in the relatively shallow waters west of Lancaster Sound. **I.** The annual harvest is based upon filled quotas of 100 at Pond Inlet, 100 at Arctic Bay, 12 at Creswell Bay, and an average kill of 3 at Resolute (Strong, 1988); we used a struck and lost rate of 40% (Weaver and Walker, 1988). The mean weight of the catch (954 kg) was calculated from the length frequencies of 58 narwhal (Weaver and Walker, 1988) combined with weight:length (Hay, 1984).

Beluga. D. Sergeant and Hay, 1978; Smith *et al.*, 1985. **E.** Smith *et al.*, 1985. **F.** Mean size in the population was calculated using an annual survival of 0.9 (Sergeant, 1973) to age 30 (Doidge, 1990); and a Gompertz growth model where weight (kg) = (1453)(1-e^(-0.12)(age)). The weight:age model was derived from 25 male beluga from Cumberland Sound, which are similar in size to Grise Fiord beluga (R.E.A. Stewart, Freshwater Institute, pers. comm. 1992). Asymptotic lengths of females from three populations, northern Quebec and Alaska (Doidge, 1990), and southwest Hudson Bay (R.E.A. Stewart, pers. comm. 1992) averaged 0.71 of male length. Given a 1700 kg asymptotic weight for Cumberland Sound males (R.E.A. Stewart, pers. comm. 1992) and a 1:1 sex ratio (Sergeant, 1973), the mean asymptotic weight for LSR beluga is (1.0 − 0.71) ÷ 2 = 0.855 × 1700 = 1453. **G.** Stomach contents of beluga killed in the Resolute and Creswell Bay areas have been virtually 100% Arctic cod (Welch, unpubl. data; see also discussion). **I.** Yield is 39 (Strong, 1989) plus 6 for nil reports, at a loss rate of 0.30. The size of harvested beluga was calculated for 113 hunter-killed animals in the LSR (Sergeant and Brodie, 1969:Fig. 3) using weight:length equations for Grise Fiord whales (R.E.A. Stewart, pers. comm. 1992), where log₁₀wt (kg) = 2.33 log₁₀length −3.13; N = 10 ♀, and log₁₀wt (kg) = 2.32 log₁₀length − 3.09; N = 17 ♂.

Walrus. E. Davis *et al.*, 1978b, cited in Davis *et al.*, 1980. **F.** Freeman, 1974/75, cited in Davis *et al.*, 1980. **G.** Vibe, 1950; Welch, unpubl. data. **H.** *Mya truncata* siphons are 3.592 kJ·g⁻¹ ww, *Serripes groenlandicus* feet are 2.742 kJ·g⁻¹ ww (Welch and Martin-Bergmann, 1990). **I.** The 1980-87 8 yr average kill is from Strong (1989) and has decreased in recent years. A 40% loss rate was assumed (Orr *et al.*, 1986).

Harp seal. E. Abundance in the LSR is poorly known and appears to vary from year to year. **F.** Lavigne *et al.*, 1982. **G.** Although a variety of crustacea are sometimes found in harp seal stomachs taken at Arctic Bay (G. Williams, Arctic Bay, pers. comm. 1990), 95% or more of harp seal food in the LSR is Arctic cod (Finley *et al.*, 1990; Sergeant, 1991; Welch, unpubl. data). **I.** The high kill of the 1970s decreased in the late 1980s. An average of 163·yr⁻¹ were taken at Pond Inlet, Arctic Bay and Resolute 1980-84 (Patimore, n.d., cited in Weihs and Okalik, 1989:Table 5). We used a loss rate of 50% (discussed in Davis *et al.*, 1980).

Bearded seal. E. No population estimates exist and the numbers counted from aircraft in the LSR (Kingsley *et al.*, 1985; Smith *et al.*, 1979) have not been much higher than the known kill, which averaged 26·yr⁻¹ for nine years at Resolute (Smith, 1981). Some overwinter in thin, fast ice in McDougall Sound (H. Kalluk, Resolute, pers. comm. 1988) and in polynyas; others probably move into the LSR in spring (Sergeant and Hay, 1978). **F.** Burns, 1967, cited in Davis *et al.*, 1980. **G.** Finley and Evans, 1983. **I.** An average of 89 bearded seals per year were taken in Arctic Bay, Pond Inlet and Resolute 1980-84 (Patimore, n.d., cited in Weihs and Okalik, 1989:Table 5). The loss rate was assumed to be 50% (Smith, 1981).

Killer whale. E. Campbell *et al.*, 1988. **F.** Kastelein and Vaughan, 1989.

Ringed seal. E. The mean number of hauled-out seals per km² for the High Arctic and Stratum 6 (Barrow Strait) aerial surveys (Kingsley *et al.*, 1985:Table 14; Hammill, 1987:Table 3) was 0.96. Seal densities estimated aerially averaged 60% of the densities calculated from the known number of breathing holes per seal (3.38) and hole density (Hammill, 1987), so 0.96/0.6 = 1.60 seals·km⁻². **F.** Mean weight in the population and catch was calculated from the age-frequency distribution at Holman Island (Smith, 1987:Table 25), the length:age from Smith (1987:Table 18), and the weight:length from McLaren (1958). **G.** Food habits were determined for 65 ringed seals killed by hunters at Resolute from September 1986 to September 1987. The percent stomach volume contributed by each prey type was averaged to obtain a

(continued)

TABLE 6. Notes continued

single distribution of prey types for the year. This was 60% Arctic cod, 25% *Parathemisto* spp., 6% sympagic amphipods, 2% benthic amphipods, 6% mysids and 1% other crustacea (Curtis, unpubl. data), at a mean energy density of 4.61 kJ·g^{-1} for crustacea (Percy and Fife, 1981). **H.** The ADMR was calculated for each of 20 age classes from mean weight at age, multiplied by the fequency distribution, and summed to obtain the mean population ADMR. **I.** The pre-snow-mobile take of ringed seals was on the order of 450·yr^{-1} for Resolute, 4500·yr^{-1} for Pond Inlet, and 2300·yr^{-1} for Arctic Bay (calculated from Bissett, 1967, 1968), or about 7500 seals annually for the LSR. The annual average for 1980-84 was 371 for Resolute, 3631 for Pond Inlet, and 2421 for Arctic Bay (Patimore, n.d., cited in Weihs and Okalik, 1989:Table 5), for a total of 6423 in the LSR. The seal harvest generally declined (and is probably still declining) during this period. We therefore used an average of 6000 ringed seals as the recent annual catch, divided by 0.8 to account for loss rate (Smith, 1987).

Polar bear. E. Schweinsburg *et al.* (1982) estimated 1031 bears in about 40 000 km^2 of LSR waters, or 0.026 bears·km^{-2}. Stirling *et al.* (1978) estimated 1647 bears for their region F, about 160 000 km^2, or 0.0103 bears·km^{-2}. We used the mean of the two estimates. **F.** The mean weight for 2242 bears at first capture (excluding cubs) was 198.5 kg (computed from Ramsay and Stirling, 1986:Tables 1 and 2). **G.** Bears take small numbers of bearded seal and occasionally other marine mammals (Smith and Sjare, 1990), but ringed seals constitute practically all the diet (I. Stirling, Canadian Wildlife Service, Edmonton, pers. comm. 1990). **H.** Denning females have about 25% lowered metabolic rates (Watts *et al.*, 1987), but the uncertainty associated with a single standard metabolic equation encompasses this relatively minor potential error. **I.** The current quota for Resolute, Arctic Bay and Pond Inlet totals 38 bears.

TABLE 7. Energy flow through seabirds in the Lancaster Sound region[1]

A	B Distribution, water bodies	C Area (km^2)	D Residence time (d)	E Abundance	F Size (g)	G Prey composition %		H Ingestion·m^{-2}·yr^{-1} kJ	g ww
Thick-billed murre (adults)	LS, BS	43 643	105	452 000	900	Arctic cod	85	1.496	0.2749
Thick-billed murre (juveniles)	LS, BS	43 643	75	218 000	900	*Parathemisto*	10	0.1760	0.0382
						Sympagic amphipods	5	0.0880	0.0191
Thick-billed murre (chicks)	LS, BS	43 643	—	169 500	200	Arctic cod	100	0.0233	0.0043
Black guillemot (adults)	Entire LSR	97 697	105	34 000	400	Arctic cod	80	0.021	0.0039
Black guillemot (juveniles)				17 000	400	*Parathemisto*	20	0.0054	0.0011
Northern fulmar (adults)	LS, BS, WC,	78 925	105	320 000	650	Arctic cod	100	0.556	0.1022
Northern fulmar (juveniles)	AI, PRI		75	160 000	650				
Black-legged kittiwake (adults)	LS, BS	43 643	105	200 000	365	Arctic cod	100	0.336	0.0618
Black-legged kittiwakes (juveniles)			75	100 000	365				

[1]See Table 1 for abbreviations of water bodies. Data sources are listed below after each species and column heading.

Thick-billed murre. E. Nettleship and Evans (1985) reported 226.000 breeding pairs in the LSR region, present at the colonies 15 May–1 September (105 d). Immature birds older than one year visit the colonies late in summer, arriving earlier and earlier as they age (Hudson, 1985). Annual adult survival is 0.91 (Hudson, 1985), equalling 40 700 birds entering the adult population at age 5. At 0.34 juvenile to adult survival (Hudson, 1985:Table 5.8), this equals 120 000 juveniles required at 0.77 survival per year to give about 41 000 birds reaching age 5, or approximately 218 000 juveniles 2-4 years old on the feeding grounds for an assumed 75 d. This equals an adult:juvenile ratio of about 2:1. 226 000 chicks at 0.75 survival to fledging = 169 500 chicks. **F.** Gaston and Nettleship, 1981. **G.** Bradstreet and Cross, 1982; Bradstreet and Brown, 1985. 169 500 chicks require 1100 g of arctic cod each (Gaston and Nettleship, 1981), or 186 450 kg cod, excluding that required for non-surviving chicks and for 2260 kg egg production (Gaston and Nettleship, 1981; Furness, 1978). This is less than 2% of the total population energy flow for thick-billed murres during this period.

Black guillemot. E. Nettleship and Evans, 1985; Gaston and Nettleship, 1981. We assumed the same 2:1 adult:juvenile ratio as was calculated for thick-billed murres. **F.** Harris and Birkhead, 1985. **G.** Ingestion was calculated as for murres but food habits are poorly known. Intake of chicks was ignored (see murres above).

Northern fulmar. E. Brown *et al.*, 1975. We assumed the same 2:1 adult:juvenile ratio as for thick-billed murres. **F.** Gabrielsen *et al.*, 1988. **G.** Ingestion was calculated as for murres, ignoring chicks (see murres above). Bradstreet and Cross (1982) found the food of northern fulmars in the LSR to be nearly all arctic cod from a small sample. Our observations suggest that northern fulmars in Barrow Strait eat mostly cod, plus copepods and amphipods, and that they are very opportunistic, resulting in extreme variability of stomach contents for birds taken within a few kilometres of each other. Major feeding bouts occur when schools of arctic cod appear in shallow water (Hobson and Welch, 1992).

Black-legged kittiwake. E. Brown *et al.*, 1975. We assumed the same 2:1 adult:juvenile ratio as for thick-billed murres. **F.** Gabrielsen *et al.*, 1988; Brekke, 1989. **G.** Ingestion was calculated as for murres, ignoring chicks (see murres above). Kittiwakes in northern Norway eat almost all capelin (Furness and Barrett, 1985, cited in Erikstad, 1990), which are not present in the LSR. We have assumed black-legged kittiwakes eat only arctic cod in the LSR, which is somewhat in error since they exhibit opportunism similar to that of fulmars, with scattered feeding on large zooplankton, coupled with major feeding bouts on schooling arctic cod.
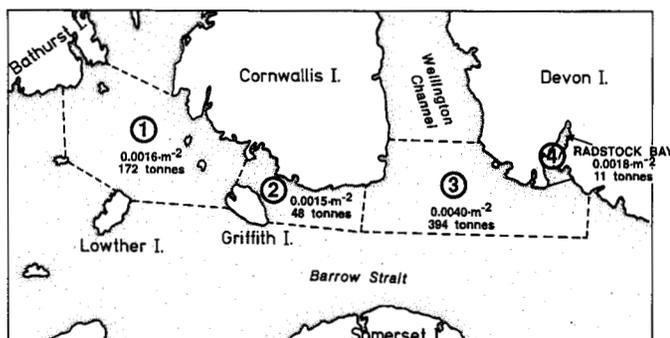
FIG. 10. Abundance of arctic cod in the Resolute area as determined by hydro-acoustical surveys.

inter-annual variability is also important and has not been assessed in the "static" picture we present here. Arctic cod have shown considerable variability in their year-to-year distribution in the Beaufort (Craig *et al.*, 1982) and Chukchi seas (Quast, 1974). Ringed seals and bearded seals were about twice as abundant in 1974 as in 1975 in the Beaufort Sea, probably related to abnormally heavy ice conditions in 1974, which caused reduced productivity, survival, ovulation rate, and pregnancies (Stirling *et al.*, 1977, 1982). The 1973 and 1974 ringed seal year class strengths were far below the annual mean (Smith, 1987). The distribution of polar bears also varied between years due to the changes in abundance and accessibility of their seal prey. The low seal productivity and availability in 1974 was reflected in a lower survival of

TABLE 8. Total annual predation on Arctic cod in the Lancaster Sound region (tonnes)

Marine mammals	Tonnes	Seabirds	Tonnes
Narwhal	23 000	Thick-billed murres	12 180
Beluga	23 000	Black guillemots	380
Harp seal	8 000	Northern fulmars	8 070
Ringed seal	70 000	Black-legged kittiwakes	2 700
Total	125 000	Total	23 330
	Grand Total	148 330	

polar bear cubs and changes in polar bear distribution in 1975 (Stirling et al., 1975). For the LSR, a twofold interannual variability in phytoplankton production (Table 2) and a threefold interannual range in copepod biomass (Conover, unpubl. data) do not appear to result in marked interannual fluctuations in energy flow through arctic cod, ringed seals, polar bears, or seabirds (Welch, Hobson, and Conover, unpubl. ms.).

GENERAL CONCLUSIONS

Little significance can be attached to much of the energy flow data synthesized herein because of high variability and the inability to put meaningful confidence limits on most of the data. Nonetheless there are some relatively robust results. First, there is more than adequate primary production to supply the food web supporting sea mammals and birds. Second, major planktonic and benthic components are missing from the analysis, since calculated consumption by the second trophic level is only half of production. Third, our estimates of arctic cod abundance are far too low to account for the production consumed by sea mammals and birds, as discussed earlier. Fourth, marine mammals are consuming much more arctic cod than are seabirds (Table 8). Fifth, the consumption of ringed seal production is probably close to the maximum possible, leaving little leeway for increased yield to either polar bears or man. Should ringed seal production be reduced, it should be manifested in bear condition factors and reproductive status. Sixth, food chains supporting higher vertebrates are generally long, with bears occupying a clearly defined fifth trophic level (this has been corroborated by nitrogen stable isotope analysis; Hobson and Welch, 1992). Long food chains help explain the relatively high concentrations of organochlorine contaminants in arctic marine mammals compared with concentrations in water and plankton (Muir et al., 1992).

There are many major data gaps in this trophic analysis of the LSR. Important needs include data on the abundance of most zooplankton and benthos; growth estimates for most invertebrate species; year-round data on respiration rates for all invertebrates; information on arctic cod abundance and distribution; and data on fluxes of allochthonous and autochthonous energy as they are driven by water currents. Better data on birds and mammals — for example, the energy balance of each species in the LSR in summer and the location of mortality throughout the year — will improve the analysis but in some cases may be difficult or impractical to obtain. Last, we note that there is little information on interannual variability, especially as the abundance of a prey affects the subsequent abundance of a predator (the documented change in ringed seals and polar bears in the Beaufort Sea cited above is

a notable exception). It would be exciting to be able to predict the year class strengths of birds and mammals from information about food supplies (e.g., arctic cod year class strength) or, even better, from the fluctuations in the physical environment that controls production processes. This will require annual data collection using the same methods in the same locations for a number of years, which is not likely to happen in the present climate of poor funding and fragmented biological oceanographic research in the Canadian Arctic.

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