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Occurrence of Arctic Cod (*Boreogadus saida*) Schools and Their Vulnerability to Predation in the Canadian High Arctic

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ABSTRACT. We document the occurrence of large schools of Arctic cod (*Boreogadus saida*) in the Barrow Strait region of the eastern Canadian Arctic during the open water season. Schools were most frequently observed near shore, often in depressions inside bays. Schools ranged up to 130 000 m^2 surface area and contained on the order of 4×10^8 fish, weighing 12 000 tonnes. Evidence indicates that schools form before the arrival of predators, but when they occur in shallow water, they are often subjected to intense predation by thousands of seabirds and marine mammals, primarily black-legged kittiwakes (*Rissa tridactyla*), northern fulmars (*Fulmarus glacialis*), harp seals (*Phoca groenlandicus*), beluga (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*). The reasons for such schooling behavior are unknown.

Key words: arctic Canada, Arctic cod, schooling, marine mammals, seabirds, predation, beluga, harp seals, ringed seals

RÉSUMÉ. On étudie la présence de grands bancs de morue arctique (*Boreogadus saida*) dans la région du détroit de Barrow située dans l'Arctique canadien oriental durant la saison d'eau libre. On a observé que les bancs se tenaient le plus fréquemment près du rivage, souvent dans des dépressions à l'intérieur des baies. Les bancs couvraient jusqu'à 130 000 m^2 et comptaient en gros 4×10^8 poissons, pour un poids total de 12 000 tonnes. L'étude révèle que les bancs se constituent avant l'arrivée des prédateurs, mais lorsqu'ils se trouvent dans des eaux peu profondes, ils sont souvent la proie de milliers d'oiseaux et mammifères marins voraces, en particulier la mouette tridactyle (*Rissa tridactyla*), le fulmar boréal (*Fulmarus glacialis*), le phoque du Groenland (*Phoca groenlandicus*), le béluga (*Delphinapterus leucas*), et le narval (*Monodon monoceros*). On ne connaît pas les causes du regroupement des poissons en bancs.

Mots clés: Arctique canadien, morue arctique, regroupement en bancs, mammifères marins, oiseaux marins, prédation, béluga, phoque du Groenland, phoque annelé

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INTRODUCTION

The Arctic cod (*Boreogadus saida* Lepechin, 1774) is abundant throughout circumpolar arctic seas, being found as far north as the pole itself (Andriyashev *et al.*, 1980) and south to Newfoundland in the western North Atlantic (Scott and Scott, 1988). It is an extremely important component of arctic marine food webs, transforming small invertebrates into packets of energy large enough to be exploited by marine mammals and seabirds. Arctic cod is a major food source for ringed seals (*Phoca hispida*), harp seals (*Phoca groenlandicus*), narwhal (*Monodon monoceros*), beluga (*Delphinapterus leucas*), thick-billed murres (*Uria lomvia*), northern fulmars (*Fulmarus glacialis*) and black-legged kittiwakes (*Rissa tridactyla*) (Bradstreet *et al.*, 1986; Welch *et al.*, 1992). Arctic cod is not commercially important in Canada but has been exploited in the Barents Sea (Gjosaeter, 1973; Filippov, 1974; Falk-Petersen *et al.*, 1986).

Despite the importance of Arctic cod within the arctic marine food web, surprisingly little is known about its natural history. In general it achieves sexual maturity at age 2+ (males) or 3+ (females) and 12-15 cm fork length (Lear, 1979; Craig *et al.*, 1982). It spawns in winter beneath the ice in Russian waters (Moskalenko, 1964; Barenkova *et al.*, 1966; Rass, 1968) and does not live beyond age 7 (Bradstreet *et al.*, 1986; Hop *et al.*, in press). It feeds primarily on planktonic copepods and amphipods, ice-associated amphipods and epibenthic crustacea (Bradstreet *et al.*, 1986; Lønne and Gulliksen, 1989). Arctic cod are often associated with ice, particularly rough jumbled ice around pressure ridges (Moskalenko, 1964), but they are also found throughout the water column to the bottom. They are usually dispersed (Crawford and Jorgenson, 1990), but small schools consisting of 10-100 fish, as well as larger aggregations, have also been detected in hydroacoustic surveys beneath the ice of Barrow Strait in May–June (Crawford, unpubl.) Small aggregations have also been reported as appearing beneath the ice of the polar basin (Andriyashev *et al.*, 1980) and in ice cracks along the coasts of Greenland (Jensen, 1948) and Spitsbergen (Lønne and Gulliksen, 1989).

Arctic cod (hereafter referred to as "cod") do, however, occasionally form very large and dense schools in the Canadian Arctic during the open-water season, sometimes approaching shore and becoming visible to people on land, in boats or in aircraft. Large aggregations also have been observed in the fall in Russian coastal waters (Ponomarenko, 1967, 1968; Rass, 1968). Aggregations of marine mammals and seabirds are often associated with the schools in Canadian waters, exploiting the temporarily abundant food source (Finley *et al.*, 1990). Craig *et al.* (1982) obtained some very large fyke net catches (up to 40 000 per night) in Simpson Lagoon on the north coast of Alaska but did not directly observe the schools and did not comment on any associated predators.

Because large schools have been infrequently reported, it has been assumed that they are sporadic events that do not occur regularly in the same time and place from year to year (Bradstreet *et al.*, 1986), and detailed descriptions are scarce.

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Anecdotally, Inuit in the eastern Canadian Arctic tell of schools exploited by marine mammals and seabirds, the schools often being described as having been "driven ashore" by beluga to leave thousands of dead cod on the beaches. For example, S. Akeeagok (Grise Fiord; Northwest Territories [N.W.T.], pers. comm. 1990) states that such events occur annually during open water in the vicinity of Grise Fiord, Ellesmere Island. G. Williams, Renewable Resource Officer, Arctic Bay, N.W.T. (pers. comm. 1989) has also seen similar events occurring annually in the vicinity of Arctic Bay, north Baffin Island. Informally one of us (HEW) has been told of cod schooling events at Repulse Bay (NW Hudson Bay) and at several communities on south Baffin Island. In NW Greenland, small schools about 5 × 10 m were observed in shallow water near Quarjarquissarssuaq Island at the head of Inglefield Fiord (77.5°N, 63°W) in August 1993. Thousands of harp seals and kittiwakes were associated with the schools. Local Inuit were gaffing the fish for personal consumption and did so regularly (J. Allen, pers. comm. 1993).

We have been researching the marine food web in the Barrow Strait/Lancaster Sound region near Resolute, N.W.T., part of the Lancaster Sound regional marine ecosystem (Fig. 1), and have studied the occurrence, distribution, abundance and feeding ecology of dispersed and schooling Arctic cod. We summarize our observations of schooling events and associated predation phenomena and incorporate some of the traditional knowledge provided by Inuit observers.

METHODS

Studies were done in Barrow Strait along the southern shores of Cornwallis and Devon islands (Fig. 1), 1984-91. Schooling events were typically observed by chance while collecting other biological oceanographic data aboard a 6.3 m boat, in a helicopter or from shore. Observations were often sketchy and incomplete due to their ancillary and opportunistic nature. We made more detailed examinations of several schools in Allen Bay, Cornwallis Island, in 1989.

The areal dimensions of schools were estimated visually when the schools could be clearly seen in shallow water. When schools were too deep to see from the surface, subjective estimates of school size were made by repeatedly passing over the school in different directions while we monitored the presence of fish with a boat-mounted depth sounder (Sci-Tex Honda "flasher" unit and/or Furuno chart recording unit). Vertical dimensions were determined from echograms generated from the Furuno chart recorder, a BioSonics hydroacoustical unit (Crawford and Jorgenson, 1993) or visually from the flasher unit.

Data on school composition were taken from fish captured by small otter trawl (5 m wide aperture, 5 cm mesh, 1.3 cm mesh cod end liner), cast net (2 cm mesh), dip nets and trap nets (8 m^3 box, 6 m wings, 20 m lead). The bottom trawl was lowered part way to the bottom and towed horizontally to obtain a pelagic sample. The trap nets were typically set perpendicular to shore, with the end of the lead at <2 m depth and the box at 5-8 m depth.

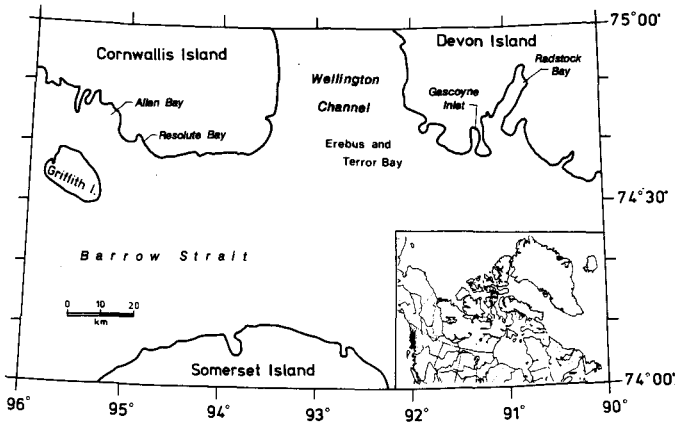

FIG. 1. Map of the Barrow Strait area, Northwest Territories, Canada. Arctic cod schools were seen in Allen, Resolute, and Radstock bays and Gascoyne Inlet.

Fish densities within the schools were approximated in two ways. In the first method, we observed that shallow-water schools formed opaque masses that completely obscured the bottom when viewed from above (by boat or helicopter). Therefore we determined the projected dorsal surface area of cod by photographing the dorsal aspect of known-length cod swimming in an aquarium and planimetering the silhouettes. The relationship between fish length and projected dorsal surface area was: DA = 3.03 FL−27.46; (r^2 = 0.84, n = 12; <0.001), where DA = dorsal surface area (cm^2) and FL = fork length (cm); range 14.5-21.5 cm. The mean size of cod (n = 3023) collected from 13 schools of adults was 16.4 cm fork length and 33.4 g weight (Hop *et al.*, in press). For FL = 16.4, DA = 22.2 cm^2 and 10 000 cm^2/22.2 = 450 cod·m^{-2}, the minimum number of non-overlapping fish required to obscure the bottom when viewed by an observer above. Because the fish must overlap considerably, surface densities must be at least twice that number to completely obscure the bottom. We have therefore used 1000·m^{-2} as an order of magnitude estimate of surface density for schools in shallow water.

In the second method for calculating the density of schooling cod, we assumed that when they are pursued by predators they congregate at densities near the maximum values reported for fish, where the space occupied by an individual fish would be approximately equal to its body length cubed (Pitcher and Partridge, 1979). For fish of 16.4 cm length, this density is 227·m^{-3}. Therefore we have conservatively set the volume density to 200·m^{-3} when deriving estimates of biomass for schools in deep water.

RESULTS

School Composition

All the large open-water schools that we observed were comprised of age 2+ or older individuals, with mean ages of 3-4+ and a modal age of 3+ (Fig. 2). The similarity of size frequencies among schools and years suggests that there is little interannual variation in the size of schooling cod (see also Hop *et al.*, in press). The overall sex ratio of schooling

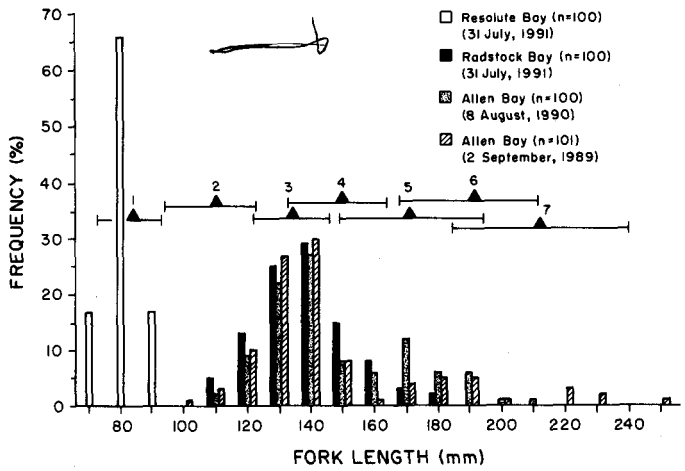

FIG. 2. Size distribution of schooling Arctic cod. The age distribution is given by the mean (triangles) plus one standard deviation (each horizontal line is two standard deviations long). Sampling gear was: dip net, Resolute Bay, 1991; cast net, Radstock Bay, 1991; trap net, Allen Bay, 1990; and otter trawl, Allen Bay, 1989.

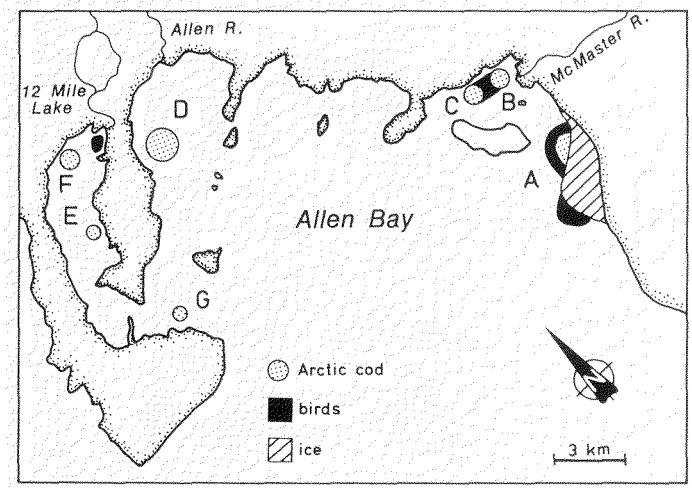

FIG. 3. Locations of Arctic cod schools, seabirds and grounded ice in Allen Bay, Cornwallis Island, on 28 August 1989. Schools located at A-G are described in the text under 1989 Allen Bay schooling events.

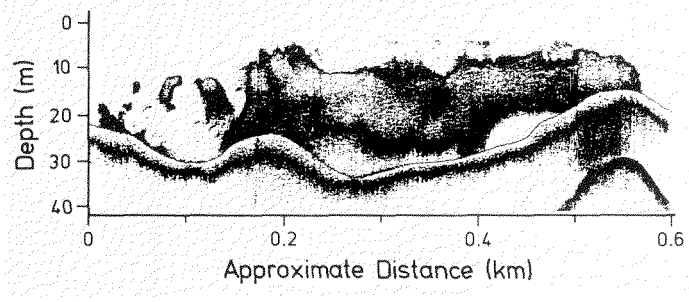

FIG. 4. Echogram of Arctic cod school (A in Fig. 3) on 31 August 1989, recorded at transect A in Figure 6 with BioSonics dual beam hydroacoustic unit.

fish deviated significantly from 50:50, with a slight surplus of females (Hop *et al.*, in press).

We have observed only two large schools of age 1+ fish. One occurred 14-20 July 1989 beneath the ice of Resolute Bay, and a much smaller school was seen in Allen Bay on 23 July 1989, also while fast ice was still present (Table 1). Aggregations of small (7-9 cm) cod corresponding to age 1+ have also been reported in ice cracks before ice-out in Arctic Bay (G. Williams, pers. comm. 1989).

1989 Allen Bay Schooling Events

Schooling cod were present continuously in Allen Bay from 23 July through 16 September 1989 (Fig. 3; Table 2). One small school of age 1+ fish was initially observed among ice floes along shore. Schools of adults were observed later, in August and September, in open water of the deeper basins of the bay. The modal fork length of a trawl sample on 2 September was ~14 cm (Fig. 2). Observations throughout most of the day and night (and of schools at Gascoyne Inlet) indicated that the schools did not disperse and reaggregate diurnally. Harp seals were present nearby continuously after ice-out, and narwhal and beluga were present in large numbers on at least two occasions. Fulmars and kittiwakes increased in abundance through late August, after which their numbers gradually decreased. A few adult glaucous gulls (*Larus hyperboreus*) were always present, and increasing numbers of young-of-year gulls appeared by late August.

On 28 August 1989 we surveyed the waters of Allen Bay with a recording echo sounder. We found one school at the edge and beneath grounded pack ice 3 km south of the McMaster River, with fulmars diving for cod through holes and gaps in the ice (Fig. 3A). We estimated the area of the school to be about 110×10^3 m^2 (Table 3), with an average thickness of 15 m (Fig. 4). Two smaller schools (Fig. 3B,C) were present in the bay NE of May Island, where seabirds were feeding on cod carried upward by visible local tidal current upwellings. Acoustics revealed that nearly all the fish remained deeper than 3 m, which is about the maximum diving depth of northern fulmars (Hobson and Welch, 1992). The main bodies of these schools were concentrated in deep basins (Figs. 5, 6). Another large school, estimated to be 300-400 m diameter with only a few attendant birds, was at D (Fig. 3) and several smaller schools were found at E, F and G (Fig. 3). Some of the latter schools were visible in shallow (3-4 m) water and were attended by birds. We estimated the total surface area of all the schools to be about 3×10^5 m^2, with a mean thickness of 10 m. At 200 fish·m^{-3} and a mean weight of 33 g, the total fish weight was on the order of 20 000 tonnes (Table 3). An independent analysis of the Allen Bay schools with BioSonics dual beam acoustics on 31 August supported these estimates (Crawford, unpubl.).

In the afternoon of 31 August 1989 we observed intensive feeding activity by beluga and birds in Allen Bay, interrupted by hunters who killed eight of the whales. One small school fragment immediately south of the McMaster River delta appeared to be driven ashore by whales. Kittiwakes and fulmars then fed to satiation, leaving an 80 m strand line of intact cod on the beach as the tide dropped. Hundreds of eviscerated fish were also left on the bottom, at 1600-1800 h. All dead fish had disappeared (presumably scavenged by birds) 24 h later. A similar stranding event, which we did not observe, probably occurred 1 km to the north after 1900 h on 31 August; by 1900 the next day, fulmars and gulls were dipping and diving for the eviscerated carcasses as the tide fell.

TABLE 1. Occurrences of Arctic cod schools, 1985-91, in the vicinity of Resolute, N.W.T. (refer to Figs. 1 and 7 for locations)

Date	Location	Depth of school	School size	Associated predators; comments
9 Aug 1985	"Cape Cod"	≈4 m	5 × 200 m	20 beluga; 100s of harp seals; several ringed seals; 1000s of fulmars and kittiwakes
9 Aug 1985	Gascoyne Inlet	4-6 m	Unknown	200 beluga; 100s of harp seals both inside and outside inlet; 1000s of fulmars and kittiwakes
21 Aug 1985	"Cape Cod"	≈4 m	5 × 250 m (possibly much larger)	≈500 beluga nearby; 100s of harp seals offshore; 1000s of fulmars and kittiwakes nearby
21 Aug 1985	Gascoyne Inlet	≈4 m	Unknown	≈500 beluga; 100s of harp seals offshore; 1000s of fulmars; some kittiwakes
23 Aug 1985	Gascoyne Inlet	≈4 m	75 × 75 m	A few harp seals; several ringed seals; 1 bearded seal; 100s of fulmars
11-22 Aug 1986	Resolute Bay	10-20 m	Large	No large numbers of predators were ever seen near the school
2 Aug 1987	Allen Bay	Shallow	Large	Reported by Inuit hunters; a search of Allen Bay on 4 Aug revealed only a few fulmars feeding on single cod carried by currents over "Dynamite Shoal"
5 & 12 Aug 1988	Resolute Bay (trap net)	2-8 m	Unknown	Overnight trap net catches of 6000 and 16 000, indicating the presence of large schools
18 Aug 1988	"Cape Cod"	1-4 m	2 × 100s m	300-400 beluga; a few harp seals offshore; 1000 fulmars; a few kittiwakes and guillemots; school disappeared after 3 h
19 Aug 1988	Erebus and Terror Bay	1-4 m	Several large schools	No marine mammals; 10s of fulmars, kittiwakes, and guillemots; very little feeding activity
23 Aug 1988	Scallon Cove (obs. from helicopter)	Shallow	15-20 × 4-500 m	382 beluga (counted from a helicopter); ≈500 harp seals nearby; 1000s of fulmars and kittiwakes
15 July 1989	Resolute Bay (obs. from ice)	Shallow	100-150 m long, very high density	100s of terns, kittiwakes, and gulls
7-9 Aug 1989	Resolute Bay (trap net)	2-10 m	Unknown	7000-10 000 fish trapped daily
11 & 12 Aug 1989	Resolute Bay	8-15 m	5 × 50 m	No associated predators
28 & 29 Aug 1989	Resolute Bay (trap net)	2-10 m	Unknown	Overnight trap net catches of 2800 and 8880 fish
17 Sept 1989	Resolute Bay	1-5 m	A few schools, 5-100+ m^2	≈25 harp seals; 600-800 fulmars and kittiwakes
1989	Allen Bay	—	—	See Table 2
8 Aug 1990	Allen Bay	6-10 m (over 14-30 m depth)	>200 × 400 m	≈10 fulmars; 20 kittiwakes
11 Aug 1990	Allen Bay among ice and tide cracks (obs. from ice and shore)	Shallow	Unknown, large	≈500 ringed seal, a few bearded seals and 1000s of kittiwakes
15 Aug 1990	Allen Bay (south of May Island)	8-25 m	100 × ? m	A few ringed seals (seals full of cod) and kittiwakes
19 Aug 1990	Allen Bay	Midwater, in water 27 m deep	≈10 m^2	20 fulmars
21 Aug 1990	Allen Bay	10 m thick over bottom @ 25 m	≈30 × 50 m, plus other schools	A few fulmars and kittiwakes
24 Aug 1990	Allen Bay	—	—	At 2000 h, 30 beluga, 5 harp seals, 100 fulmars and 300-500 kittiwakes appeared to be feeding on cod
		—	—	At 2045 h, 250 fulmars, 500 kittiwakes, 100 glaucous gulls, 5 pomarine and 10 parasitic jaegers were present, plus the beluga and harp seals
		—	—	At 2100 h the beluga departed
25 Aug 1990	Allen Bay	—	—	At 0900 h one small pod of beluga was seen among pack ice; at 2123 h about 50 beluga returned to same place as on 24 Aug
4 Sept 1990	Allen Bay	10-20 m, over deeper water	Several small schools	10 fulmars, 6 kittiwakes, 20 gulls
31 July - 2 Aug 1991	Radstock Bay (Patrol Point)	Shallow	≈5000 m^2	100s beluga and harp seals; ≈15 narwhal, 1000s fulmars and kittiwakes (see Results)

TABLE 2. Schools of Arctic cod in Allen Bay, 1989

Date	Location	Depth of school	School size	Associated predators; comments
23 July 1989	Near McMaster River (obs. from ice)	Shallow (among ice floes and cracks near shore)	Small	10s of kittiwakes, terns; age 1+ cod
23 July 1989	Near McMaster River (obs. from shore)	Shallow	Unknown	100s of kittiwakes, terns, gulls; birds satiated; 10 large (≈20 cm) cod dead on gravel delta
24 July - 4 Aug 1989	Near McMaster River (trap net)	2-10 m	Unknown	1000s of cod trapnetted daily
20 Aug 1989	Near McMaster River (obs. from shore)	Deep	Unknown	≈2000 fulmars, 300 kittiwakes, 60 glaucous gulls preying on a school of cod; a single immature beluga feeding against shore in cove NE of McMaster River
23 Aug 1989	Inner basin and west side of Allen Bay (obs. from boat)	Deep	Several, sizes unknown	200-300 narwhal and beluga; one adult male narwhal killed and contained several kg cod remains only; 1000s fulmars and kittiwakes
28 Aug 1989	See Fig. 3	Deep and shallow	Several (see text)	≈100 harp seals, some ringed bearded seals; 1000s fulmars, kittiwakes (see Results)
31 Aug 1989	Deep basins NE and SE of May Island	Deep and shallow	Several, al least one large	At least 10s of beluga (8 killed by hunters, 3 of which contained only cod); several 1000s fulmars, kittiwakes; a few gulls; 2 mass strandings (see Results)
2 Sept 1989	Off McMaster River (obs. from boat)	10-20 m	Large	≈1500 fulmars, kittiwakes
16 Sept 1989	Off McMaster River	10-20 m	Large	A few ringed and harp seals; 1000 fulmars, kittiwakes; a few glaucous and Thayer's gulls

TABLE 3. Approximate dimensions and numbers of schooling Arctic cod in Allen Bay, Cornwallis Island, on 28 August 1989, as determined with an echo sounder (mean fish density was assumed to be 200·m^{-3} at a mean fish weight of 33 g [see text])[1]

Arctic cod school (Fig. 3)	School length (m)	School width (m)	School thickness (m)	Surface area ($m^2 \times 10^3$)	Approximate volume ($m^3 \times 10^4$)	Numbers of fish ($\times 10^7$)	Biomass (tonnes)
A	450	300	10-20	110	165	33	11 000
B	300	125	4-6	35	18	35	1 200
C	190	190	5	20	10	2	600
D	425	400	10-20	133	200	40	13 000
							25 800

[1]Schools E, F, and G: Total surface area ≈5 × 10^3 m^2. School volumes are not known.

1990 Allen Bay Schooling Events

One or more large schools also formed in Allen Bay in 1990 and persisted for at least a month (Table 1), but fast and pack ice hindered our ability to survey the entire extent of the school(s). Relatively few harp seals were seen, perhaps because of the ice, but an extraordinary number of ringed seals were present in late July to early August, when we counted over 300 on the ice and observed many more in the water (Table 1). There were very few kittiwakes or fulmars relative to the large number of birds exploiting the schools under similar circumstances the previous year. Possibly other food sources attracted the birds, although simultaneous surveys of southwest Devon Island and south Cornwallis Island revealed no cod schools or major concentrations of birds. Relatively light predation by marine mammals may have allowed the schools to persist for a long time in both 1989 and 1990.

1991 Radstock Bay Schooling Events

The schooling events sometimes appeared to be ephemeral. For example, on 31 July 1991 at 1030 h, a school over relatively deep water near Patrol Point, Radstock Bay, was composed of three indistinct groups each about 100 m in diameter (location A in Fig. 7). Thousands of harp seals were present, and hundreds of beluga were seen swimming toward the schools. Hundreds of fulmars and kittiwakes were present, but feeding opportunities were few (about 10 000 northern fulmars occupy the colony at nearby Cape Liddon [Brown *et al.*, 1975]).

We returned to observe and film the event between 1430 and 1800 h by helicopter and from shore, by which time the the cod had formed four distinct schools in shallow (2-5 m) water (B-E in Fig. 7). Many beluga were seen elsewhere at the mouth of Radstock Bay by that time, and fewer harp seals were nearby than in the morning. The school at location B was estimated from photographs to be >500 m long and the school at location C to be about 400 m long. Thousands of fulmars and kittiwakes and hundreds of beluga were feeding intensively on the schools at locations B and C (Fig. 8a,b), and about 15 narwhal patrolled the two schools. A smaller school at location D (~200 m^2) was largely free of predators. About 50 beluga and a few birds were feeding on the school at location E (Fig. 8c). As measured from aerial video and still photography, that school was 500 m long and

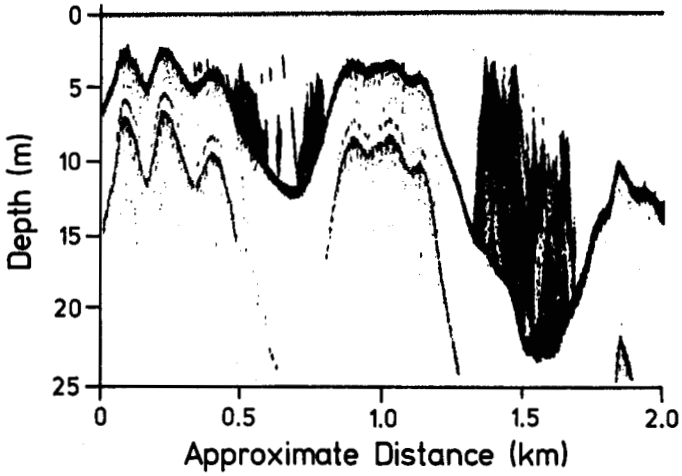

FIG. 5. Echogram of Arctic cod school (B in Fig. 3) on 31 August 1989, recorded at transect B in Figure 6 with BioSonics dual beam hydroacoustic unit.

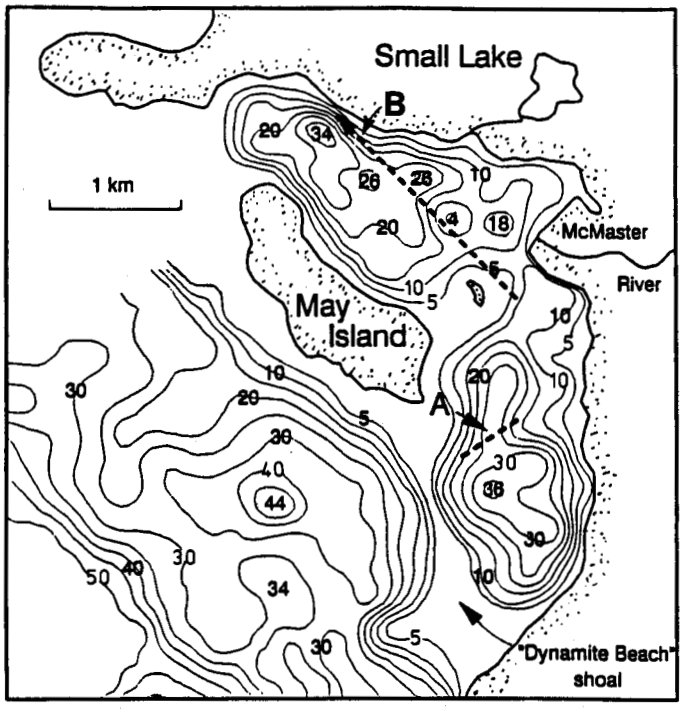

FIG. 6. Bathymetry of the eastern part of Allen Bay where schools of Arctic cod were found in 1989. Fish congregated in the basins between May Island and the mainland. The echograms in Figures 4 and 5 were made on transects A and B.

averaged 5 m wide, covering an area of 2500 m². At 1000 cod·m⁻², with a mean weight of 18.7 g each from this schooling event, this equalled 46 tonnes of fish.

By 1800 h fewer than 20 beluga were still feeding, on the school at location B, which had been decimated and fragmented into a dozen or so smaller schools (Fig. 8d). On the second day of observations (1 August) there were fewer beluga nearby, bird activity had decreased but was still intense, and the number of cod visible from the air had decreased by a factor of five. By the third day (2 August), cod were not visible from shore or helicopter, there were far fewer birds in the area, and only a few beluga and harp seals remained in Radstock Bay.

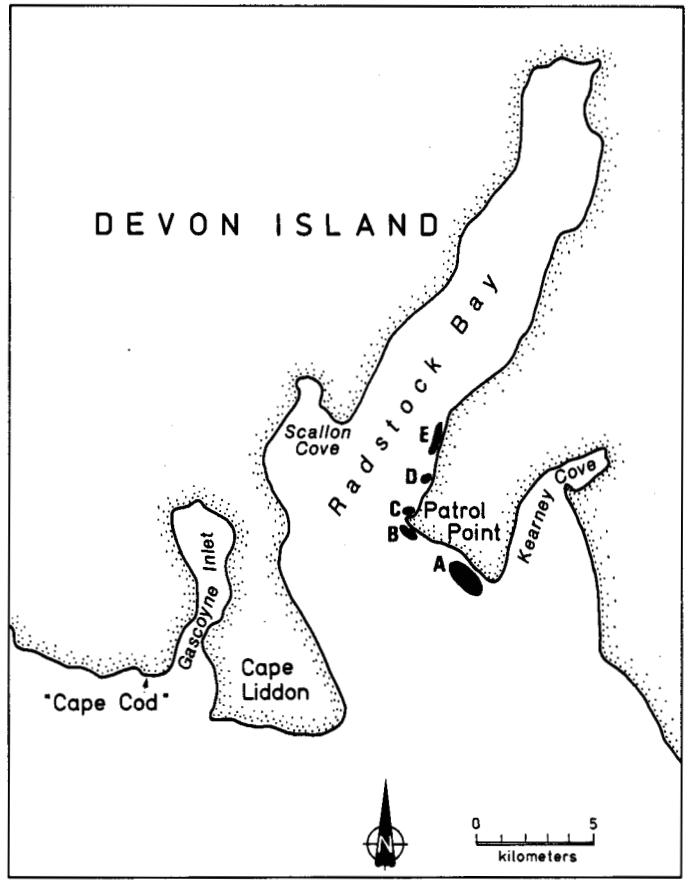

FIG. 7. The Radstock Bay area of southwest Devon Island, N.W.T. Schools of Arctic cod were discovered at A on the morning of 31 July 1991. Later that afternoon schools were at B, C, D and E (see photographs in Fig. 8).

In general the schools of Arctic cod tend to be found in bays and inlets, where they pool in deep basins. When they occur on open coast lines or off points they are moving along the shore in shallow water and end up in bays. For example, the schools off "Cape Cod" near Gascoyne Inlet on 9 August 1985 and on 18 August 1988 (Table 1; Fig. 7) were moving eastward along the coast and ended up in Gascoyne Inlet.

DISCUSSION

Significance of Schooling to Predators

Arctic cod are a major prey of chick and adult fulmars in the Lancaster Sound region (Bradstreet and Cross, 1982; Hobson, 1991). Fulmars also take other planktonic prey, but the availability of Arctic cod in late summer may be important to fulmar chick survival in the same way cod are important to thick-billed murre chick survival, where invertebrate prey are sufficient to support adults but do not constitute large enough energy packets for efficient transport back to the nest (Gaston and Nettleship, 1981). Arctic cod are also an important component of black-legged kittiwake diet, along with planktonic crustaceans. Both kittiwakes and fulmars can feed on cod only when the fish are near the water surface, which occurs primarily when the fish are schooling in shallow water. In the presence of cod schools the kittiwakes fly continuously, dipping and aerially seizing cod from the

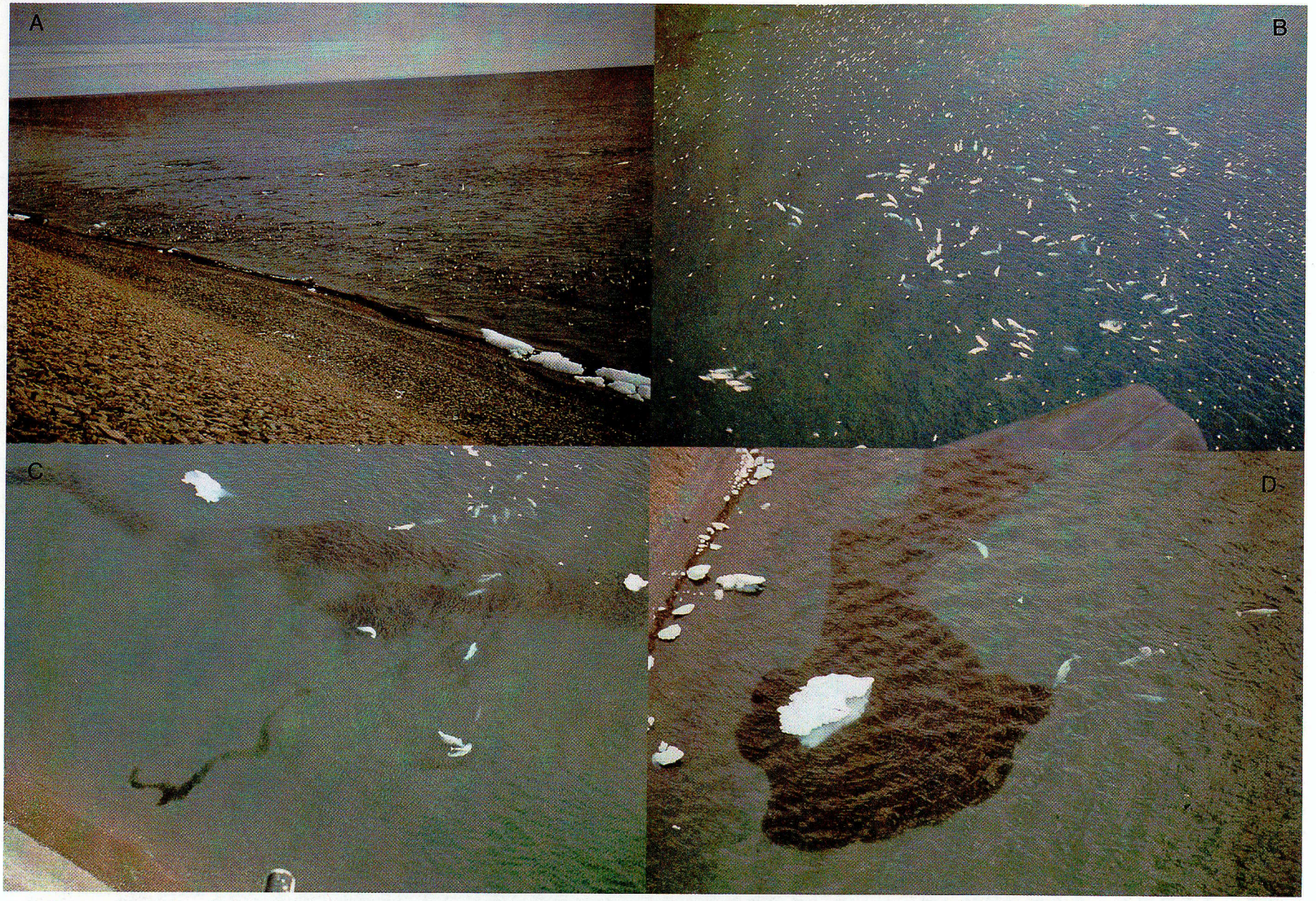

FIG. 8. Photographs of cod, seabirds and beluga near Patrol Point, Radstock Bay, the afternoon of 31 July 1991 (locations in Fig. 7). A) View south from the shore of Patrol Point at school B about 1500 h on 31 July 1991, showing intense feeding activity by kittiwakes, fulmars and beluga. Beluga densities are similar to those in Figure 8B but are difficult to see from this perspective. A dark mass of cod extending down the coast on the right side of the picture can be discerned. B) Aerial view of beluga and flying seabirds 100-200 m offshore from Figure 8A, seaward of school B. There are >130 whales in the picture. They are probably feeding on Arctic cod, which are too deep to see. Remnants of a school in shallow water are visible in the top left. C) A few whales and birds feeding on the remnants of school B about 1800 h. Note the fragmentation and dispersion of the school. Three hours earlier it appeared like that in Figure 8D. D) The forward end of school E about 1430 h. Predation pressure is light (note the absence of birds). The school is 500 m long, of which about 50 m is shown.

surface. Fulmars catch fish by surface seizing and plunging, and they can also dive at least three metres in pursuit of cod; kleptoparasitism is frequent among fulmars feeding on cod (Hobson and Welch, 1992).

When cod are hugging the shore in the presence of beluga, we have observed fulmars, presumably near satiation, eviscerating the fish and consuming only the entrails, mostly the oil-rich liver, leaving the carcasses on the bottom in shallow water (see also Finley *et al.*, 1990). These eviscerated carcasses are then scavenged on the next tidal cycle, if live cod are not available and the dead fish come into the diving range of gulls and fulmars. These events may leave strand lines of dead cod along the high-tide mark (see also Bain and Sekerak, 1978; Bradstreet *et al.*, 1986).

Beluga in the Barrow Strait area feed almost exclusively on Arctic cod (Bain and Sekerak, 1978; Finley *et al.*, 1990; Welch *et al.*, 1992). The maintenance ration for a beluga of average size (880 kg) is about 22 kg cod daily (Welch *et al.*, 1992:Table 6). Therefore a pod of 500 whales such as were observed feeding on the cod school at Gascoyne Inlet on 21 August 1985 (Table 1) would eat about 11 tonnes daily, and likely more if the whales were feeding in excess of maintenance. Narwhal also feed on Arctic cod in the area of Barrow Strait (Welch *et al.*, 1992), but only twice (23 August 1989 and 31 July 1991) have we seen them exploiting large schools near shallow water. Narwhal are also said to enter Creswell Bay, Somerset Island (240 km south of Resolute), to feed on schools of cod. Narwhal stomachs are empty if the animals are killed before entering the bay, whereas the stomachs are full of cod if the whales are allowed to feed in the bay before being killed. The narwhal occasionally drive the cod schools ashore (A. Atagotaaluk, Pond Inlet, N.W.T., pers. comm. 1991).

Arctic cod constitute about 60% of ringed seal prey throughout the year at Resolute (Welch, unpubl.); the relatively small ringed seal can prey efficiently on dispersed cod. Large numbers of ringed seals are not usually associated with cod schools, with the notable exception of the Allen Bay event in 1990 (Table 1). Smith (1987) reported observing small pods of ringed seals presumably pursuing schools of Arctic cod in the Amundsen Gulf area of the western Arctic, the seals being gorged with fresh fish, although the cod themselves were in water too deep to be seen from the surface.

Harp seals also feed intensively on Arctic cod in the Barrow Strait area (Finley *et al.*, 1990; Welch *et al.*, 1992). One thousand harp seals, such as were present in Radstock Bay on 31 July 1991, would eat an estimated 4.5 tonnes per day at maintenance ration (Welch *et al.*, 1992, model results), but this is probably an underestimate considering that harp seals fatten in the Lancaster Sound region in summer and often feed far above maintenance levels when they encounter cod schools (Finley *et al.*, 1990). The combined removal of cod by vertebrate predators from large schools by marine mammals during feeding frenzies (e.g., in Radstock Bay on 31 July 1991) could be on the order of 20 tonnes or more per day.

General Sequence of Schooling Events

Schools of Arctic cod probably do not form initially as a result of predation pressure by marine mammals or seabirds, because we have observed three schools present in Resolute Bay in the absence of predators. In one case the school persisted for a month before being found by a pod of harp seals on 17 September 1989, at which time at least some of the fish moved into shallow water and were visible from shore (Table 1).

In the Lancaster Sound region, harp seals are often the first aggregated predators to exploit Arctic cod schools. We have observed, and have been told by three other observers (S. Akeeagok, G. Williams and L. Pudluk, of Resolute) that harp seals are rarely seen in shallow water with the cod. Rather, a small pod of animals dives in synchrony hundreds of metres offshore from the school, remain submerged for 4-7 minutes while they presumably feed on cod, then resurface near the place they dove, often headed offshore. This sequence has also been observed at Grise Fiord by Finley *et al.* (1990). Thus harp seals may serve to consolidate the fish and drive them closer to shore.

Beluga do not hesitate to enter water as shallow as 1 m in pursuit of schooled cod, feeding on the outer edges and even passing through the school, fragmenting it into smaller pieces (Fig. 8C,D).

The mass strandings that we have observed, noted above, appeared to have resulted from heavy predation. However, mass strandings in the fall along the Alaskan (Craig *et al.*, 1982) and Russian coastlines (Klumov, 1937; Shibanoff, 1958; Moskalenko, 1964) have been attributed to storms.

Why Do Arctic Cod School?

We can offer no likely reason for Arctic cod to school. Schooling probably has little to do with the reproductive cycle, since they spawn in late winter (Barenkova *et al.*, 1966; Rass, 1968). Schooling cod have gonads that are far from mature, and there is only a small increase in the gonado-somatic index for schooling cod in Allen Bay from August to September (Bain and Sekerak, 1978; Hop *et al.*, in press). Feeding opportunities inside large schools are reduced, as shown by the 65% frequency of empty stomachs in schooling cod compared with 3% for dispersed cod (Hop *et al.*, in press). The abundance of large planktonic crustacea (copepods and amphipods) is also reduced in the vicinity of cod schools (Hop *et al.*, in press).

Schooling behavior of fish is thought to confer protection against predators (Cushing and Harden Jones, 1968; Major, 1978; Burgess and Shaw, 1979). At first glance this seems unlikely for Arctic cod, because aggregated predators target cod schools, causing predation rates on the order of 20 tonnes and half a million fish daily. However, the probability of an individual falling prey may still be very low if the school size is like the one documented on 28 August 1989, a thousand times larger than maximum expected daily predation rates.

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