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Schooling behaviour of arctic cod, *Boreogadus saida*, in relation to drifting pack ice

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Synopsis

Concentrations of arctic cod were detected with a hydroacoustic system in Resolute Bay, NWT during 2 weeks in August of 1986. Fish biomass within the bay was about 30 t. The fish were feeding primarily on amphipods, which were abundant. When the daily location of the schools was examined in relation to the extent and position of drifting pack ice, a pattern emerged suggesting that the distribution of the fish was influenced by the amount and location of ice cover. If the bay was relatively ice-free, the density of schooling cod was high and the size of the schools, as 2-dimensional surface area, was generally small. When ice covered the bay, density within the schools was lower and they occupied more area. Arctic cod were most dispersed after the bay had been filled with pack ice for several days. It is postulated that this behaviour is a response to potential predation by seabirds and marine mammals.

Introduction

The arctic cod, *Boreogadus saida* (Lepechin, 1773), is considered to be a pivotal member of the arctic food web, yet relatively little is known about its numbers or habits in the Canadian Arctic (Bradstreet et al. 1986). Its distribution is circumpolar at high northern latitudes and in the limited diversity of the arctic marine food web, this fish represents the major link between the secondary producers (zooplankton) and the top carnivores (marine mammals and seabirds) (Andriashev 1964, Bradstreet[1], Hobson & Welch 1992b, Mansfield et al. 1975, Moore & Moore 1974, Sergeant 1973). The diet of arctic cod consists mainly of copepods and amphipods (Bradstreet et al. 1986). It is unusual among Arctic species in that its growth pattern is r-selected and it is short-lived (maximum age = 7 + years).

In the Canadian Arctic, arctic cod have been observed in two general types of distributional patterns: (a) scattered in low densities (Crawford & Jorgenson 1990, Lowry & Frost 1981, Pereyra &

[1] Bradstreet, M.S.W. 1977. Feeding ecology of seabirds along fast-ice edges in Wellington Channel and Resolute Passage, N.W.T. Report by LGL Ltd., Toronto, for Polar Gas Project, Toronto. 149 pp.

Wolotira[2] and (b) aggregated in schools (Bradstreet et al. 1986, Welch et al. 1992). It is not known whether dispersed individuals gather periodically to form schools or whether some individuals remain dispersed while others form schools as distinct entities (Bradstreet et al. 1986). The type of behaviour considered in this report is schooling that occurred in the late Arctic summer.

Between 1985–1990, the Department of Fisheries and Oceans (DFO) conducted a program designed to gather information on the biology and behaviour of arctic cod in the Canadian Arctic. A hydroacoustic system was the major tool for these studies. Numerous observations of schools of arctic cod in various locations and circumstances have been made (e.g. Welch et al. 1992). During the 'open water' summer season, school location ranged from the nearshore shallows of small bays to the middle of the channels of the Arctic archipelago. Their depth distribution ranged from the surface waters to the bottom, with depths exceeding 150 m. The density of fish within the schools can be extraordinary, concentrating very large numbers of fish in small areas (Welch et al. 1992). Other schools have consisted of comparatively loose aggregations (e.g. this study).

Ponomarenko (1968) postulated that late summer nearshore concentrations of arctic cod may be a result of pre-spawning behaviour, although the species does not actually spawn until mid-winter. Workers in the Beaufort Sea have observed an apparent positive relationship between the abundance of arctic cod and the summertime onshore movement of marine water masses (Craig et al. 1982, Griffiths et al.[3], Moulton & Tarbox 1987). However, others have reported the opposite pattern in the same waters (Fechhelm et al.[4], Craig & Schmidt[5]). It has also been suggested that the movement of arctic cod into bays and inshore areas during the summer may be related to the abundance of food organisms there (Craig et al. 1982).

In other fishes, an important function of schooling behaviour is thought to be the reduction of risk to predation (Neill & Cullen 1974, Duffy & Wissel 1988). Sometimes, the schools we observed in Resolute Bay were preyed upon with great intensity and commotion by seabirds (northern fulmar, *Fulmarus glacialis;* arctic tern, *Sterna paradisaea;* black guillemot, *Cepphus grylle*) and marine mammals (ringed seal, *Phoca hispida;* bearded seal, *Erignathus barbatus;* and beluga whale, *Delphinapterus leucas*) (Welch et al. 1992). At other times, the schools were relatively unmolested. We have yet to observe the aggregation of a dispersed group of fish into a school.

During the course of these studies, we have noted apparent differences in the density distribution of this fish, depending on local sea ice conditions. Although we have attempted to conduct specific research on this topic, appropriate circumstances (e.g. coincident ice and fish distributions) have not occurred during these times. As a preliminary effort, we have conducted an a posteriori analysis of a unique data set obtained in 1986. During that year, ice pans and arctic cod schools remained in Resolute Bay throughout the summer and we observed them during a twelve day period in August. These data were originally collected as part of a larger study of Arctic fish abundance. This new analysis was done to examine whether arctic cod affect their behavioural distribution in relation to the amount and location of ice in their immediate environment.

[2] Pereyra, W.T. & R.J. Wolotira. 1977. Baseline study of fish and shellfish resources of Norton Sound and southeastern Chukchi Sea. pp. 288–319. *In:* Environmental Assessment Alaskan Continental Shelf, Annual Report Principal Investigators, March 1977, Vol. 8, Receptors-Fish, NOAA/BLM, OCSEAP, Boulder.

[3] Griffiths, W.B., D.R. Schmidt, R.G. Fechhelm & B.J. Gallaway. 1983. Fish ecology. Vol. 3. pp. 19–342. *In:* B. Gallaway & R. Britch (ed.) Environmental Summer Studies (1982) for the Endicott Development, Report by LGL Alaska Research and Northern Technical Services for Sohio Alaska Petroleum Company, Anchorage. 342 pp.

[4] Fechhelm, R.G., P.C. Craig, J.S. Baker & B.J. Gallaway. 1984. Fish distribution and use of nearshore waters in the northeastern Chukchi Sea. NOAA, OMPA/OCSEAP, Anchorage. 178 pp.

[5] Craig, P. & D. Schmidt. 1985. Fish resources at Point Lay, Alaska. Report by LGL Alaska Inc. for North Slope Borough Materials Source Division, Barrow. 105 pp.

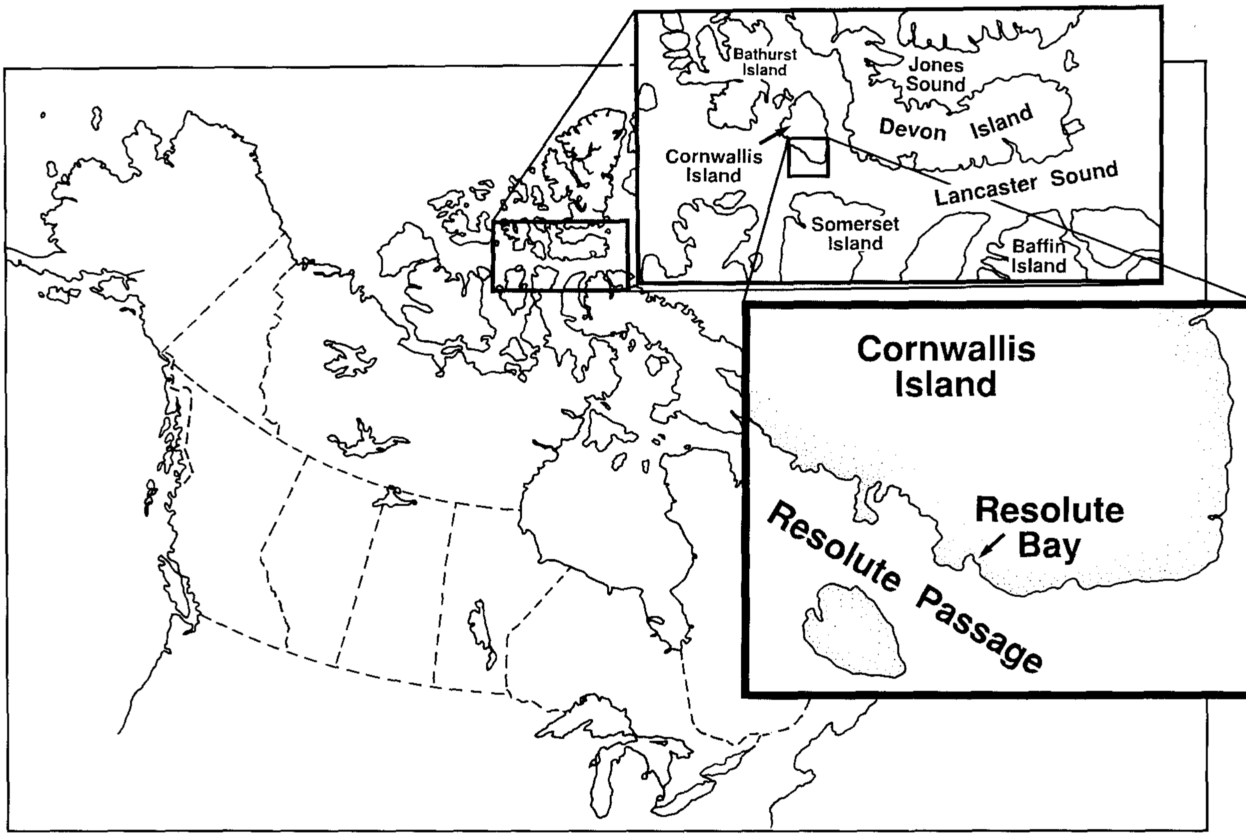


Fig. 1. Location of Resolute Bay, Cornwallis Island in the Canadian High Arctic.

Materials and methods

Study area

Resolute Bay is a small embayment (about 5 km^2) on the south coast of Cornwallis Island, N.W.T. (74°42′ N, 94°50′ W) (Fig. 1). It is part of Resolute Passage in Barrow Strait, an extension of Lancaster Sound, and is in the eastern portion of that body of water commonly referred to as the Northwest Passage. There is a shallow sill (about 2–7 m) across most of the entrance to the bay and a deeper basin (maximum depth = 28 m) in its northern portion (referred to hereafter as the northern basin). The Inuit village of Resolute is located on the bay's northern shore.

The hydroacoustic study

We used a dual-beam hydroacoustic system (Table 1) to study fish abundance and distribution in the bay. The transducer was mounted in a vee fin which we towed about 1.5 m below the surface. We followed a set of zig-zag transects across the bay (Fig. 2), as ice conditions would allow.

Occasionally, we had to detour around floating ice but such deviations were minor. They were considered to have no adverse affect on our surveys. Boat speed was typically 7 km h^{-1} in open water. When working near ice, we slowed to about 5 km h^{-1} for safety. We did not actually hit the ice so there were no undue loud noises from our passage beyond that of the engine.

We examined the bay on six dates in 1986: August 11–15, and 22. On each date, two recordings were executed consecutively (3 h total time re-

Table 1. Fisheries acoustics system specifications.

Transmitter/receiver	BioSonics, Inc. Model 101
Frequency	200 kHz
Transducer	circular, dual-beam, 6° × 15° (nominal)
Source level (dB/uPa at 1 m)	220.6
Pulse length (ms)	0.3 – 0.4
Pulse repetition rate (sec^{-1})	2.5 – 10
TVG	20 log R or 40 log R @ 12.5 – 125 m
Absorption coefficient	46 db km^{-1}
System-receiving sensitivity, 40 log R (dBv/uPa at 1 m)	– 122.2
Water temperature (C)	0.5°
Estimated speed of sound in water (m sec^{-1})	1445.7
Echo integrator	BioSonics, Inc. Model 121
Target strength analyzer	BioSonics, Inc. Model 181

quired). The first was to collect data for dual-beam target strength (TS) analysis (Ehrenberg 1974). The second was to estimate biomass by echo integration (EI). During each we recorded wind direction and mapped the distribution of the ice pack in and near the bay. The amount of ice cover, as tenths of the total bay area, was estimated from these maps. On all dates but the 15th, we examined as much of the bay as the ice would allow. On the 15th, we studied only the southern portion of the bay and its mouth, although the northern basin was ice-free.

We calibrated the acoustic system at the start of each survey by standardizing it to – 41.5 dB with echoes from a ping pong ball (Johannesson & Mitson 1983). During data collection, a chart recorder made echograms of fish and zooplankton detections. Acoustic signals were stored digitally on magnetic tape for later analysis. Unwanted small signals were eliminated from our biomass estimates by thresholding at the – 63 dB signal level. The equivalent size fish target (see below) for this echo level was about 2.8 cm, the size of an early juvenile arctic cod (Sekerak 1982).

We acquired data for TS analysis on August 22 when many fish were adequately spaced for the detection of individual targets. The mean value of all echoes detected (as fish backscattering cross section) was used with data from all dates to scale the echo integrator for estimations of fish abundance and density, following standard methodology (Johannesson & Mitson 1983). Estimates of biomass were derived by multiplying abundance estimates with the derived mean size of the acoustically detected fish (see below).

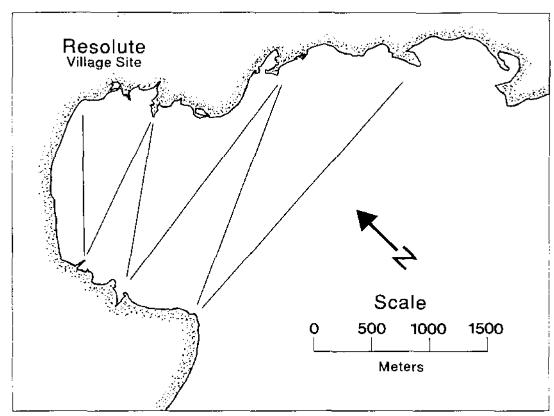


Fig. 2. Approximate vessel path followed during the hydroacoustic recording of arctic cod distribution in Resolute Bay. Adjustments were occasionally required to avoid ice.

Echo integration analysis proceeded, after BioSonics, Inc. protocol[6], as follows. Data were depth stratified into 1 m intervals and grouped into units representing 40 m of distance travelled by the survey boat. These units were horizontally averaged for each transect to derive an estimate of fish abundance as:

[6] BioSonics, Inc. 1985. Fish density and biomass estimates from echo integration data using CRUNCH software. BioSonics, Seattle.

$$Q_k = M_k V_k / C_e \bar{\sigma}_{bs},$$

where Q_k = fish abundance in the kth depth stratum, M_k = mean value of the echo integrator output for the kth depth stratum, V_k = total volume of water in the kth depth stratum, C_e = equipment scaling factor, and $\bar{\sigma}_{bs}$ = mean value of fish backscattering cross section. Total abundance was the sum of fish in all depth strata.

A confidence interval (95%) for this estimate was calculated by first deriving the variance for each depth stratum estimate:

$$\text{var}(Q_k) = Q_k^2 * [\text{var } M_k / M_k^2 + \text{var } \bar{\sigma}_{bs} / \bar{\sigma}_{bs}^2].$$

The confidence interval for each stratum estimate was defined as:

$$CI_k = Q_k \pm 1.96 \sqrt{\text{var}(Q_k)}.$$

From these, a confidence interval for the estimated fish stock in the bay (for (p) depth intervals) was computed as:

$$Q = \sum_{k=1}^{p} Q_k \pm 1.96 \sqrt{\sum_{k=1}^{p} \text{var}(Q_k)}.$$

During EI analysis, erroneous data (e.g. bottom echoes) were excluded with graphically aided editing techniques (Crawford & Fox 1992). Similar data visualization methods were used for data interpretation and presentation. For example, we superimposed EI derived 2-dimensional contour plots of fish abundance onto a scaled map of Resolute Bay and used them to estimate the area (m^2) of fish schools. Fish biomass was estimated by multiplying these areas by the corresponding mean 'surface density' (fish m^{-2}) within the schools. We also determined the water column cross-sectional 'volume density' (fish m^{-3}) to examine vertical fish distribution. The mean fish volume densities for each day were examined with analysis of variance (alpha = 0.05) and compared with Tukey's multiple pairwise comparison (Steel & Torrie 1980).

An acoustically-derived estimate of fish-size distribution in the bay was done with custom post-processing software which grouped echoes into sequences which were assumed to represent individual fish (so-called echo tracking), after Traynor & Ehrenberg (1979). First, the echo classification algorithm of BioSonics, Inc.[7] was used to sort echoes into two groups: 'single fish' echoes, which are suitable for target strength analysis; and 'multiple fish' echoes, which are not suitable for such analysis. For echoes to be grouped into a 'fish sequence', they must have occurred in successive pings (ping = a transmission of pulsed sound energy into the water column by the acoustic system) and their depths must agree within 0.2 m. A sequence must contain a minimum of two 'single fish' echoes but these could be associated with two others which did not meet this standard. That is, the smallest sequence consisted of either two 'single fish' echoes in 2 pings or two 'singles' and one or two 'multiple' echoes in 3 or 4 pings. [Tests done on tracking echoes from fish detected beneath landfast sea ice have indicated that not all echoes from single fish are successfully classified by the algorithm, justifying the inclusion of 'multiple' echoes (R. Crawford unpublished data)]. For each sequence, we determined the mean target strength (tracked TS) and its standard deviation, the median depth of the echoes, and the number of pings.

Fish size (total length = L) was estimated from the tracked TS values according to the following relation (Anon[8]):

$$TS\ (dB) = 21.8 * \log L\ (cm) - 72.7\ (dB).$$

Fish weight was derived from power function analysis (Sprugel 1983) of fish size groundtruth data (see below):

$$\text{Weight (g)} = 5.5E\text{-}0.3 * (L^{3.06}),$$

where r = 0.997, n = 168). The size/depth distribution of tracked targets was examined with linear regression analysis.

[7] BioSonics, Inc. 1986. Model 181 dual-beam processor with ACQUIRE and TARGET STRENGTH software. BioSonics, Seattle.

[8] Anon. 1988. Report on the joint Norwegian/USSR acoustic survey of pelagic fish in the Barents Sea: September – October 1988. Institute of Marine Research, Bergen.

Groundtruthing the acoustic data

To identify and scale targets detected acoustically, we caught fish with a bottom trawl and gill nets, and we sampled plankton with a plankton trawl. The bottom trawl (4.9 m ground sweep) was constructed of 5.1 cm mesh netting, except the cod end was 3.8 cm mesh with a 1.3 cm knotless mesh liner. We used the trawl on August 11, 12, and 22, when there was adequate ice-free water. Most sampling was done in the northern basin. We towed the net along the bottom in water depths between 4–20 m.

The gill nets were sinking-type, 1.8 m high, made of five 13.7 m long panels of different mesh sizes: 20, 37, 65, 90, 110, and 120 mm (stretched mesh). We used them on August 21, when a narrow 'moat' developed along the northern basin shoreline as the ice pack slowly moved out of the bay. The nets were used where we detected schools of fish with the navigational echo sounder of the survey boat. Water depth ranged from 5–15 m and pack ice cover in the northern basin was about 4/10 – 6/10. The rest of the bay was ice choked. Set duration was about three hours.

The plankton net was a 0.4 m^2 Tucker-type trawl of 0.500 mm mesh with a 0.750 mm mesh lined cod end bucket. We used this net on August 11, 12, and 22, also. During a tow, avoiding ice often required changing direction. To avoid contact with the bottom, we lowered the net to about the middle of the water column, slowly brought it to the surface, and lowered it again before retrieval. Tow duration was about 15 minutes. We estimated the depth of the net from the length and angle of the tow wire.

Fish were brought ashore where they were weighed, measured and frozen at −20° C. Total time between capture and freezing was less than four hours. Plankton samples were preserved in seven percent seawater-formalin for later examination.

In the laboratory, the fish were thawed and otoliths were removed. These were heated in glycerine (Lawler & McRae 1961) and the darkened rings (assumed to be annuli) were counted to determine age. Stomachs were also removed from a randomly selected sub-sample from the gill net catches. The degree of stomach fullness was estimated (scale of 0–4, 4 = full) and the contents were identified to genus, if possible.

Results

General conditions

Several schools of arctic cod remained in Resolute

Table 2. Ice cover, wind direction, and mean fish volume density in Resolute Bay during the August 1986 study period. Tukey's multiple pairwise comparison identified two groups with homogeneous means (A and B), with overlap between the two groups for August 11–13. The association of each mean to the groups is indicated (*).

Date	Ice cover[a]	Wind dir	Fish·m^{-3}		Pairwise comparison		Remarks
			Mean	SD	Group A	Group B	
11	1/10	NE	1.341	3.201	*	*	· Bay relatively ice free
12	1/10	NE	1.928	1.492	*	*	· Bay remains ice free
13	7/10	NW	0.894	1.118	*	*	· Northern half ice free; southern half of bay fills with pack ice
14	3/10	NNE	0.176	0.173		*	· Overnight, bay was ice choked; by afternoon, bay was relatively ice-free except for eastern side
15	1/10	NE	2.942	5.416	*		· Bay ice-free
16–21	9/10	W	–	–			· Bay ice-choked, unnavigable, study suspended
22	6/10	NW	0.122	0.185		*	· Ice slowly leaves northern half of bay, southern half remains ice-choked
23	9/10	W	–	–			· Bay ice choked, study ended

[a] Approximate values based on a scale of 0/10 (no ice) to 10/10 (solid ice).

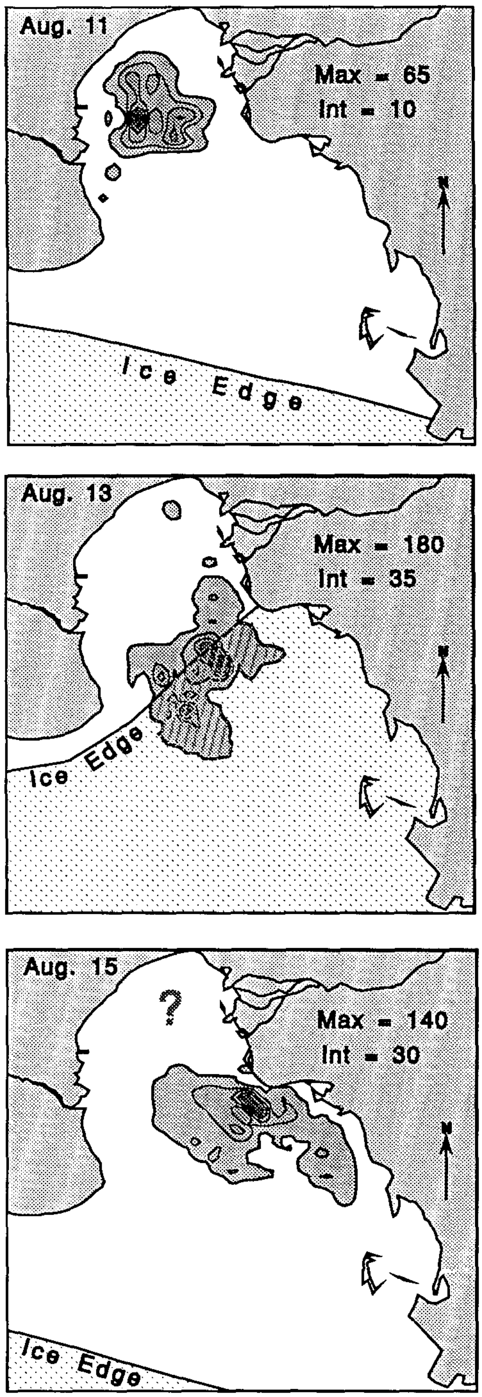


Fig. 3. Distribution of fish and ice in Resolute Bay on several dates in August 1986. Minimum surface density plotted = 1 fish m^{-2}. Isopleth scale (maximum and interval values in fish m^{-2}) noted on each panel. Ice edge on August 13 was penetrable by boat and fish distribution under ice is plotted. Ice edge on August 14 and 22 was impenetrable; fish distribution under ice unknown. Northern basin (marked with ?) was not examined on August 15.

Table 3. Surface densities, stock size and biomass estimates in schools of arctic cod in Resolute Bay on several dates in 1986.

Date	Fish m^{-2}		School area (m^2)[a]	Stock		Biomass[b] (tonnes)
	Mean	SD		Mean	95% CI	
8/11	6.7	1.7	8.8E + 05	5.9E + 06	1.4E + 06	18
8/12	15.9	5.6	7.8E + 05	1.2E + 07	8.5E + 06	37
8/13	10.6	2.2	1.5E + 06	1.6E + 07	6.6E + 06	49
8/14	2.5	0.3	1.3E + 06	3.2E + 06	4.1E + 05	10
8/15[c]	8.1	1.3	1.7E + 06	1.4E + 07	4.4E + 06	42
8/22[d]	0.6	0.1	1.2E + 06	6.6E + 05	2.3E + 05	2

[a] Combined area of all schools.
[b] Extrapolated from estimates at 3 g fish^{-1}.
[c] Based on incomplete survey of the bay (see text).
[d] Based on that portion of schools which were in open water; many fish were under ice (see Fig. 3).

Bay through the study period. When we began our study (August 11), seabirds, mostly northern fulmars and black guillemots, were feeding on the fish but no marine mammals were observed. By the next day, only a few northern fulmars remained in the bay. Bird abundance remained low for the rest of the study period.

Although the amount of drifting pack ice in Barrow Strait in the summer is always unpredictable, the strait is generally navigable by small boat during August. However, 1986 ice conditions were exceptional; the northern shore of the strait was choked with ice virtually the entire summer. Ice pans drifted into Resolute Bay almost continuously: navigable 'open' water in the bay was often very limited.

The distribution of the ice was influenced by the direction and duration of the prevailing wind (Table 2). When it was from a northerly direction, ice was pushed away from the southern shore of Cornwallis Island, and the amount of open water in the bay increased. When the wind direction had a westerly component, ice was blown into the bay, impeding the passage of our 6.7 m boat (and presumably marine mammals as well).

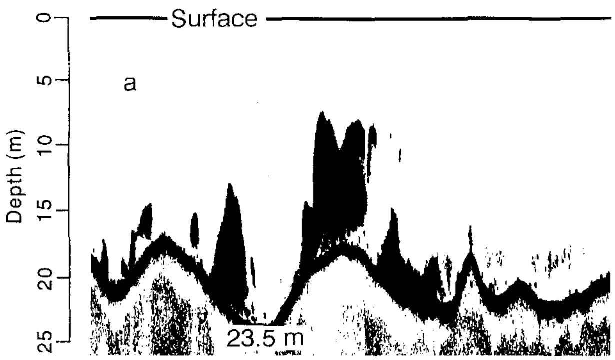
Fish distribution

During the first two days of our study (August 11–12), 6–12 million arctic cod occasionally filled the lower half of the water column in the north basin (Fig. 3, Table 3) in schools > 15 m thick (Fig. 4a). The bay was generally ice-free. Fish ranged between 3 m from the surface to the bottom on the 11th, but they descended soon after we began our transects. On all other dates, fish were detected no closer than 5 m from the surface.

By the morning of the 13th, the southern half of the bay was covered with pack ice (Table 2). Nevertheless, there was sufficient space between ice pans for passage of our boat and we were able to examine the entire bay. Compared to the situation on August 11–12, there were few fish in the ice-free northern basin and many were under the ice (Fig. 3).

During the morning of the 14th, a change in wind direction (Table 2) began to move the ice out of the bay. By the afternoon, the bay was generally clear and the fish were scattered in several schools (Fig. 3); the largest two were in the east-central area and the northern basin. Mean surface density had decreased (Table 3).

By the 15th, the bay was completely ice-free. Although we did not traverse the standard set of transects, we examined the southern half of the bay and its mouth during the execution of other unrelated work. We found a large school in the east-central portion of the bay and the fish volume density there was the highest we recorded during



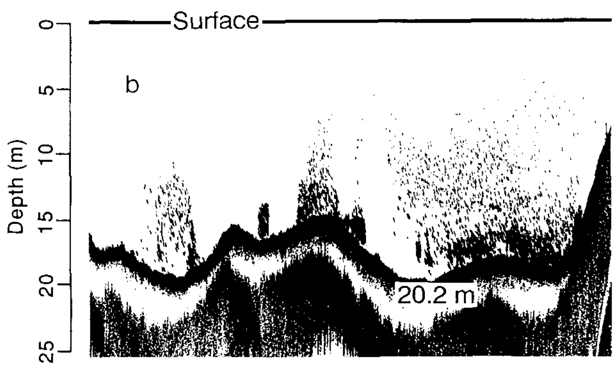


Fig. 4. a –Echogram of arctic cod schools in Resolute Bay, 11 August 1986. Distance displayed = 378 m. Minimum resolved fish separation = approx. 0.58 m. b – Echogram obtained in Resolute Bay, 22 August 1986. Distance displayed = 408 m. Minimum resolved fish separation = approx. 0.14 m. Compared with a, higher resolution emphasizes fish separation.

the study (Table 2). Fish abundance in the northern basin on that date was unknown but there were no seabirds feeding in that area.

During the night of the 15th, a wind shift carried large amounts of ice into the bay, precluding hydroacoustic observations until the 22nd. On the afternoon of that date we had access to only the northern half of the bay. Fish were relatively scattered (Fig. 4b). No dense schools were found and the volume and surface densities were the lowest recorded. Total abundance was also low (Table 3), suggesting that fish which we detected previously may have been under the dense ice pack that we could not enter with our boat.

Fish density

The mean volume densities (fish m^{-3}) for each date were significantly different ($F = 2.92$, $df = 5{,}150$, $p = 0.0152$). The means comprised two groups (Table 2) and there was overlap between the two groups for means from August 11–13. The lowest values were obtained after ice had covered the bay. The highest values coincided with open water periods.

Fish size

There were a total of 629 'single fish' echoes detected on August 22 (mean backscattering cross section = 8.4372E-06, sd = 1.5122E-05; mean TS = −54.1 dB, sd = 5.1). From these, 134 tracked echoes were identified by the echo tracking software. Target strengths of tracked echoes ranged from −40.1 dB to −62.4 dB (mean = −54.1 dB, sd = 3.7, mean pings per target = 3.1), corresponding to fish sizes of 3.0–31.3 cm (mean = 7.8 cm, sd = 3.8). This range is similar to that of other data sets obtained from Resolute Bay, before and since (R. Crawford unpublished data) but the mean value is 1–2 dB (0.8–1.7 cm) less. The distribution of the acoustically derived fish lengths was unimodal (Fig. 5) and there was no relation between tracked fish size and depth ($r^2 = 0.002$, mean depth = 14.2 m). Most fish echoes, tracked or not, were from the lower half of the water column (Fig. 4).

Artic cod was the only pelagic fish species caught in the nets. Unlike the acoustic data, the length frequency distribution of the combined net catches was bimodal (Fig. 5) and the mean size was larger (mean length = 13.3 cm, sd = 5.9, n = 184; mean weight = 27.6 g, sd = 24.8, n = 169). Fish in the smaller group (5–10 cm total length), caught with the bottom trawl, were primarily age 1+. These specimens were found among long (up to 4 m) fronds of ribbon kelp in the by-catch, an association consistent with SCUBA observations (R. Crawford unpublished data).

The larger arctic cod (13–25 cm) came from the

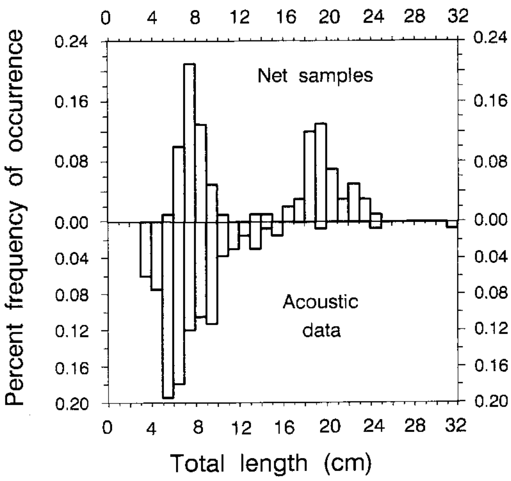


Fig. 5. Length-frequency distributions of arctic cod collected with nets from Resolute Bay on August 11, 12, 21, and 22, 1986 and the derived lengths from acoustically tracked targets detected on August 22 (see text).

gill net and the majority of these were captured in the 37 mm mesh panel. They were predominantly age 3 + to 5 +. These fish were poorly represented in the acoustic data. It was not known if this difference was an accurate reflection of the situations occurring on the two sampling dates or if it was a result of the different sampling methods (August 21 = gill nets; August 22 = TS data). Very few age 2 + fish were captured in the net samples. The gonads of all the arctic cod specimens examined were undeveloped.

Fish biomass

The acoustically derived mean fish size was about 8 cm or 3 g. Average fish biomass for August 11–13 was about 35 t (Table 3).

Other observations

Throughout the study period, the fish schools moved slowly; most stayed in the same general area for several hours of a day. Although a school may have occupied a large portion of the water column, fish were concentrated near the bottom (Fig. 6).

Echograms indicated there were also high numbers of zooplankters in the bay. Our plankton net was not equipped with a flow meter so quantifica-

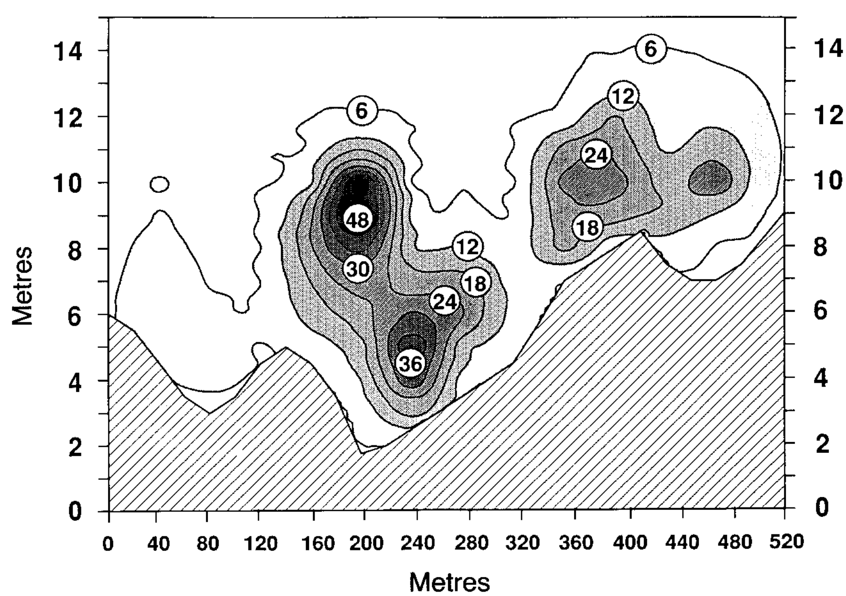


Fig. 6. Cross-section of the main body of fish in Resolute Bay on 13 August 1986. Results were obtained by echo integration of hydroacoustic data which were depth stratified into 1 m intervals and totalled every 40 m along the track of the survey vessel. Isopleths indicate fish 40 m^{-3}.

tion of these samples was not possible. We caught primarily copepods (*Calanus hyperboreas*), amphipods (*Onisimus litoralis*, O. *glacialis* and *Parathemisto libellula*), and ctenophores (*Mertensia ovum*). We also caught a few fish larvae, mostly Cyclopteridae (*Liparis fabricii*, L. *tunicatus*), and a few bigeye sculpin, *Triglops nybelini*. There were no young-of-the-year arctic cod in our samples.

The arctic cod we collected with the gill net had been feeding almost exclusively on *Onisimus* sp., although smaller P. *libellula* were also consumed. The stomachs of these fish were more than half full (mean fullness = 2.26, sd = -1.16, n = 43).

Discussion

During our observations, when ice drifted into the bay, the schools of arctic cod appeared to move under it. Later, as the ice was leaving, the fish in the schools were found to be spread out, covering more area of the bay. By the time the bay was relatively ice-free, the fish had re-assembled into a denser school. We concluded that when under ice, arctic cod became less aggregated and increased their nearest-neighbour distance (NND).

The distribution of the loosely aggregated schools was patchy. This apparent lack of structure was interpreted to be a reflection of foraging behaviour. However, because they altered their distribution in relation to the distribution of ice in the bay, the schools appeared to be sufficiently close together to maintain sensory communication within the whole group. The change in school density relative to ice conditions was interpreted to be a reaction by the fish to adjust their NND according to their circumstance. When foraging in open water, the arctic cod decreased their NND.

Because they apparently respond to the presence or absence of ice, arctic cod may form schools in shallow ice-free water as a defensive social posture, a behaviour which balances risk and reward (Pitcher et al. 1988). Although it may be risky for an arctic cod to venture where predators feed, joining an aggregation would decrease the chance of an individual being discovered there (Neill & Cullen 1974). The reward might be enhanced feeding opportunities in the shallow bays or along the coast. However, feeding is not likely to be the only stimulus for the movement of these fish into shallow areas. Although it was not observed in this study, the stomachs of densely schooled arctic cod are often empty (H. Hop personal communication). In such cases, the cause for schooling remains unexplained.

During our observations of the schools, they were occasionally preyed upon by fulmars. Because these birds are shallow divers, only those fish within about 3 m of the surface would be vulnerable to them (Hobson & Welch 1992b). When compared with the intense feeding forays we have observed when marine mammals were present, we do not believe that the few seabirds we observed were significantly affecting the behaviour of the fish.

The fish responded to the presence of the boat by descending slightly. Rapid lateral movement was not detected and would be inconsistent with observations of other arctic cod schools (R. Crawford unpublished data). We concluded that vessel avoidance behaviour was not the cause for the change in fish NND spacing we observed.

Pitcher & Partridge (1979) suggested that schooling fish typically pack into a volume that can be estimated as the body length cubed (1 BL^3). These authors noted that foraging fish may be assembled in a rather loosely organized social group and frightened fish may be more densely packed. If we assume that the highest mean density we recorded (2.9 fish m^{-3}) was comprised of the larger size arctic cod from the gill nets (mean length = 19.3 cm), the mean volume occpuied by each fish was about 48 BL^3. If the arctic cod were threatened by a foraging predator, they would probably school more tightly than those we detected. At a volumetric spacing of 1 BL^3, their density would have been 139 fish m^{-3}.

The fish obtained with the gill nets from under drifting ice pans had been feeding primarily on *Onisimus* sp. Although this amphipod is typically associated with the under-ice (epontic) community, it was also found in our plankton samples which were obtained from waters with no ice cover. Also, the rate of gastric evacuation for arctic cod is slow (H. Hop unpublished data); these fish may have fed several days prior to capture. Thus, the few stomach samples offer no clue as to feeding behaviour in the circumstances of this study.

Although sound is not normally a between-fish stimulus for schooling behaviour (Shaw 1978), arctic cod could be orienting their distribution under drifting pack ice according to the sound generated by the collision of floating ice pieces. Also, arctic cod have drumming muscles on their gas bladder (Hawkins & Rasmussen 1978). Sound is an important orientation or communication stimulus to other Arctic animals and it may also be important to this species. Paradoxically, group behaviour (and sound orientation) is also used by predators of arctic cod (e.g. beluga whales; Pippard & Malcolm[9]), to enhance feeding opportunity when they attack a school of prey.

The low number of age 2 + fish in our samples was consistent with other collections from Resolute Bay and adjacent areas (H. Hop personal communication). Other workers (Lønne & Gulliksen 1989, Bradstreet 1982) observed small arctic cod among crevices and other rough undersurface ice features. It is possible that (1) the age 2 + fish in Resolute Bay were concentrated immediately under the drifting pack ice (or were in the kelp beds on the bottom) and were not detected by our sampling methods, (2) that variable recruitment to the stock was a cause for the low numbers of that year-class, or (3) that this age group does not inhabit this bay. We considered it unlikely that so many of these fish would have escaped capture to be so poorly represented in our samples but our data did not provide sufficient information to resolve this question.

The fish we detected in Resolute Bay were only a small portion of the population extant in Barrow Strait during the time of our study. Though our observations outside the bay during the study period were limited, we estimated there were many more fish in the strait than in the bay at the time. The fish outside the bay were non-schooling and were scattered throughout the water column (> 100 m deep). There may have been movement between these two groups of fish during our study, which would explain some of the variability in our biomass estimates. Also, fish under ice were not counted, further contributing to variability in our results.

The biomass data are considered approximate and conservative because of the poor representation of larger fish sizes in the acoustic data compared with the net catches. This inconsistency was considered an artifact of the difficult sampling conditions and its resolution was not possible here given the a posteriori nature of this analysis. Accordingly, a first order estimate of the amount of arctic cod in Resolute Bay during August 1986 was about 30 t. With a caloric content of 1.3 $Kcal \cdot g^{-1}$ (Lavigne et al. 1985), this would represent about 4E + 07 Kcal to the predators of this fish.

Although the schools were neither large nor dense, the considerable amounts of biomass contained within them in a relatively small bay underscores the importance of this species to the energy flow of the arctic ecosystem. These schools represented a concentration of energy that can be effectively and efficiently exploited by predators fortunate enough to locate them. They may also be an effective means for the fish to cryptically avoid predation. Those schools that are not preyed upon store large amounts of energy in the ecosystem, but that storage is very temporary in this short-lived species.

[9] Pippard, L. & H. Malcolm. 1978. White whales: observations of their distribution, population and critical habitats in the St. Lawrence and Saguenay rivers. Dept. of Indian and Northern Affairs, Parks Canada, Proj. c1632, Contract 76–190. 160 pp.

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