

Quantitative Studies of Arctic Cod (*Boreogadus saida*) Schools: Important Energy Stores in the Arctic Food Web

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ABSTRACT. Aggregations of Arctic cod (*Boreogadus saida*) in Allen Bay, on the southern coast of Cornwallis Island, Lancaster Sound were studied with fishery acoustics techniques in 1989 and 1990. Nonschooling fish were also examined in several Cornwallis and Devon Island bays. Although acoustic signal shading within the schools minimized abundance estimates (error may exceed 50%), measurements in 1989 indicated that two aggregations of adult Arctic cod together comprised at least 900 million individuals. Combined surface area of these two schools was 59 hectares, and total biomass was 30 715 tonnes (520 t·ha⁻¹). Mean density in one school was 91 fish·m⁻³. In the other it was 307 fish·m⁻³, each fish occupying a space equivalent to about one body length cubed. A smaller school studied in the same location a year later had a mean density of 72 fish·m⁻³. Mean length of net-captured fish from that school was 18.7 cm (TL), and mean weight was 44.5 g. School surface area was about 4.6 hectares, and it contained an estimated 2835 t of biomass (616 t·ha⁻¹). Given that significant concentrations of biomass occurred in this small portion of the Lancaster Sound region, we concluded that, in theory, sufficient biomass was sequestered in fish schools within the region to support energy flows through the food web. Acoustic measurements indicated that fish at a school edge were larger (target strength [TS] = -44.7 dB, equivalent size = 19.3 cm) than nonschooling fish elsewhere (TS = -53.4 dB, equivalent size = 8.4 cm). Zooplankton abundance near a school was markedly reduced. Near Cornwallis Island, where water temperatures throughout the water column were > -1.3°C, fish were scattered from surface to bottom. But near Devon Island, fish were common only in warmer surface waters (> 2.0°C) above a marked thermocline at about 35 m, but not deeper, where water temperature was -1.5°C.

Key words: fish, Arctic cod, *Boreogadus saida*, biomass, trophic, predation, zooplankton, grazing, Lancaster Sound, Canada

RÉSUMÉ. En 1989 et 1990, on s'est servi de techniques acoustiques utilisées dans l'industrie de la pêche pour étudier des concentrations de morue arctique (*Boreogadus saida*) dans Allen Bay, sur la côte méridionale de l'île Cornwallis (déroit de Lancaster). On a également étudié des poissons non rassemblés en bancs dans plusieurs baies des îles Cornwallis et Devon. Bien que l'ombre acoustique due aux bancs ait réduit les estimations de l'abondance (la marge d'erreur peut dépasser 50 p. cent), les mesures de 1989 montraient que deux concentrations de morue arctique adulte totalisaient au moins 900 millions d'individus. La superficie combinée de ces deux bancs était de 59 hectares et leur biomasse totale d'environ 30 000 tonnes (520 t·ha⁻¹). La densité moyenne dans un banc était de 91 poissons·m⁻³. Dans l'autre, elle était de 307 poissons·m⁻³, chaque individu occupant un volume équivalent à un cube dont l'arête mesure environ la longueur de son corps. Un plus petit banc étudié au même endroit un an plus tard avait une densité moyenne de 72 poissons·m⁻³. La longueur moyenne des individus capturés au filet dans ce banc était de 18,7 cm (longueur totale), et le poids moyen était de 44,5 g. La superficie occupée par le banc était d'environ 4,6 hectares, et elle contenait une biomasse approximative de 2835 tonnes (616 t·ha⁻¹). Vu que d'importantes concentrations de biomasse existent dans ce secteur restreint de la zone du déroit de Lancaster, on conclut qu'en théorie il y avait, dans la région, suffisamment de biomasse fixée dans les bancs de poissons pour soutenir des transferts d'énergie dans le réseau trophique. Les mesures acoustiques indiquaient que les poissons situés à la périphérie du banc étaient plus gros (intensité de cible [IC] = 44,7 dB, taille équivalente = 19,3 cm) que les poissons non rassemblés en bancs ailleurs (IC = 53,4 dB, taille équivalente = 8,4 cm). L'abondance du zooplancton près d'un banc était nettement réduite. Près de l'île Cornwallis, où la température de l'eau dans toute la colonne d'eau était > -1,3 °C, les poissons étaient répartis de la surface au fond. Mais près de l'île Devon, les poissons étaient abondants seulement dans les eaux de surface plus chaudes (> 2,0 °C) au-dessus d'un thermocline établi à environ 35 m, mais pas plus, où la température de l'eau était de -1,5 °C.

Mots clés: poisson, morue arctique, *Boreogadus saida*, biomasse, trophique, prédation, zooplancton, broutage, déroit de Lancaster, Canada

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INTRODUCTION

In the limited diversity of the Arctic, the Arctic cod (*Boreogadus saida* Lepechin 1774) is an important conduit of energy flow from the zooplankton to tertiary consumers (summarized by Bradstreet et al., 1986). Otoliths of this fish are often a dominant item in the stomach contents of many arctic seabirds and marine mammals (Bradstreet et al., 1986). In spite of its vital role in the food web, the biology and habits of this fish in Canadian arctic waters remain poorly understood.

Estimates of annual energy flow in Lancaster Sound have suggested that predators consume the energy equivalent of about 150 000 t of Arctic cod annually (Welch et al., 1992). Although Hobson and Welch (1992) found that this fish was one of several important prey items in the Lancaster Sound food web, preliminary estimates of Arctic cod abundance derived from studies with fisheries acoustics in offshore Lancaster Sound and Resolute Passage (Crawford and Jorgenson, 1990, 1993) accounted for only a small fraction of the standing stock required to support this level of energy flow (Welch et al., 1992).

It has long been known that Arctic cod aggregate into schools in the coastal waters of Arctic Canada (Bradstreet et al., 1986) and Russia (Ponomarenko, 1967, 1968), but most observations in Arctic Canada have been anecdotal. Recently, Welch et al. (1993) estimated fish densities were about 1000 fish·m⁻² and 200 fish·m⁻³ within schools of Arctic cod found in Allen Bay, Cornwallis Island in August 1989. Biomass, calculated with these numbers, totalled about 26 000 t. These values were subjectively derived estimates and were considered rough approximations.

This paper reports the first quantitative analysis of Arctic cod schools in the Canadian Arctic. It also includes analyses of data obtained from nonschooling fish (presumably also Arctic cod) that were detected (during the search for aggregations) as single targets scattered within the water column. Interpretations of hydrologic conditions provide suggestions about environmental cues eliciting the near-surface aggregations of this fish in the arctic summer. The volume density and community composition of zooplankton collected near and distant from fish schools were also observed. Although adverse field conditions limited its scope, this research sought to explain the apparent imbalance of the Welch et al. (1992) trophic model. The goal was to better understand the ecological significance of these schooling events to the flow of energy through the arctic food web.

METHODS

We used echo integration and target strength analysis to study fish abundance and density in schools of Arctic cod along portions of the south coasts of Cornwallis and Devon Islands (Fig. 1). The primary study tool was a 200 kHz dual-beam fisheries acoustics system (see Crawford and Jorgenson, 1993) aboard the CSL *Ogac*, a 13.7 m research vessel stationed at Resolute Bay. The acoustic transducer, in a vee-fin,

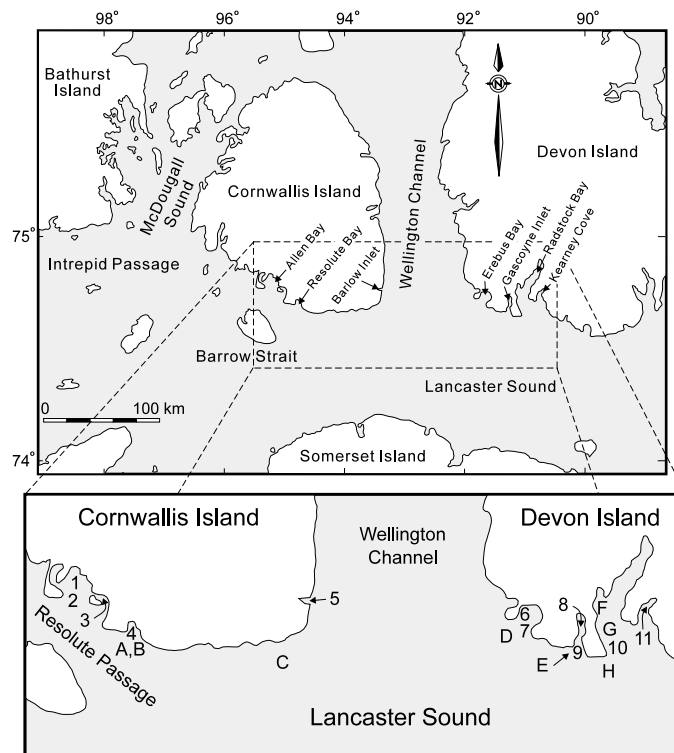


FIG. 1. Study area location in western Lancaster Sound, Arctic Canada. Letters locate temperature and salinity profiles (see FIG. 2). Arabic numerals locate plankton sampling sites (see Table 1).

was towed at 8 km·h⁻¹ at a depth of about 1.5 m. The system was calibrated (Johannesson and Mitson, 1983) to a target strength of -41.5 dB with echoes from a standard target (a ping pong ball). We endeavored to pattern cruise tracks on a parallel or zigzag transect survey grid (Simmonds et al., 1992), but because amounts of navigable water varied (the vessel was not ice-strengthened), it was occasionally necessary to alter search patterns.

During data collection, detected echoes were displayed and recorded on a chart recorder. Signals were also digitized and stored on magnetic tape for later analysis. Time varied gain (TVG) was 20 log R during echo integration and 40 log R during target strength data collection, where R = echo range (Johannesson and Mitson, 1983).

Locating and Measuring Fish Schools

On 31 August 1989, we used a parallel transect survey grid to examine two of several schools of Arctic cod (see Welch et al., 1993) that were in Allen Bay, Cornwallis Island (Fig. 2). The studied fish were aggregated in a cove between May and Cornwallis Islands (Fig. 3), an area hereafter called May Island Cove (MIC). During the hydroacoustic study, our strategy was to maintain the parallel transect survey plan regardless of the occurrence of detected fish echoes (nonadaptive sampling).

The following summer, on 27–28 August 1990, we used a zigzag survey pattern to search the same area of Allen Bay. We found one school in MIC in the same location studied the

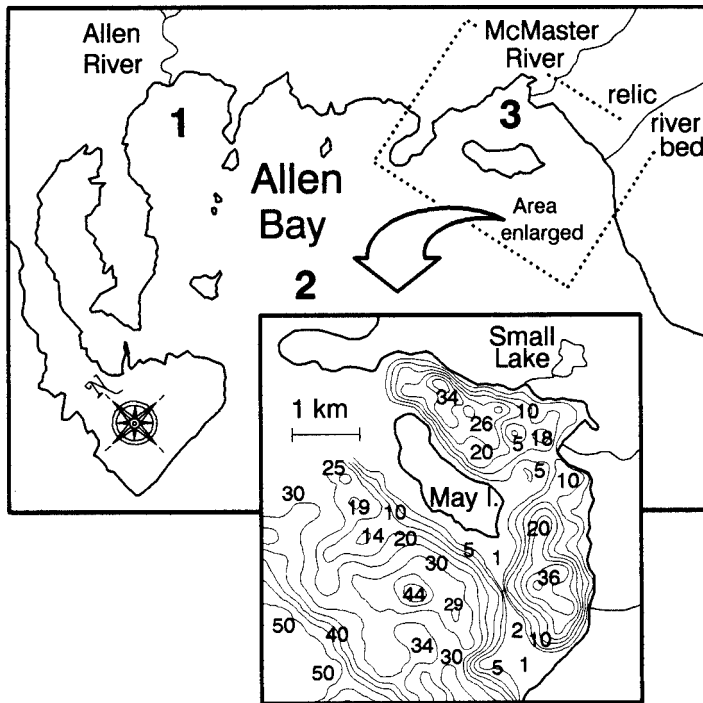


FIG. 2. Allen Bay (Cornwallis Island) configuration and bathymetry (m). The Arctic cod schools that were the subject of this study were located between May Island and the outlet of Small Lake, Cornwallis Island, an area referred to as "May Island Cove."

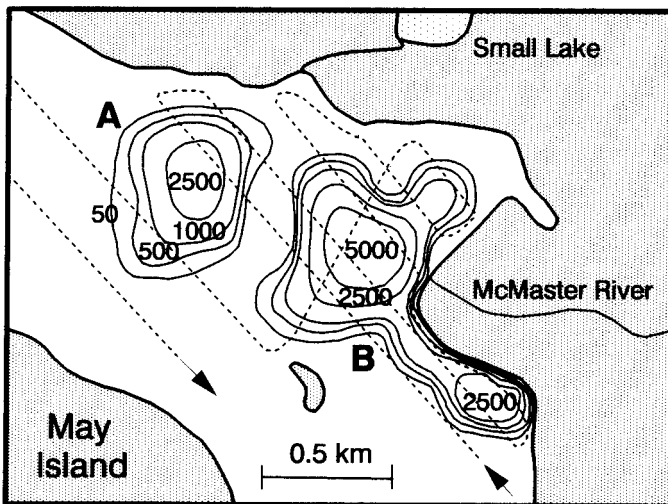


FIG. 3. Two aggregations of Arctic cod studied in May Island Cove on 31 August 1989. Isolines indicate fish density (fish·m⁻²) within the schools. Dotted line shows the cruise track of the hydroacoustic survey vessel.

previous year. In the 1990 search, we adopted a revised strategy: after marking the location of the school with an anchored buoy and orienting on this marker, we studied the school using a pattern of three evenly spaced transects that intersected roughly at their center. Each transect extended just past the edges of the school (adaptive sampling). We derived the surface area and shape of the school as we had done for the 1989 study, but the new survey pattern (after Buerkle, 1985) generated better information on school dimension.

Studies of Five Other Embayments

In 1990, between 29 August and 5 September, after sea ice had blocked further efforts to study fish schools in Allen Bay, we searched for fish aggregations in other embayments (Fig. 1). We used a parallel transect survey to examine Barlow Inlet, and a zigzag pattern in Resolute Bay (after Crawford and Jorgenson, 1993) and Gascoyne Inlet. The two largest bays, Erebus and Radstock, were studied less completely by tracing an irregular course along the shoreline, between the 5 m and 35 m isobaths. Study of Radstock Bay was limited to the bay mouth. During the hydroacoustic explorations, we also searched nearshore areas for schools either by direct visual observation (e.g., dark masses in the water) or by pinpointing gatherings of actively feeding Arctic cod predators (marine mammals and seabirds). During the searches, we collected data for analysis of echos from nonschooling pelagic fish we detected along the way.

Determining Fish Biomass

Biomass estimation with echo integration (EI) is a function of the sum of echo intensities in energy reflected by an insonified ("illuminated" by sound; Johannesson and Mitson, 1983) assemblage of fish. Echo intensity is scaled to the acoustic reflectivity (expressed in units of backscattering cross section or CS) of individual fish. Acoustic reflectivity is determined by performing target strength (TS) analysis of echoes from single fish or by deriving a scaling factor from net samples, using the TS/size relation that is representative of the fish size in the subject school, according to:

$$TS = a + b \log L$$

where L is fish length and a and b are the linear constants particular to the species of concern. TS is related to CS (symbolically represented as σ) by:

$$TS = 10 \log (\sigma / 4\pi)$$

Therefore, the equivalent CS/size relation is:

$$\sigma = 4\pi 10^{((a + b \log L) / 10)}$$

The mean CS ($\langle \sigma \rangle$) for the aggregation is calculated by applying the size relation for the species to the size distribution of fish collected in net samples, as:

$$\langle \sigma \rangle = 4\pi \sum_i f_i 10^{((a + b \log L_i) / 10)}$$

where L_i is the mid-point of the n th size class and f_i is the average fraction of the catch the n th group represents. The volume or area density (F) of the fish aggregation (in either fish numbers or weight) is derived by using the mean CS to develop a conversion factor (K) for the echo integrator and applying it to the formula

$$F = (K / \langle \sigma \rangle) E$$

where E is the mean echo integral, the integrated sum of the echoes received from the subject aggregation. Data are collected in segments along the survey track, and each segment is considered a “data block.” The general concept of this analytical approach is diagrammed in Figure 4.

Fish volume density describes the aggregation density of fish within a specific portion of the water column. It can be specific to depth or to distance from the transducer (e.g., when comparing density at the center of a school with density at its top or bottom). *Mean volume density* refers to the mean aggregation density within the entire insonified water column or the portion of concern (e.g., the depths occupied by a fish school). *Area density* describes the number of fish per unit cross section area of the acoustic beam. Since it contains the region “seen” by a downward-looking hydroacoustic transducer, area density is derived from a cumulative sum of echoes within the beam.

Many factors affect the accuracy of estimates of fish size and abundance estimates calculated with hydroacoustic methods. For example, one needs to know the true relation between TS and fish size. TS depends on echo sounder frequency and the species, size and orientation of the fish. It is also affected by the accuracy and precision of echo detection, which depends on equipment operation, performance and hydrographic conditions. An excellent overview of the hydroacoustic method and its associated errors has been compiled by Simmonds et al. (1992). Suffice it to say that in this study of Arctic cod, numerous uncertainties came into play. In acknowledgment of these biases, generous “rounding” has been applied in reporting these results, a practice that is appropriate for exploratory applications of the type reported here.

Bioacoustic Analysis of Fish Schools

In 1989, the Allen Bay sampling plan consisted of a series of parallel transects designed to cover the area of MIC where schools of Arctic cod were known to occur. Because the sampling strategy was nonadaptive, a large portion of the EI data set included more than just the two areas of fish aggregation. To focus data analysis toward the schools, we analyzed each transect separately and used a graphic technique (Crawford and Fox, 1992) to derive the shape of the schools and their surface area. Contour maps (Surfer Computer Program, Golden Software Inc., Golden, Colorado 80401-1866, U.S.A.) derived from the interpolation of values > 1 fish·m⁻² displayed the distribution of fish abundance within MIC. The cumulative surface area within the 1 fish·m⁻² contour and the relevant data blocks within the area were considered to be descriptive of a school. Lack of coherence within the boundary was minimal; only 3 of 101 blocks within the schools had area densities < 1 ·m⁻².

Area density (fish·m⁻²) and volume density (fish·m⁻³) for each 50 m data block from the portion of the cruise track that passed over a school were calculated by standard methods

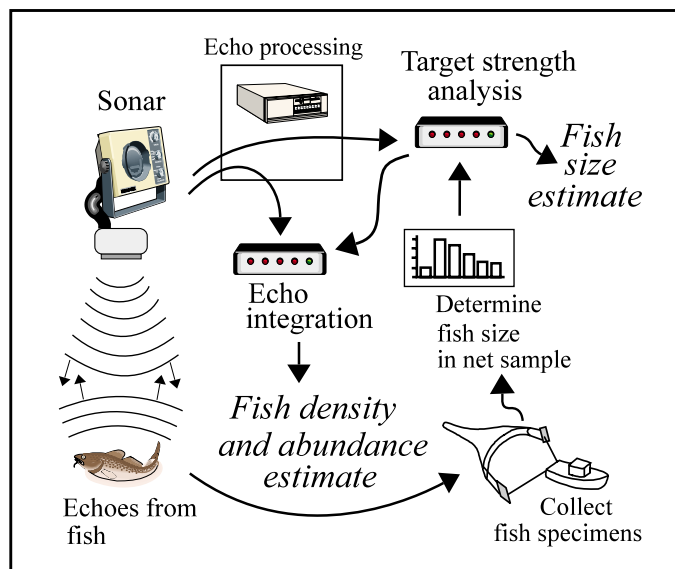


FIG. 4. Scheme of the concept for fisheries acoustics data acquisition and analysis. Echo integration, to determine abundance or density, can be scaled with a predetermined value. It can also be scaled with a value derived from target strength (TS) measurements that are obtained from the subject school and related to the size of the fish in it. TS analysis subsequently provides estimates of the size of fish detected elsewhere.

as implemented for the BioSonics Model 121 Echo Integrator (BioSonics, Inc., 1985). The data of each block were depth-stratified into 2 m intervals, and volume density was determined separately for each. Fish abundance was estimated by expanding the grand mean area densities to the surface areas of each school. Confidence intervals for fish abundance were derived from the errors associated with the mean area densities.

The adaptive sampling characteristic of the survey pattern resulted in fewer “empty” data blocks in the 1990 data set. Rather than treat each transect separately as we had done previously, we combined data and calculated fish density and abundance with standard methods for BioSonics, Inc. equipment (after Crawford and Jorgenson, 1993). Two analyses were performed, using different values to scale EI. The first used a CS value derived from the mean fish size obtained from catches with an Isaacs-Kidd midwater trawl lined with 12.7 mm knotless netting (I-K). The equivalent TS of this fish size was -45.0 dB ($CS = 3.1813E-05$ m²·fish⁻¹). The second analysis used the results of TS analysis of echoes from fish targets detected near the edge of a school. Echo tracking (see below) was not used. The results calculated with the two scaling factors were compared using the Mann-Whitney test (Sokal and Rohlf, 1969).

Acoustic Fish Size Determination

TS can also be used to estimate the size of a fish in an insonified population. The primary requisite is that fish echoes be derived from the insonification of individual fish. Another requisite is a definition of the true relation between TS and fish size. We did not determine such a relation for this

study. Because a definitive relation was not in the literature, we used a process of deduction to choose a substitute, as follows. At a 1988 meeting in Murmansk, V. Mamylov presented the following equation for the TS/size relation for Arctic cod (E. Ona, pers. comm. 1992):

$$TS = 21.8 \log L - 72.7 \text{ dB} \quad (1)$$

where TS is target strength (in dB) and L is total length (cm). It was purportedly an improvement on the relation that was being used for Arctic cod stock assessments at that time (Anon. 1988), namely

$$TS = 21.8 \log L - 74.9 \text{ dB} \quad (2)$$

A more recent and reportedly preferable relation (H. Gjøsæter, pers. comm. 1994) is

$$TS = 20.0 \log L - 70.0 \text{ dB} \quad (3)$$

However, all of these equations were derived from measurements of Atlantic cod (*Gadus morhua* Linnaeus) with 38 kHz hydroacoustics rather than the 200 kHz of this study. In absolute terms, the differences between the equations are small; when applied to Arctic cod, length estimates by equations 1 and 3 differ by < 1 cm. However, Foote et al. (1993), studying herring (*Clupea harengus harengus* Linnaeus), found that the use of 200 kHz data with these formulas could produce an error equivalent to about 2 cm for this study, a nontrivial discrepancy. Likewise, in his determination of equation 3, Ona (1994) found that Atlantic cod TS measured at 120 kHz is lower than at 38 kHz. Because of this, he recommended adjusting equation 3 when used with higher frequencies. Finally, Lear (1979, 1980) has reported that Arctic cod from more southern latitudes grow larger, with a proportionately deeper body shape, than fish in the High Arctic study area, an observation we have confirmed during several years of research. This morphic variation is likely to affect target strengths (Ona, 1990), which brings into question the applicability of using an equation for Atlantic cod to analyze data from Arctic cod.

Given this array of contingent factors, we concluded that the best equation would be determined by using a 200 kHz system to measure specimens of Arctic cod from Lancaster Sound. Without such a formula, we chose equation 1. It offered appropriate “adjustments” compared to equation 3 (namely slightly smaller TS values). It also had produced acoustically derived lengths of Arctic cod that were in general agreement with the size range of High Arctic net-captured fish during previous research in the study area (R. Crawford, unpubl. data). Recognizing that this choice incorporated errors that would affect the accuracy of our abundance and biomass estimates, we attempted to accommodate these errors by rounding. Given the challenge presented by the acoustic study of dense aggregations of fish and the myriad other sources of error we had to consider (see Discussion), we concluded that the

use of this approximate TS/size relation would not, in itself, seriously compromise this exploratory bioacoustic study of fish schools.

To reduce error from another source, we minimized the introduction of extraneous bioacoustic and electrical noise in recorded data by choosing -64 dB as the minimum signal level for computer analysis. The equivalent minimum derived fish length was 2.5 cm, the size of very young Arctic cod that live in the plankton. No minimum signal level was used when creating echograms so they included signals from smaller organisms.

Because hydroacoustic fish size determination improves with multiple insonifications of single fish (Dawson and Karp, 1990), we examined the size and depth distribution of nonschooling fish by developing an echo-tracking procedure. First, a classification algorithm (used by the BioSonics, Inc. Model 181 Dual Beam Processor) was used to identify “single fish” echoes (40 log *R* data; *R* = range from transducer in meters). These echoes were grouped into a “fish sequence” if they met the following criteria: echoes occurred in successive pings (ping = one transmission of pulsed sound energy); *R* values between pings agreed within 0.2 m; and a sequence contained a minimum of two single fish echoes (which could be separated by a “non-single fish” echo). Each fish sequence was reported as: mean tracked TS; standard deviation; median depth of echoes; number of pings; and fish size (total length) as derived by substituting tracked TS into equation 1. Equality of mean sizes found in different bodies of water was tested with ANOVA and Least Significant Difference (L.S.D., $\alpha = 0.05$). To homogenize variance, the log transformation was applied to the data before testing.

Net Sampling

In 1990, we used the I-K trawl to collect fish samples from the studied school. We determined desired sampling depth by locating “targets” as revealed by echograms and confirmed sampling depth with an acoustically linked depth indicator (Vemco VR-60) fitted to the trawl. Tow duration was typically 5 min. The catch was subsampled by taking random pailfuls, which were returned in sea-ice slurry to a laboratory, where fish were weighed ($n = 100$) and measured (total length; $n = 200$).

Plankton Sampling

In 1990 we sampled zooplankton with a bongo sampler (2 nets of 60 cm diameter). Maximum sampling depth was determined from the echograms and monitored as for the midwater trawl. The tow pattern consisted of lowering the sampler to the maximum sampling depth and then raising it to the shallow limit of the predetermined sampling range (Table 1). The nets were then lowered again and the routine was repeated (the so-called “tow-yo pattern”). Tow duration was 5–10 min. Samples from only one net (0.5 mm mesh) fitted with a calibrated flow meter (General Oceanics Model 2030R) were used for analysis.

TABLE 1. Dates, locations in the western Lancaster Sound region (Fig. 1), depth ranges and areas sampled with a bongo net plankton sampler. For some locations, water temperatures for the middle of the depth range (unless otherwise noted) are included.

Site	Date	Waterbody location	Depth range (m)	Area (km ²)
1	27 Aug.	Allen Bay, near Allen River	10–12	≈ 80
2	27 Aug.	Allen Bay, center of bay proper	10–15	≈ 80
3	28 Aug.	Allen Bay “May Island Cove”	10–25	≈ 2
4	31 Aug.	Resolute Bay, northern basin	10–20	≈ 5
5	2 Sept.	Barlow Inlet, center; -0.3°C	20–26	≈ 3
6	3 Sept.	Erebus Bay, westside; 2.0°C	15–20	≈ 25
7	3 Sept.	Erebus Bay, eastside; 2.2°C	15–25	≈ 25
8	4 Sept.	Gascoyne Inlet, center; 2.2°C	10–15	≈ 15
9	4 Sept.	Gascoyne Inlet, near mouth; 1.7°C	10–15	≈ 15
10	4 Sept.	Radstock Bay, mouth, w. side; 2.5°C	10–20	≈ 200
11	4 Sept.	Radstock Bay, Kearney Cove; 2.0°C @ 2 m; -0.2°C @ 25 m	5–30	≈ 2

Cod end contents were rinsed into 7% seawater formalin and fixed for 7–10 days before being transferred to 70% ethanol for preservation. Organisms were identified to species (if possible) and counted. For those organisms which were prominent in the plankton, and whose various life stages are known prey for Arctic cod (e.g., copepod copepodites), life stages were counted separately. Counts were expressed as number·100 m⁻³. Juvenile Arctic cod (young-of-the-year, or YOY) were also measured and mean length (total length) was determined. Organisms were ranked according to the order of their cumulative abundance in all the samples. Species richness at each site was defined as the number of species collected there.

Measurement of Environmental Parameters

In 1989, Resolute Bay temperature profiles for the study period were obtained from H. Hop (unpubl. data). In 1990, we used a CTD (conductivity, temperature, depth) system (Bergmann, 1989) to obtain depth profiles of salinity (conductivity) and temperature. Water temperature data were also obtained from the net-mounted sensor used during net sampling operations. Intermittent operation of both instruments interfered with temperature and salinity data collection from Allen and Resolute Bays, and salinity data collection from Devon Island bays. Two- and three-dimensional bathymetric maps developed from depth measurements obtained during hydroacoustic data collection (Crawford and Fox, 1992) allowed visualization of the bottom topography in MIC.

RESULTS

Environmental Conditions

In 1989, Allen Bay was relatively ice-free throughout the study period, with ample open water for navigation and for seabirds and marine mammals. In 1990, sea ice was profuse to the west of Resolute Bay (Fig. 1), our base. Allen Bay was

partially navigable during only the first two days (August 27–28) of the study period. By 29 August ice had blocked our passage to the bay, so we headed east to examine other embayments of Cornwallis and Devon Islands. Although ice was not a direct factor in the other embayments, its presence posed a constant threat to the completion of the expedition. We opted to search for Arctic cod over as wide an area as possible and to curtail certain aspects of the research plan (e.g., the collection of replicate plankton samples).

Hydrographic conditions in 1990 were similar to those of 1984–86 (Bergmann, 1989), with differences on opposite sides of Wellington Channel. Near Cornwallis Island, west of the channel, there was a weak thermocline. Water temperatures varied about 1.0°C in the mixed surface layer to about 30 m; deeper waters were almost isothermal (Fig. 5). Near Devon Island (east of the channel), the thermocline was much more pronounced. Surface waters (to about 20–30 m) were > 2.0°C warmer than deeper waters, with the warmest surface water occurring in the embayments (Fig. 5). Deeper waters near Devon Island (about -1.5°C), were 0.3–0.5°C colder than waters at similar depths near Cornwallis Island. Salinity data were insufficient to search for trends in that parameter. Near Cornwallis Island, salinity was about 32‰, except in the upper 20 m where it declined to about 29–30‰.

Water temperatures in Resolute Bay during the summer of 1989 (Hop et al., in press) were similar to those we measured at comparable depths in Resolute Passage in 1990. Accordingly, we assumed that temperatures in all the bays were similar in 1989 and 1990. We also assumed that water temperatures in Allen Bay were similar to those in Resolute Bay and were >1.0°C colder than equivalent depths (< 30 m) in the Devon Island embayments.

Bioacoustic Studies

Schooling Fish in MIC: The fish in MIC (Fig. 3) were highly aggregated (grand mean volume density both years combined = 157 fish·m⁻³; SE = 75 fish·m⁻³). In one of the three schools studied, volume density was extraordinarily high (mean = 307 fish·m⁻³; Table 2). In the other two, aggregation was typical (~70–90 fish·m⁻³) of other densely schooling species (e.g., herring and capelin, *Mallotus villosus* Müller). Measurements of volume biomass density ranged from 3.1 to 10.6 kg·m⁻³ (grand mean = 5.6 kg·m⁻³; SE = 2.5 kg·m⁻³).

Area density and biomass of the three schools were also high (Table 2). Grand mean area density for the two 1989 schools was 1473 fish·m⁻². Area density for the 1990 school was remarkably similar (1479 fish·m⁻²). Total biomass for the two 1989 schools was 30 715 t. In 1990, biomass was 2835 t. Echograms that represented Arctic cod schools as “hollow” masses revealed that acoustic shading was prevalent in our data (see Discussion).

The Arctic cod was the only fish species we caught in the I-K trawl (used only in 1990) and the trawl was successful only when sampling a school (we did not catch fish that were scattered in the water column). The length-to-weight relation for specimens from the 1990 school, using the correction of

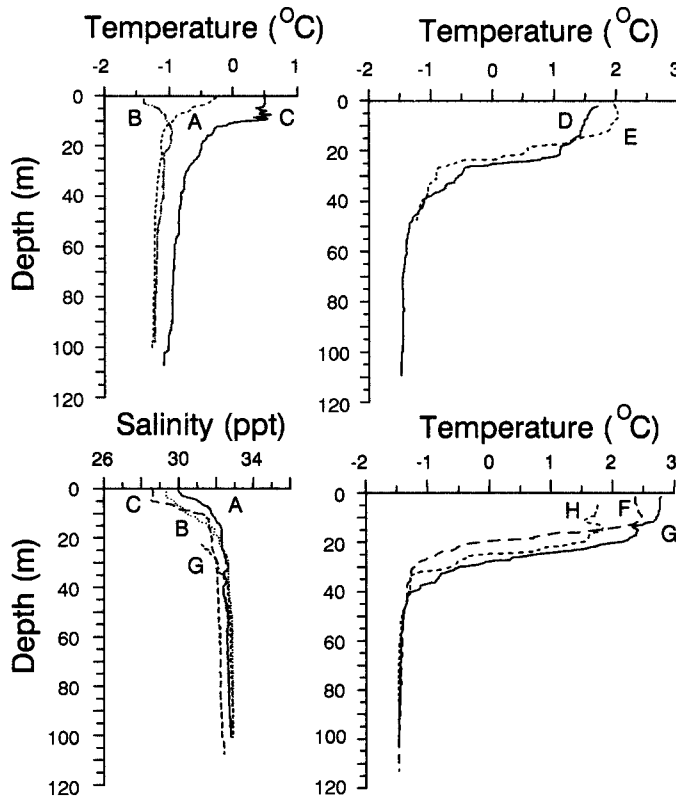


FIG. 5. Temperature and salinity profiles (summer 1990) for several locations within the study area. Letters correspond with the site markers on Figure 1.

Sprugel (1983), was:

$$W = 1.19E-02 \times L^{2.76} (r = 0.969, n = 100)$$

Mean fish size was: total length (TL) = 18.7 cm (SD = 3.5 cm, $n = 200$; Fig. 6); weight = 44.5 g (SD = 26.5 g, $n = 100$). The derived TS of this fish size was -45.0 dB, which had an equivalent CS of $3.1813E-05 \text{ m}^2 \cdot \text{fish}^{-1}$. This CS value was used to scale one EI analysis. The second analysis was performed using the results of TS analysis of echoes from 210 single fish targets detected near the edge of the subject school. These results gave a mean measured CS of $3.3932E-05 \text{ m}^2 \cdot \text{fish}^{-1}$ (SD = $3.8399E-04 \text{ m}^2 \cdot \text{fish}^{-1}$) and an average TS of -44.7 dB (equivalent fish length = 19.3 cm).

The separate EI analyses produced estimates of volume densities that were not significantly different ($p > 0.05$, Mann-Whitney test). We report the results scaled with TS analysis because the results were obtained from measurements of fish in a single-species aggregation (i.e., no ambiguity about the echo source). Also, the method of error estimation allows straightforward calculation of confidence limits (Table 2) without the incorporation of uncertainties associated with derivations used in the other analysis. In all cases, variability was high, as is typical of hydroacoustic studies in general (Simmonds et al., 1992).

Nonschooling Fish: Where fish aggregations were not detected, nonschooling fish (Table 2) were generally dispersed in a water body. The exception was Gascoyne Inlet:

TABLE 2. Results of echo integration analysis ($\pm 95\%$ CI) of three dense aggregations of Arctic cod which occurred in the same area of Allen Bay, Cornwallis Island in 1989 and 1990.

	1989		1990
	School A	School B	
Volume density ¹			
fish·m ⁻³	91 ± 42	307 ± 92	72 ± 44
range (fish·m ⁻³)	0 to 584	0 to 1146	0 to 269
kg·m ⁻³	3.1 ± 1.5	10.6 ± 3.2	3.2 ± 2.0
Area density ¹			
fish·m ⁻²	775 ± 429	2170 ± 523	1479 ± 455
range (fish·m ⁻²)	4 to 4918	2 to 8325	2 to 3612
kg·m ⁻²	26.7 ± 14.8	74.9 ± 18.0	66.6 ± 20.5
Fish numbers ^{2,3}	2.2E08 ± 1.2E08	6.7E08 ± 1.6E08	6.3E07 ± 3.7E07
Surface area (m ²)	2.8E05	3.1E05	4.6E04
Total biomass (t) ^{2,3,4}	7600 ± 4140	23 115 ± 5520	2835 ± 1665

¹ Based on means of values obtained from each 50 m segment of the cruise track across each fish school.

² 1989 confidence intervals were based on the variance of the values derived from echo integration analysis. 1990 confidence intervals were based on a combination of variances: one from echo integration analysis and another from target strength determination (variance of backscatter cross section; BioSonics, Inc. 1985).

³ Abundance and biomass estimates are first order approximations because of acoustic shading and other errors. It is reasonable to multiply estimates by a factor of 2.

⁴ Based on 45 g·fish⁻¹.

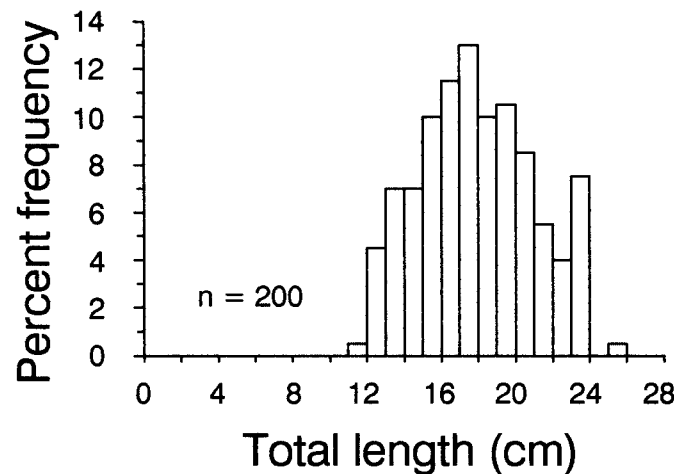


FIG. 6. Length frequency distribution of Arctic cod captured in May Island Cove (Fig. 3) with an Isaacs-Kidd midwater trawl on 28 August 1990.

200 tracked targets were detected on the south (Lancaster Sound) side of the shelf that extends across the inlet mouth; only a few targets, 12 of which were trackable, were detected inside the inlet proper.

Fish depth distribution ranged between 3 and 30 m except in Resolute Bay, where fish were not shallower than 10 m (Fig. 7). The acoustically estimated sizes (Fig. 8) of tracked targets (grand mean length = 7.7 cm) were not significantly different (ANOVA, $F = 0.43$, $df = 563$, $p = 0.73$) in four

TABLE 3. Echo-tracking analysis of fisheries acoustics data (see text for details) obtained from nonschooling fish in several Lancaster Sound embayments (Fig. 1).

	Allen Bay (n = 15, 20 m)		Resolute Bay (n = 80, 28 m)		Erebus Bay (n = 188, 22 m)		Gascoyne Inlet (n = 212, 75 m ¹)		Radstock Bay n = 149, 140 m)	
	Mean	STD	Mean	STD	Mean	STD	Mean	STD	Mean	STD
Fish length (cm) ²	7.9	2.2	10.2	3.1	7.6	3.1	7.6	3.0	7.8	2.9
Target strength (dB)	-53.6	-2.9	-51.1	-2.7	-54.2	-3.6	-54.1	-3.5	-53.8	-3.3
Target median depth (m)	10.9	2.8	14.3	2.3	11.5	2.7	12.2	4.3	14.9	6.4
Pings per target	2.6	1.0	2.7	1.1	3.2	1.5	2.7	0.9	2.6	1.0

¹ Maximum depth in the mouth of Gascoyne Inlet where fish were most abundant. (Maximum depth inside inlet proper is about 20 m.)

² Derived from target strength.

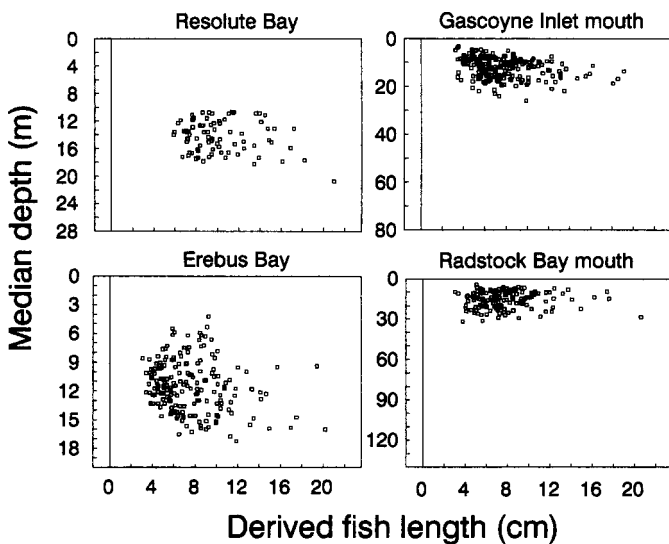


FIG. 7. Depth distribution of nonschooling fish acoustically detected in four Canadian Arctic embayments (Fig. 1) between 29 August to 5 September 1990 (see Table 3).

embayments (Gascoyne Inlet; Allen, Erebus and Radstock Bays). The derived size of fish in Resolute Bay (mean = 10.2 cm) was significantly larger (L.S.D.).

Plankton Study Results

Plankton sampling (Table 1) yielded a total of 58 zooplankton categories, comprising various life-cycle stages of 48 species (Table 4). Although the tow-yo sampling pattern mixed the catch across the depth ranges sampled, the samples reflected the zooplankton that occurred where the fish were because sampling was limited to depths where most fish echoes occurred on the echograms. The most common species was the copepod *Calanus hyperboreus* Krøyer. YOY Arctic cod ranked 14th. The next most common fish species was the cyclopterid *Liparis fabricii* Krøyer, ranked 33rd. Although smaller-sized categories (e.g., copepodites) were prominent in our collections, they were probably under-represented because the sample net mesh was comparatively large.

The plankton communities on the two sides of Wellington Channel, which separates Cornwallis and Devon Islands (Fig. 1), had different species compositions. Disregarding ambiguous identifications, 32 species were

collected south of Cornwallis Island, west of Wellington Channel; but eight of these were not found to the east. South of Devon Island, 41 species were collected, and 14 of these were not found to the west.

Average zooplankton species richness in the two Allen Bay samples taken outside of MIC was 31 species. In MIC (n = 1), it was only five species (Fig. 9), the lowest in the study. When compared with records from all other areas examined, the echograms from MIC were also uncharacteristically devoid of echoes typical of those from zooplankton-sized organisms, reinforcing the netting results.

The distribution of YOY Arctic cod, like that of the adults, was quite variable. We found the highest numbers in Allen Bay (Table 4), away from May Island, but they were also common in the mouth of Gascoyne Inlet. They were not common in Gascoyne Inlet proper or in the other embayments. Mean TL of all YOY Arctic cod was 23 mm (SD = 4.4 mm, n = 78). For all sites combined, mean density (\pm 95% CI) was 18.2 ± 20.6 fish·100 m⁻³. At stations where YOY were abundant, echograms revealed that small plankton-size organisms had coalesced into a dense layer near the thermocline. There were relatively few echoes elsewhere. This suggested that YOY were associated with the zooplankton community near the thermocline.

DISCUSSION

Fish Density in Arctic Cod Schools

Three very dense aggregations of Arctic cod were found in a specific area of Allen Bay, Cornwallis Island, within about one kilometer from shore. On almost the same dates in two consecutive years, schools were in the same location in the same bay, suggesting a very site-specific residence by this species in that area.

The aggregation densities (70–90 fish·m⁻³) in two of these schools were similar to those reported for other densely schooling fish, such as herring (Olsen, 1986). These measured values were also similar to the subjectively derived estimate of volume density determined by Welch et al. (1993). In one school we examined, however, the volume density was much higher: 307 fish·m⁻³. Using optical methods, Pitcher and Partridge (1979) determined that, in general,

individual fish within a densely packed school occupy a space that is roughly equivalent to their body length cubed (1 BL³). Although we did not obtain measurements of fish lengths from the most densely packed school, Hop et al. (in press) collected Arctic cod of about 155 mm TL from the same area (and presumably from the school we studied) one to two weeks after our acoustic studies. At 1 BL³ spacing, fish of this size would pack together at 280 fish·m⁻³, a value close to the highest measured density. With similar spacing, fish of the size (18.7 cm) we collected from a less dense aggregation in 1990 would pack together at about 150 fish·m⁻³. As Pitcher and Partridge (1979) pointed out, responses to predation affect fish spacing in a school. Although predators (marine mammals and seabirds) were present during our studies, we did not observe predator activity that obviously affected our findings. However, the range of values in our measurements indicates the high variability in the aggregation densities assumed by schools of Arctic cod.

Limitations in the Bioacoustic Study of Fish Schools

Challenges Specific to Dense Aggregations: The shading of more distant fish in a dense aggregation results in the

attenuation or extinction of transmitted sound passing through the school (acoustic shading). As a result, targets further from the sound source receive less energy and contribute less to the reflected signal (Davies, 1973; Armstrong et al., 1989; Olsen, 1990; Appenzeller and Leggett, 1992).

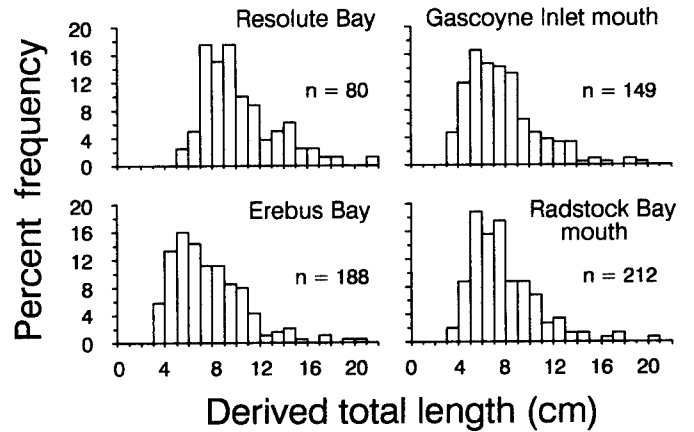


FIG. 8. Acoustically derived fish lengths (from echo tracking) of nonschooling fish detected in four Canadian Arctic embayments in summer, 1990 (see Table 2). Depth ranges for each of the four embayments are scaled to the maximum depth of the area examined with hydroacoustics.

TABLE 4. Concentration (number·100m⁻³) of 20 of 58 categories of zooplankters¹ collected with a bongo net plankton sampler (0.5 mm mesh) at several sites (Table 1) south of Cornwallis and Devon Islands, listed according to the rank of cumulative density.

Rank	Group	Genus and Species ^{2,3}	Loc. ⁴	Sample site location code (see Fig. 1)										
				Allen Bay		Resolute Bay	Barlow Inlet	Erebus Bay		Gascoyne Inlet		Radstock Bay		
				1	2	3 ⁵	4	5	6	7	8	9	10	11
1	Calanoida	<i>Calanus hyperboreus</i> , cop.	B	1105	8718	42	2440	9182	564	198	51	273	25	9048
2	Calanoida	<i>Calanus glacialis</i> , cop.	B	127	647	6	138	1909	150	21	3354	393	18	839
3	Calanoida	<i>Pseudocalanus minutus</i> , cop.	B	121	376	0	153	909	0	1	61	5	1	728
4	Larvacea	<i>Oikopleura vanhoeffeni</i>	B	0	24	2	0	0	0	2	1556	0	0	552
5	Chaetognatha	<i>Sagitta elegans</i>	B	16	193	44	333	15	4	102	142	106	7	450
6	Calanoida	<i>Acartia longirenis</i> , adult	B	358	141	0	0	0	0	0	707	16	0	0
7	Larvacea	<i>Fritillaria borealis</i>	B	0	94	0	0	0	0	7	222	0	0	563
8	Calanoida	<i>Pseudocalanus minutus</i> , adult	W	24	294	0	346	0	0	0	0	0	0	0
9	Amphipoda	<i>Parathemisto libellula</i>	B	7	90	1	57	235	5	1	2	72	14	41
10	Mollusca	<i>Limacina helicina</i> , adult	B	28	16	0	0	0	134	7	21	22	58	24
11	Cirripedia	Barnacle nauplius	B	0	224	0	0	0	0	0	2	3	0	61
12	Amphipoda	<i>Onisimus nanseni</i>	B	10	114	0	22	69	11	0	0	10	4	23
13	Mollusca	<i>Limacina helicina</i> , veliger	E	0	0	0	0	0	0	0	2	9	0	221
14	Gadidae	<i>Boreogadus saida</i> , post larvae	B	99	50	0	6	0	4	10	0	22	8	1
15	Calanoida	<i>Calanus glacialis</i> , adult	B	2	0	0	0	36	5	3	8	9	5	55
16	Calanoida	<i>Acartia longiremis</i> , cop.	B	0	12	0	0	0	0	0	101	2	0	0
17	Cnidaria	<i>Aglantha digitale</i> , juv.	E	0	0	0	0	0	0	1	101	8	0	0
18	Calanoida	<i>Calanus hyperboreus</i> , adult	B	0	0	0	10	36	1	2	0	0	1	44
19	Cnidaria	<i>Aglantha digitale</i> , adult	E	0	0	0	0	0	38	7	6	16	10	1
20	Amphipoda	<i>Onisimus glacialis</i>	B	7	0	0	5	9	0	0	0	0	0	44
21–58	Others	Various	-	-	-	-	-	-	-	-	-	-	-	-
Volume filtered (m ³)				490	136	83	81	88	74	230	99	173	163	145
Species richness ⁶				23	28	5	16	13	14	13	15	15	11	16

¹ For a complete listing of all 58 categories (48 species) contact R. Crawford.
² As zooplankter category according to various life-cycle stages.
³ Organism life stage identification code: cop. = copepodite; juv. = juvenile.
⁴ Loc. = Location of organism occurrence in relation to Wellington Channel which separates Cornwallis and Devon Islands: E = east only; W = west only; B = both sides.
⁵ Sample 3 was taken near a dense aggregation of Arctic cod.
⁶ Based on the 48 species of the entire collection, not the partial listing given here.

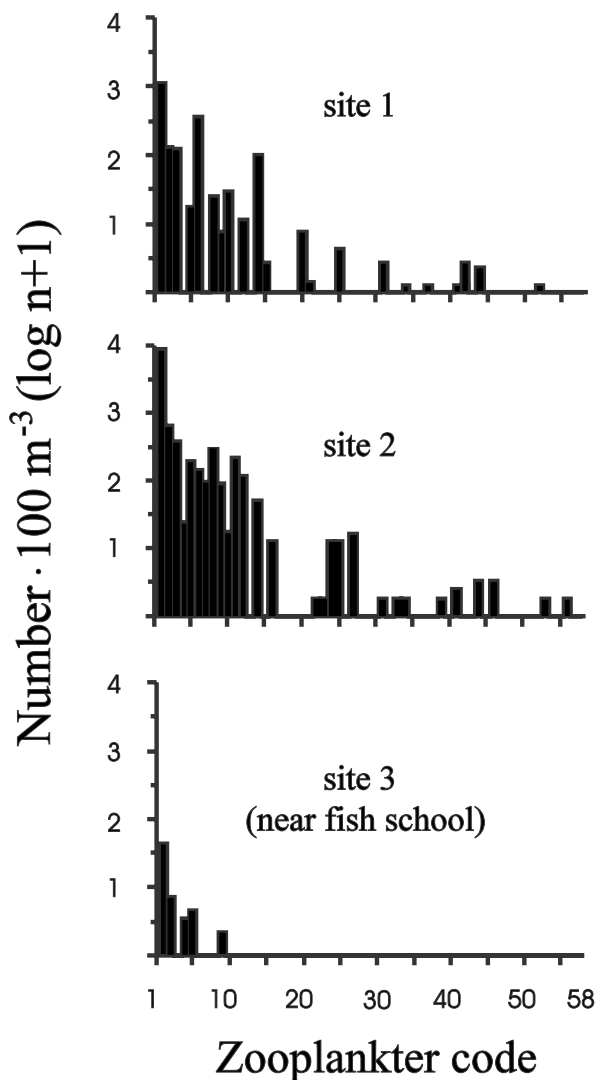


FIG. 9. Zooplankton density in August 1990 at two sites (1 and 2) in Allen Bay as compared with a site (3) in May Island Cove (Allen Bay) near a school of Arctic cod. Site location is given on Figure 1. See Table 4 for organism code index (partial).

When extinction of sound occurred in our study, Arctic cod within the deeper portions of the schools were under-represented in our data sets.

This so-called “shadow effect” is properly considered a function of area density (MacLennan and Forbes, 1984), not one of volumetric density as it is sometimes presented (e.g., Appenzeller and Leggett, 1992). The critical density value required to cause extinction depends on factors such as species, orientation, and size (Røttingen, 1976). Additional echo losses from multiple scattering effects are assumed to be negligible (Foote, 1982, 1990a). Studying 33 cm herring (*Clupea harengus* L.), Foote (1990a) and Toresen (1991) found that shadowing occurred when area densities were less than 100 fish·m⁻² (at 38 kHz). Røttingen (1976) observed shadowing when the density of 12 cm sprat (*Sprattus sprattus* L.) was about 4300–4800 fish·m⁻² (38 kHz). We measured densities of Arctic cod up to 8325 fish·m⁻², and we used a relatively high frequency (200 kHz), which exacerbates the effect of extinction (Foote, 1984).

In addition, the signal levels of echoes returned from the schools were occasionally so unexpectedly high as to saturate the bioacoustic receiver circuitry. Signal saturation essentially restricts the maximum allowable echo intensity to be incorporated into the EI analysis. With this limit on the input level, the integrated sum of received echoes is an underestimate of the true value.

Signal saturation can be avoided by appropriately manipulating the hydroacoustic system circuitry, a skill that develops with experience. Collecting data during the various conditions of this study—from waters adjacent to a school (no fish), to waters at the edge of the school itself (where we sought data from individual fish), to the center of the school (which may or may not be extraordinarily dense)—involved a large dynamic range of signal acquisition and processing experiences. Learning the appropriate techniques to accommodate this range required more study than we were allowed, given the ice conditions. On the other hand, two approaches to correct for acoustic shading have been devised. One requires special data collection (e.g., Olsen, 1986; Toresen, 1991); the other involves post-processing techniques (Foote, 1990a, b). Our 1990 plans for collecting data that would adjust for extinction and signal saturation were curtailed when sea ice blocked access to the schools of fish. We did not attempt post-processing correction because those methods are not effective when extinction is severe (Foote, 1990b), as in the case of this study.

Finally, EI analysis is accurate only when there is linearity (proportionality) between integrated echo intensity and fish density. This relationship does not apply when fish are densely aggregated (Røttingen, 1976; Foote, 1978, 1982, 1983, 1990a). The effects of this error, those of acoustic shading and signal saturation, and the others noted below make it likely that the measurements from this study underestimate the actual densities and abundances in the subject fish schools. The total error in our estimates of biomass caused by the cumulative effect was probably greater than that caused by our use of an approximate TS/size relation.

Other Sources of Error: The potential sources of error that affect hydroacoustic studies have been summarized by MacLennan et al. (1990) and Simmonds et al. (1992). Uncertainty in the absolute value of target strength is predominant (Simmonds et al., 1992) and was certainly a factor in this study. In general, much of this uncertainty results from variation caused by fish behavior. For example, nonschooling fish in Resolute Bay were no closer than 10 m to the surface, whereas in other bays they were within 2 m. Ship activity, which is known to elicit avoidance behavior by Arctic cod (Crawford and Jorgenson, 1993), was present in Resolute Bay and may have been a cause for this difference. Likewise, schooled Arctic cod have been seen (Welch et al., 1993) to move away from an approaching beluga whale (*Delphinapterus leucas* Pallas). Thus, densely aggregated fish in Allen Bay probably avoided the passage of the survey boat as it passed over them. These behaviors and others (e.g., variations in tilt angle and swimming speed) affected

backscattering (Olsen, 1990) and contributed errors to our estimates of fish density and biomass.

As noted previously, our choice of an approximation for the TS/length relation for Arctic cod was based in part on previously acceptable results (e.g., Crawford and Jorgenson, 1993). We chose to continue with this approximation for this study because there was close agreement between the mean length (18.7 cm) of net-collected specimens from a school (Fig. 6) and the mean acoustically determined length (19.3 cm) of fish at the edge of the school. However, nonschooling fish (grand mean length = 7.5 cm) were much smaller than either of these (Fig. 7 and 8). We do not know if the magnitude of this size difference was correct, but the tendency does follow a pattern we have observed previously (R. Crawford, unpubl. data).

Uncertainty about the size difference arises from the fact that acoustically derived fish size distributions are broader than the true measures because of fluctuations in echo intensity from swimming fish (Dawson and Karp, 1990). To reduce the influence of such errors in our length measurements of nonschooling fish, we used echo tracking. However, in spite of this precaution, the acoustically derived size distributions in Figures 6 and 7 should be considered characteristic and not actual representations. Fluctuations in echo intensity probably also affected the acoustically derived size estimates considered above, but we do not believe this error alone could account for the magnitude of size differences between schooling and nonschooling fish.

In summary, the errors listed here affect all hydroacoustic studies of fish abundance. The typical accuracy of this type of survey (without acoustic shading) has been estimated to be about $\pm 35\%$ (Simmonds et al., 1992). Studies that incur significant shading can be in error by $\pm 50\%$ or more (Burczynski et al., 1990; Appenzeller and Leggett, 1992). In spite of this magnitude of uncertainty, the results of this study represent the best available estimate of the biomass stored within schools of Arctic cod in the eastern Canadian High Arctic. For the purposes of considering these ephemeral features of the Arctic food web and trophic energy flow, we suggest that doubling the values in Table 1 would produce legitimate approximations of the upper bounds in the numerical ranges of fish abundance (and biomass) in the three schools we studied.

Biomass of Arctic Cod

When Welch et al. (1992) estimated that 150 000 t of Arctic cod are consumed annually by predators in Lancaster Sound, it was speculated that fish schools, which had yet to be accounted for, contained the large biomass necessary to support this level of predation. Values intuitively derived by Welch et al. (1993) for fish biomass in the two 1989 Arctic cod schools described here were gross underestimates, primarily because these authors assumed school shape to be elliptical. Instead, the surface areas of the irregularly shaped schools were ten times as large.

Our results (roughly adjusted for extinction) indicated that one 31 hectare school of Arctic cod (School "B" of Welch et al., 1993) may have contained 45 000 t of biomass. Near that school were at least six other aggregations of Arctic cod (Welch et al., 1993), although not all were as dense as the example. And though schools much larger than the example have been seen in Devon Island waters (Welch et al., 1993), the aggregations of Arctic cod described here represented an impressive concentration of biomass of this important prey. The number of Arctic cod schools occurring at a given time in the Canadian Arctic during the summer is unknown, but they are not a rare phenomenon (Bradstreet et al., 1986; Crawford and Jorgenson, 1993; Welch et al., 1993). Given that it is likely that numerous such schools occur in the expanse of the Canadian Arctic archipelago, and that the number of fish in each school is large, it is reasonable to consider that the magnitude of the aggregate biomass of these schools represents the energy source needed to balance the trophic model of Welch et al. (1992).

Additional Observations

The Arctic cod we studied may have originally been attracted to MIC by abundant food, but that was not why they remained there. This species is a generalistic feeder (Lowry and Frost, 1981). It will consume a broad range of food items (Lilly, 1980), including many of the zooplankters collected during this study, a community corresponding to the assemblage found previously in these waters (Bain and Sekerak, 1978; Buchanan and Sekerak, 1982; Hop et al., in press).

Our limited plankton survey, done perhaps several weeks after the arrival of the fish, indicated that zooplankton was less abundant near a school than elsewhere in Allen Bay. Small numbers of organisms in plankton samples in these waters are unusual (H. Welch, pers. comm. 1990). The scarcity of zooplankters in our near-school sample, and in other samples collected near schools by vertical plankton tows (Hop et al., in press), apparently reflected the cumulative effect of grazing by the schooled fish.

This phenomenon may be common in these waters. About 65% of the fish collected from schools in bays on Cornwallis and Devon had empty stomachs (Hop et al., in press). In spite of dynamic currents that continually sweep zooplankton into these areas, long-term grazing by slow-moving fish schools may routinely deplete local food resources. This occurrence is an unremarkable characteristic of aquaculture situations (e.g., near fish cages). However, as a naturally occurring phenomenon, the subject warrants further study.

Several years of inquiry in these waters (e.g., Crawford and Jorgenson, 1993; Welch et al., 1993) produced little evidence for environmental cues to where schools of Arctic cod occur. Possible exceptions are bathymetric relief and the proximity of freshwater sources. In MIC, the cod schooled in a basin where shallow sills and an island separated them from open water. The layout resembled a refuge where Arctic cod might assemble to avoid predation (Crawford and Jorgenson, 1993). The basin in MIC received the outflow of a small

stream (the McMaster River) and the discharge from Small Lake (Fig. 2). The preponderance of water flow is springtime meltwater, and its discharge presumably reduces the salinity in the receiving waters of MIC. However, no surface freshwater flows occurred during the study period. Other cod schools have been seen near inactive streambeds and also near ice (Welch et al., 1993). Additional study is needed to determine whether the relation between the location of cod schools and features that may affect salinity is more than coincidence.

On the other hand, there was clearly a relationship between temperature and the distribution of nonschooling fish. Prinsenbergh and Bennett (1987) determined that south of Cornwallis Island, eastward flowing currents (all depths) flow into western Lancaster Sound through Barrow Strait. Currents within the mixed surface layer are generally the strongest and carry cold arctic waters into Barrow Strait from Penny Strait, Viscount Melville Sound and from Peel Sound. But along the southern shore of Devon Island, warmer currents flow westward into Lancaster Sound over even colder waters from Baffin Bay (LeBlond, 1980). The maximum penetration of the warmer currents extends to about Wellington Channel, where they mix with eastward flowing Barrow Strait water and southern flowing Wellington Channel water. The CTD data (Fig. 5) were consistent with this scenario.

Near Cornwallis Island, where water temperatures were not colder than -1.3°C , fish were scattered throughout the water column. But near Devon Island, where waters deeper than about 35 m were about -1.5°C (Fig. 5), fish were found only in the warmer surface waters ($< 2.0^{\circ}\text{C}$). These warmer surface waters are also where very large schools of Arctic cod have been sighted (see Welch et al., 1993). That no fish occurred in water colder than about -1.3°C may be a function of the limit of freezing protection afforded by the antifreeze glycoprotein in Arctic cod (Osuga and Feeney, 1978). Though our plankton sampling was limited to the mixed surface layer, YOY Arctic cod were apparently associated with a plankton community that also remained above the thermocline.

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