



***Biology Of Greenland Cod, Gadus Ogac, At  
Saqvaquac, Northwest Coast Of Hudson  
Bay; In Environmental Biology Of Fishes  
Type of Study: Species Biology Fisheries,  
Info On Other Fish Species  
Date of Report: 1988  
Author: Welch, Harold E  
Catalogue Number: 3-26-17***

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## Biology of Greenland cod, *Gadus ogac*, at Saqvaquac, northwest coast of Hudson Bay

Mansour Y. Mikhail<sup>1</sup> & Harold E. Welch<sup>2</sup>*Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada*<sup>1</sup> *Present address: C.A.R. E. Centre, 2338 Hurontario Str., Mississauga, Ontario L5B 1N1, Canada*<sup>2</sup> *Direct reprint requests*

Received 8.2.1988

Accepted 24.7.1988

*Key words:* Food habits, Distribution, Abundance, Respiration, Arctic, Growth, Age, Spawning, Marine fish

### Synopsis

The distribution and relative abundance, life history parameters, food habits, and metabolic rate were determined for *Gadus ogac* in Saqvaquac Inlet, northwest coast of Hudson Bay (63° N). Fish were demersal, non-schooling, and distributed evenly down to 35 m depth. Growth was slow (maximum age 12y) and mortality relatively low (0.5 y<sup>-1</sup>), *G. ogac* first spawned at 2-3 y and spawned annually thereafter, in late March - early April. They tended to remain in the inlet and were not taken on the open coast. They are top carnivores, taking primarily capelin when available, benthic crustacea (crabs, amphipods) when not. The metabolic rate of *G. ogac* is intermediate between the elevated rate of Arctic cod, *Boreogadus saida*, and eurythermal temperate species. Available data indicate they are not important in marine mammal and bird food webs. Their biology is contrasted with that of Arctic cod, which are short-lived, cryopelagic, feed on pelagic crustacea, and are an extremely important component of Arctic marine food webs.

### Introduction

*Gadus ogac*, Greenland cod or ogac, is a medium-sized fish with a circumpolar mid and low arctic distribution (Leim & Scott 1966). In Canada it is found on the Atlantic coast as far south as Nova Scotia, north to Baffin Island, along the mainland coast west to the Beaufort Sea, and throughout Hudson, James and Ungava bays. To the north its distribution overlaps with that of Arctic cod, *Boreogadus saida*, a slightly smaller fish with some direct economic value in Europe, and enormous importance as an intermediate in Arctic marine mammal and bird food chains. To the south *G. ogac* overlaps with *G. morhua*, Atlantic cod, which has

played a major role in north temperate fisheries for centuries. Compared to *B. saida* and *G. morhua*, *G. ogac* is poorly known; it has no present commercial importance and its status as a link in bird and mammal food chains has not been determined, but appears to be minimal. Incidental aspects of *G. ogac* biology have been discussed by various authors (Boulva 1970, Scott 1952, Craig et al. 1982, Jensen 1948), and Morin & Dodson (1986) reported growth rates, food habits and distribution in the large estuaries of James Bay and the east coast of Hudson Bay, but there have been no comprehensive investigations on the life history and general biology of *G. ogac*.

The purpose of the present work, therefore, is to

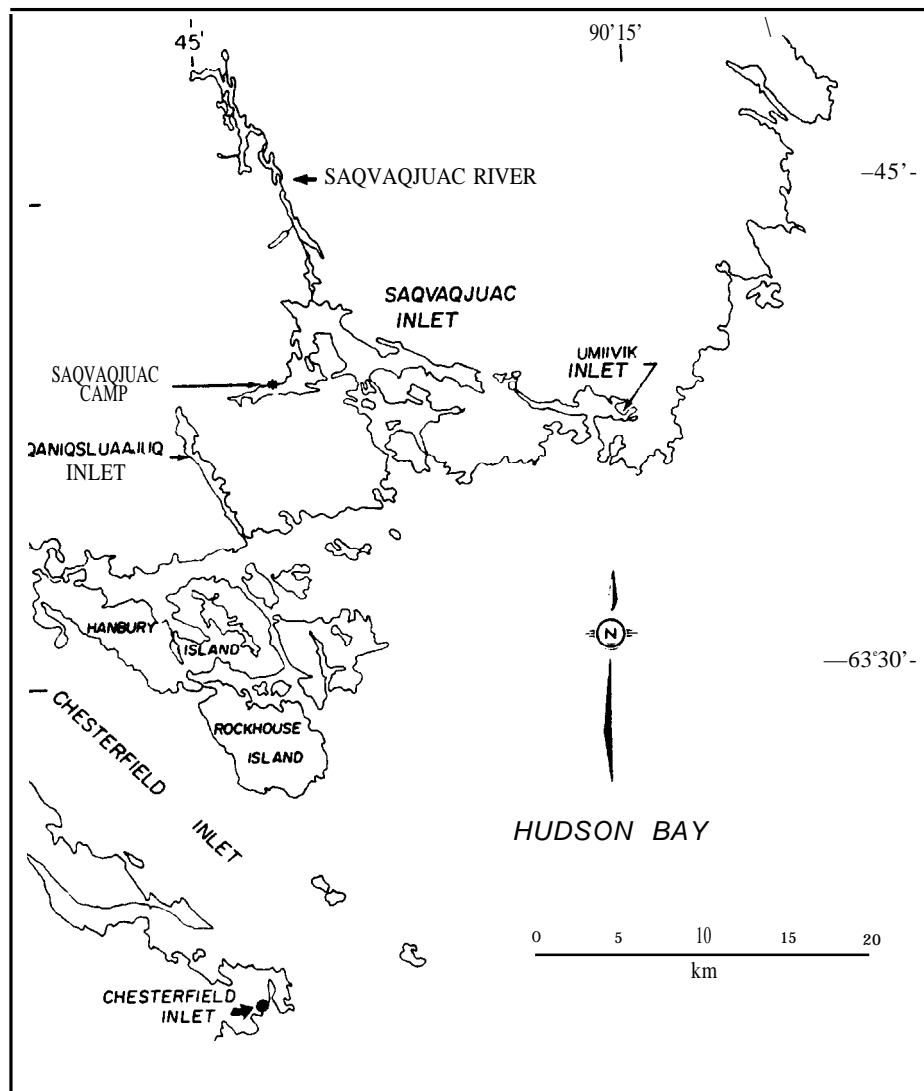


Fig. f. Saqvaquac and adjacent inlets.

determine the local distribution, growth rates, food habits, respiration rate and other life history parameters of *G. ogac* at Saqvaquac Inlet on the northwest coast of Hudson Bay (Fig. 1). We also consider the biology of the species in the context of its environment and its role in marine food chains. Comparison with *B. saida* is made where data for both species exist.

#### Materials and methods

##### *Description of the study area*

Saqvaquac is a small inlet 30 km north of Chesterfield Inlet hamlet, Northwest Territories (Fig. 1). Its climate and geography are discussed in Welch (1985). Saqvaquac Inlet is separated from Hudson Bay by a narrow outer race that experiences very strong (> 10 knot) tidal currents. The outer race damps the tidal amplitude of 3--6m on the outer coast down to 1--2 m in the Outer Basin, and further

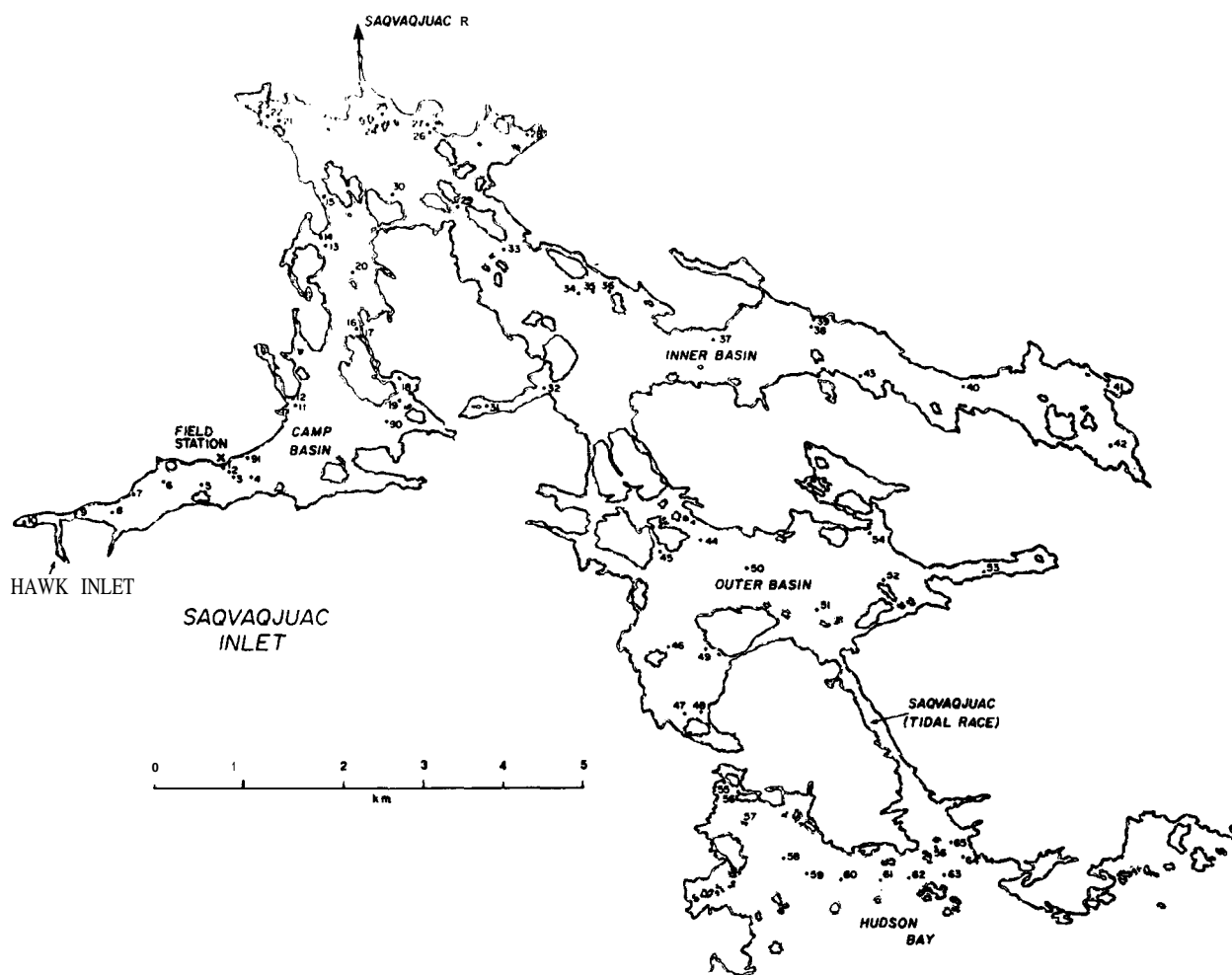


Fig. 2. Saqvaqujac Inlet, showing randomly located sampling stations for angling catch-per-unit-effort assessment of relative population density.

constrictions dampen and skew the semi-diurnal tides to about 0.6 m at the Canada Department of Fisheries and Oceans Research Station located on the innermost (Camp) basin (Dalton 1981). The small Saqvaqujac River (mean annual discharge  $1.34 \times 10^8 \text{ m}^3$  from  $607 \text{ km}^2$  drainage) enters the Inner Basin, and smaller streams enter the Inner and Camp basins (Fig. 2), which results in considerable dilution of surface waters in summer. Salinity may be near zero immediately below the ice during melt; later in the summer, tidal and wind mixing gradually lower the pycnocline. Temperatures may reach  $10^\circ \text{C}$  at the surface but do not get much above freezing below the pycnocline. Maximum depths are 57 m (Camp Basin), 56 m (Inner

Basin), and  $> 40\text{m}$  (Outer Basin).

The inlet is ice-covered from early October until early July, with channels freezing last and opening first; part of the outer race never freezes. Oxygen data indicate that deep water ( $> 40\text{m}$  in 1983) in the Camp Basin may not circulate every year, depending upon freezeup conditions (H. Welch, unpublished). Water in Hawk Inlet (Fig. 2) below the sill height of 10 m is anaerobic, dense (to 7%) and does not circulate. Otherwise all habitat in Saqvaqujac Inlet is available to *G. ogac*. Sampling was also done at adjacent Umiivik and Qaniqsluaajuq inlets (Fig. 1), both hydrologically similar to Saqvaqujac Inlet.

### Analytical

Here we outline all sampling and analytical methods; further details are given in Mikhail (1985).

Relative abundance and distribution of *G. ogac* at 78 locations in the Saqvaquac area (Fig. 2), including 54 sites chosen randomly within Saqvaquac Inlet, was determined by angling catch-per-unit-effort (CPUE) through the ice in spring 1983. Jigging a 4.8 cm long red and white spoon 1 m above the bottom for 0.5 h constituted one unit of effort. Measurements of the time required to raise and lower the lure were made and all catch data were normalized to zero depth to eliminate bias due to reduced jigging time in deep water. Additional fish growth and distribution measurements were taken in 1983 by trap nets (Beamish 1972) and gill nets (3.7, 5.0, 7.5 and 10.0 cm stretched mesh) at 15 sites chosen randomly from the 54 used for CPUE. Qualitative samples for stomach contents analysis were taken on lures during the open-water season in Saqvaquac Inlet. One to five hours after capture, each fish was measured (total length, 1 mm), weighed (total and eviscerated weight, 1 g), and sexed. Otoliths were taken and stomach contents preserved in formalin. Additional fish angled March – August 1981 and August 1982 were also analyzed for length-frequency distributions, spawning season, and food habits.

Greenland cod were aged from fin rays (Beamish & Harvey 1969) and otoliths, assuming otolith rings are deposited annually, as has been shown for other cod species (Craig et al. 1982, Bedford 1964, Keir 1962). Otoliths were broken in half through the SUICUS acusticus, smoothed with abrasive, baked at 250° C for 5 min, and immersed in 70% ethyl alcohol for 0.5 h. The broken section was viewed from above at 60x magnification by mounting it vertically in plasticize, covering it with glycerol and illuminating it from the side (modified from Keir 1962). Distances from the focus outward to each annulus on the largest radius of the section was measured with an ocular micrometer (one division = 0.17 mm). Fish length at each annulus was back-calculated according to the modified direct proportionality method (Bagenal & Tesch 1978). Analysis of age-frequency distributions (Robson &

Chapman 1961) were used to estimate survival and mortality rates.

Preserved stomach contents were washed, total volume determined by displacement in a graduated cylinder, and food specimens identified and recorded as estimated percent of total volume for each taxon. Unidentifiable digested material was not included in percent composition calculations. Percents were arcsine transformed (Elliot 1971).

Oxygen consumption was determined in 1983 for 56 cod angled near the laboratory and placed in a flow respirometer within 0.5 h. The respirometer and procedure were similar to that of Holeton (1974). Fish were held in clear acrylic tubes with diameters just small enough to prevent turning around, at about 80% oxygen saturation at 0°, 5°, and 10° C ( $\pm 0.20$ ). Fish for 0° determinations were captured in water at 0°  $\pm 0.1^\circ$  and held 24 h in the tank before beginning measurements. Fish for 5° determinations were caught at 2.5° and held three days, at 3, 4, and 5° before beginning measurements. Fish for 10° determinations were captured from 10° water and held in the tank 24 h at 10° C before beginning measurements. Oxygen was determined according to Carpenter (1965), using a photometric end point (Welch & Bergmann 1985), with an overall precision of  $\pm 0.15 \text{ mg O}_2 \text{ h}^{-1}$ .

Statistical analyses were performed using SAS (1982 a,b) procedures.

### Results

#### *Distribution and relative abundance*

The total units of jigging effort were 172, or 86.0 h. No *G. ogac* were caught immediately below the ice or in midwater during 4.5 h of effort (Table 1), nor were any taken outside the inlets during 6h of effort. Analysis of variance showed no significant ( $p=0.05$ ) differences between the two inlets, the eight fishermen, or regions of Saqvaquac Inlet, although there was a slight tendency for CPUE to increase with increasing distance from the outer coast of Hudson Bay (Table 2). Although analysis of variance showed no significant differences in CPUE with depth (Fig. 3), more intensive sam-

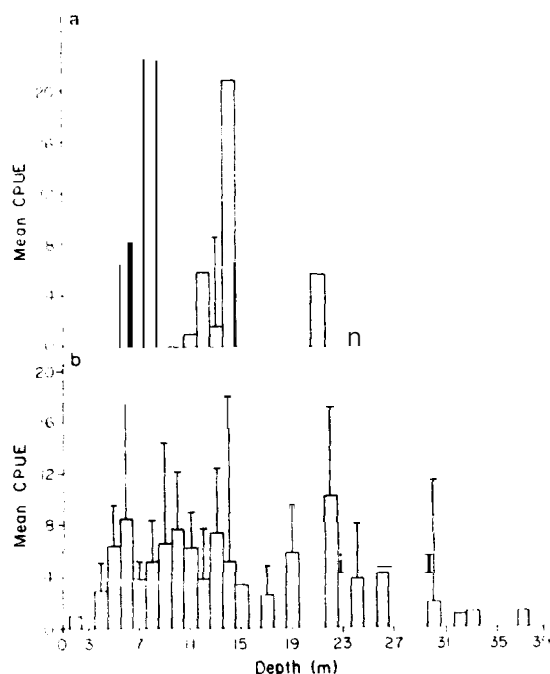


Fig. 1. Variation of mean angling catch-per-unit-effort (CPUE) of *Gadus ogac* 1 m above the bottom at various depths. Only the upper 95% (C.I.) is shown. CPUE data have been normalized for lure transit time to zero depth. a-@uriqshraajrrq Inlet, 1 June 1983; b-Saqvaquac Inlet, May - June 1983.

pling in water >30 m deep might have resulted in significant lower catches in deep water.

There were highly significant differences in CPUE with time (Fig. 4). CPUE was 7-9 in late May - early June, decreased to <4 the last week in

*Table 1.* Absolute CPUE data uncorrected for lure transit time, through the same holes where no *Gadus ogac* were caught immediately below the ice or in midwater, Saqvaquac Inlet, 1983.

Date	Hole no.	Depth m	CPUE data (1 m above bottom)
26 May	20	13	4
28 May	32	9	4
28 May	39	13	5
30 May	50	22	7
30 May	48	8	7
30 May	50	22	9
6 June	11	17	1
7 June	13	13	3
8 June	17	7	4

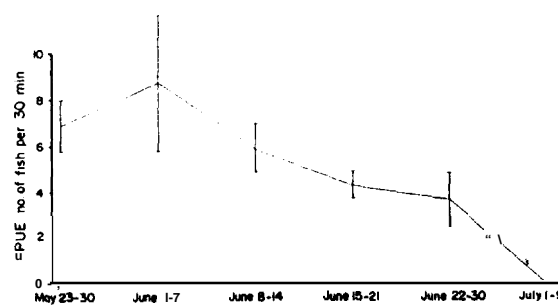


Fig. 4. Weekly variation of mean CPUE for *Gadus ogac* in Saqvaquac Inlet. 2 S.D. CPUE data are normalized for lure transit time to zero depth.

June, and became zero by 1 July. Despite intensive effort no *G. ogac* could be jigged through the ice anywhere inside or outside Saqvaquac Inlet the first week of July. Immediately after iceout on 10 July, cod were easily angled and netted throughout the Inlet.

#### Age and growth

Otolith ages were used for growth analyses although fin-ray ages were not significantly different from otolith ages for individual fish (Baird's T test,  $p = 0.0068$ ). Analysis of covariance showed no differences between sexes in the total length/otolith radius relationships ( $p > 0.1$ ); sexes were combined for further analysis. Trap nets sampled smaller fish more efficiently than angling or gill nets (Fig. 5). Recruitment appeared to be fairly con-

Table 2. Mean angling CPUE (no. of fish per 30 min, 95% at  $p = 0.025$ ) of *Gadus ogac* from Qaniqsluaajuq Inlet (1 June 1983) and Saqvaquac Inlet (May-June 1983) and outer coast of Hudson Bay. CPUE data are normalized for lure transit time to zero depth.

Location	Mean CPUE 95/0 C.I.
Qan Inlet	6.4 4.6
Saq Inlet	5.7 0.9
Camp basin	6.0 1.4
Inner basin	5.5 1.5
Outer basin	4.6 3.0
Outer coast of Hudson Bay	0.0 0.0

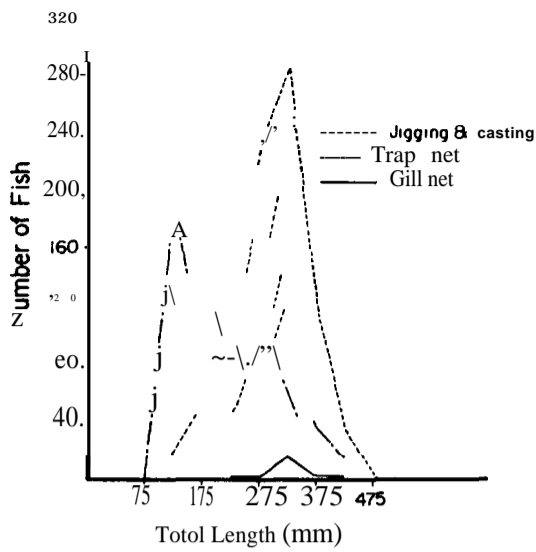


Fig. 5. Length-frequency of *Gadus ogac* caught by different types of fishing gear. Saqvaquac Inlet, 1983.

stant from year-to-year, with no great variations in year-class strengths, although the 1979 year-class may have been relatively weak (Fig. 6). Growth curves for *G. ogac* were different between Saqvaquac and Qaniqsluaajuq inlets; Qaniqsluaajuq fish grew more rapidly early in life but Saqvaquac fish became larger by age 8 (Fig. 7). The mean weight-length relationship for 1058 *G. ogac* captured 1981–1983 at Saqvaquac and Qaniqsluaajuq inlets was

$$\log_{10} W = -5.01 + 3.08 \log_{10} L,$$

where  $W$  = weight in grams and  $L$  = length in mm. Annual survival was not significantly different between the two inlets because of the relatively small sample from Qaniqsluaajuq; the annual survival for Saqvaquac fish was 0.55 for females and 0.45 for males, or about 0.5 for the population as a whole.

The sex ratios of mature *G. ogac* was 57F:43M in Saqvaquac Inlet and 33 F:67M in Qaniqsluaajuq Inlet in 1983; the difference was significant ( $p < 0.005$ , chi-square goodness of fit). Amongst immature fish in Saqvaquac Inlet, males were slightly more abundant than females.

Five gravid males and eight gravid females were jigged in Saqvaquac Inlet during March and April

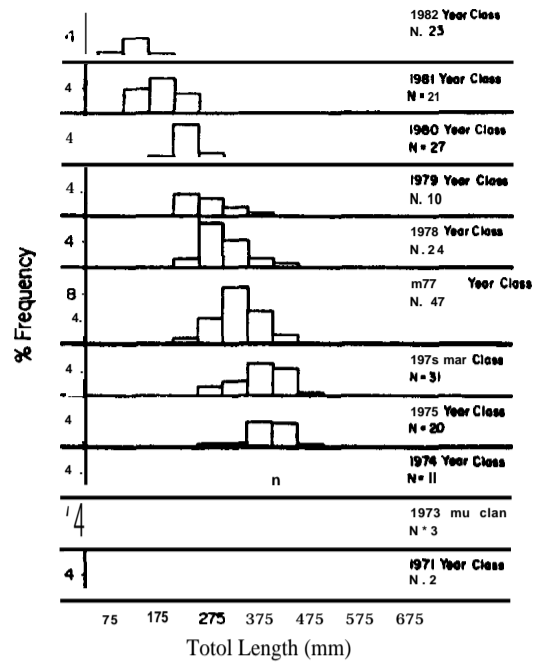


Fig. 6. Length-frequency by year class for *Gadus ogac*, Saqvaquac Inlet, 1983.  $N = 237$ .

1981. By late April no more gravid fish were caught and spawning was probably completed. Age at first maturity was estimated for fish that were known spawners (Table 3). A few females spawned in their second year and most males and females in their third year. Probably all fish older than three years spawn annually, since we found no fish older than three that were in non-spawning condition during the spawning season.

#### Food habits

Greenland cod in the Saqvaquac area were omnivorous benthic predators, feeding on a wide variety of prey species. Crabs, *Hyas coarctatus*, amphipods, polychaetes and fish comprised 77% of the food of 370 cod taken between March and September 1981–1983 (Table 4). Analysis of covariance showed no significant differences in diet composition between the inlets, or time of day and location within Saqvaquac Inlet. There were significant differences in diet composition within Saqvaquac Inlet for season of the year ( $p < 0.01$ ), ice-covered

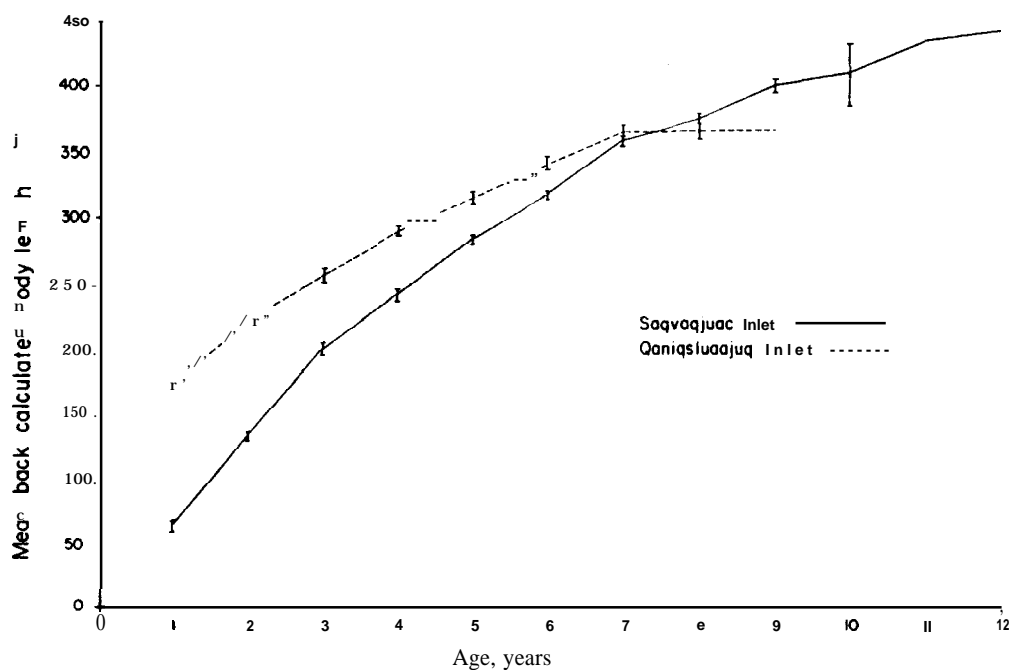


Fig. 7. Relationship between mean back-calculated body length and age of *Gadus ogac*, 95% C. I., 1983.

period between 1981 and 1983 ( $p < 0.02$ ), and length-group during the ice-covered season in 1983 ( $p < 0.05$ ). However, the differences were all relatively slight and should not be emphasized, because sampling effort was not evenly distributed across the spectrum of variables.

Table 3. Distribution of maturity stages for *Gadus ogac*. Saqvaqjuac Inlet, May - August 1983.

Age	Virgin		Spent	
	F	M	F	M
1	4	7		
2	8	17	2	
3	1	1	10	10
4			11	17
5			20	14
6			30	17
7			22	9
8			15	6
9			11	
10			3	
12			2	

#### Metabolic rate

Oxygen uptake rates were high and variable during the first hours in the respirometer, relative to later rates (Fig. 8). Serial regressions of  $O_2$  uptake were performed backward in time, to the time where inclusion of earlier points resulted in slopes significantly different from zero ( $p > 0.1$ ). At 0° C and 5° C the slopes were not significantly different from zero after 60 h, while at 10° C the slope from the start was not different from zero. Therefore the average rates after 60 h at 0° C and 5° C, and after 48 h at 10° C were used in order to minimize the effects of stress and handling.

The logarithmic relation between routine oxygen consumption rate ( $mg O_2 h^{-1}$ ) and body-weight ( $g$ ) at various temperatures is presented in Fig. 9. Multiple regression analysis resulted in the following equation:

$$\log O_2 = -1.813 + (0.750 \log W) + 0.048 T,$$

where  $O_2$  = oxygen-uptake in  $mg h^{-1}$ ,  $W$  = total weight in g,  $T$  = temperature in °C, and  $R^2 = 0.92$ .



## Discussion

### *Distribution and relative abundance*

The apparent disappearance of cod in Saqvaquac Inlet in early July could have had several causes. First, cod may have moved out of the inlet. This is highly unlikely because they disappeared in all basins simultaneously rather than the Outer Basin

last, and cod could not be caught outside the inlet at any time. Growth curves (below) also suggest that adult fish did not leave the inlet. Second, cod may have moved to deeper water to avoid sudden osmotic change. Winter salinity and temperature in Saqvaquac Inlet is essentially uniform from top to bottom at about 34.2‰ and -1.8°C (Welch, unpublished). At the onset of melt the water directly beneath the ice becomes diluted and warmer, and

**Table 4.** Food analysis of *Gadus ogac* by the volumetric method. Each number represents the percentage of the total volume of all contents in the sample. The following organisms were identified to phylum, genus or species: crab (*Hyas coarctatus*), capelin (*Mallotus villosus*), blenny (*Lumpenus* spp. ), Arctic shanny (*Stichaeus punctatus*), Greenland cod (*Gadus ogac*), American sand lance (*Ammodytes americanus*), Arctic cod (*Boreogadus saida*), slender eel blenny (*Lumpenus fabricii*), horse shoe fan worm (phylum phoronida). Saqvaquac Inlet (1981, 1982 and 1983). Qaniqluaajuaq Inlet, 1983 and Umiivik Inlet, 1983.

Food item	Saqvaquac Inlet					Umii	Qan	All data comb.
	ice cover 1981	open water 1981	open water 1982	ice cover 1983	open water 1983	Inlet ice cover 1983	Inlet ice cover 1983	
Crab	20.1	9.3		33.4	11.4	5.6	13.5	21.0
Amphipoda	4.5	18.4	14.3	18.9	35.5	4.5	4.6	18.6
Polychaeta	4.7	46.6		7.2	11.1	11.8	9.0	14.2
Fish, unident.	23.2	7.5	42.9	10.6	13.5	7.5	20.4	13.5
Capelin	37.9	2.0			1.3			5.8
Sculpin spp.	2.8	1.6		4.2	1.4	57.5	8.2	4.4
Shrimp		0.8	1.4	3.3	10.8		7.6	4.0
Fish eggs				6.3	1.3		16.1	3.9
Algae	0.2	2.2		4.3	4.8	5.0	1.9	3.2
Cumacea				2.0	1.8		12.4	1.6
Crab zoeae		2.6		0.8	4.0			1.5
Shrimp eggs		9.0						1.5
Blenny			30.0	1.7	0.3			1.3
Mysidacea	1.6			1.7		X.1	If)	1.1
Fish larvae		-		1.5	0.9		0.2	0.9
Arctic shanny	1.1			1.0	0.8			0.8
Greenland cod	0.6		11.4		1.0		1.7	0.7
Crab eggs	3.3			0.2				0.5
Tanaidacea				0.6				0.3
American sand lance				0.1			2.9	0.2
Mysid larvae				0.5			0.5	0.2
Invertebrate eggs				0.5				0.2
Arctic cod				0.5				0.2
Shrimp larvae				0.3				0.1
Slender eel blenny				0.3				0.1
Bivalvia					0.1			0.1
Horseshoe fan worm				0.1				0.1
Total percent	I(N)	100	I(U)	100	I(H)	100	100	100
Number of fish	51	61	7	150	69	x	24	370

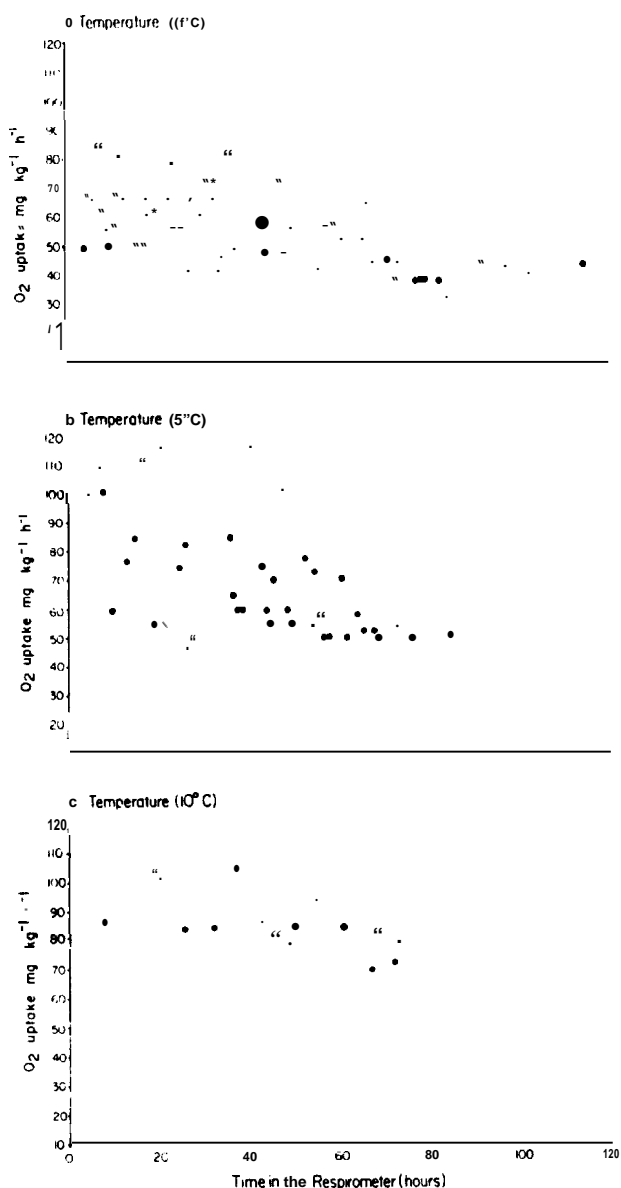


Fig. 8. Oxygen uptake of *Gadus ogac* as a function of time spent in the respirometer. Data points are means of individual oxygen uptake values for fish grouped according to the length of time spent in the respirometer.

this mixed layer gradually deepens until late August. Dead crabs, *Hyas coarctatus*, are common in late June – early July in shallow water in the inlet, where they apparently die from osmotic shock. However, angling CPUE data showed no movement toward deeper water, and low salinity water

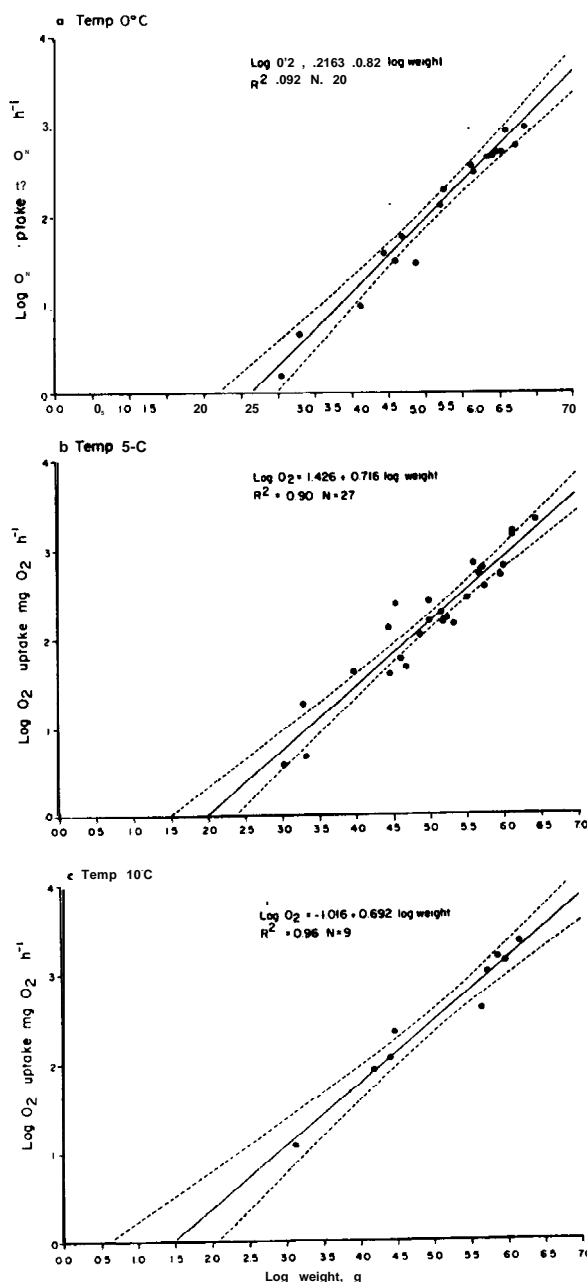


Fig. 9. Oxygen uptake versus weight for *Gadus ogac*. Dashed lines are 95% confidence boundaries for predicted values.

did not occur deeper than 10m in July 1983. The most likely reason for the decline in angling CPUE is that cod stopped feeding for a brief period, for unknown reasons. No trap or gill net sets were made during the period in question because the ice was deteriorating. On the east coast of Hudson

Bay, Greenland cod have been observed to become less abundant in gill net catches as summer progressed in the Innuksuac estuary (Mm-in et al. 1980) and in the Eastmain estuary (Lambert & Dodson 1982); the decline in the Eastmain was attributed to the progressive warming of coastal waters.

The fairly even distribution of catch from 4 to 30m water depth, and the fact that every hole fished inside the inlet yielded at least one fish per half hour, indicates that *G. ogac* were distributed along the bottom of Saqvaqjuac Inlet without any marked depth preference. However, we did not sample below 35 m depth and cod may have been less abundant in the deepest water (57 m maximum depth). Boulva (1970) caught 301 *G. ogac* in Cambridge Bay, N.W.T. by angling and gill net; 97.3% came from 0–30 m depth, 2.7% from 30–40 m, and none below 40 m, despite some effort in deep water. Jensen (1948) recorded *G. ogac* as common in the fiords of west Greenland from shoreline down to 400m, but not occurring on the outer bank of Davis Strait. We were unable to catch *G. ogac* beneath the ice or in midwater, and it appears to be strictly demersal at Saqvaqjuac. *B. saida*, of which only two were caught (by jigging) during our study, are also known to be distributed evenly along the bottom down to 400 m in the Chukchi and Bering seas (Lowry & Frost 1981) and along the bottom of Barrow Strait, Northwest Passage (R. Crawford, personal communication), but *B. saida* also forms part of the 'cryopelagic' fauna of the Arctic basin (Andriashev 1970), being abundant under ice and in mid-water throughout its range (Jensen 1948, Lear 1979). They often form massive schools in late summer and autumn (Craig 1982, Andriashev et al. 1981, Welch personal observation), when they may migrate shoreward and along the coast.

*G. ogac* appear to be relatively sedentary and do not migrate much distance, according to our data. Growth rates were quite different between Saqvaqjuac and Qaniqsluaajuq inlets (Fig. 7). If the two populations mixed to any great extent we would expect the length variance for each year to be much greater or that the two curves would not be significantly different. We did catch pelagic young-of-the-year cod in plankton nets suspended

in the tidal race at the mouth of Saqvaqjuac inlet in late June, so it may be that interchange between populations mostly occurs via the young; we were unable to angle any cod in May–June outside the inlets. *G. ogac* may move more extensively in other parts of its range; one individual tagged in Cambridge Bay was recovered in Wellington Bay 67 km distant (Hunter, in Boulva 1970). In general *G. ogac* tend to be sedentary, non-migratory, demersal and solitary, whereas *B. saida* are more mobile, pelagic, ice-associated, and frequently aggregate in large schools.

#### *Growth and maturity*

*G. ogac* from Saqvaqjuac reach about 450mm and 1.2 kg, comparable to *G. ogac* from SE Hudson Bay (Morin & Dodson 1986), but elsewhere it is reported as reaching 5 kg at Cambridge Bay (in Morin & Dodson 1986, no source given) and 'many weighing upwards of 6–7 kg' in west Greenland (Jensen 1948). Jensen also records the maximum age as 11 years, so growth rates of some *G. ogac* in Greenland must be far higher than at Saqvaqjuac. In SE Hudson Bay it reaches 21 years (Morin & Dodson 1986). There is general agreement that it spawns at 3–4 years (Table 3; Jensen 1948) about March–April. *B. saida* also reach maturity in their third year (Lowry & Frost 1981) and probably spawn annually thereafter, although the capture of two non-spawning females age 4 and 5 (Craig et al. 1982) suggest that some may spawn every second year. In any case the high mortality for post spawners (maximum age about 6 y) means that repeat spawning is much less important for *B. saida* than for *G. ogac*.

#### *Food habits*

*G. ogac* feeding habits are remarkably constant throughout its range. Although they take a great variety of prey (e.g. Table 4), fish are the primary food when available. In years when capelin were relatively abundant in Saqvaqjuac Inlet (e.g. 1979, Welch, personal observation), cod fed on them

almost exclusively. In other years, or beneath ice cover before capelin began their summer migrations into the inlet, crabs, benthic amphipods and polychaetes were major prey. Elsewhere *G. ogac* have also been found to feed on fish near the bottom, supplemented by common benthic crustacea (e.g. capelin, sand lance, sculpin, *G. ogac* in the Innuksuac estuary; capelin, sand lance, sticklebacks and benthic amphipods in the Eastmain estuary; sculpin, sea snails, and benthic invertebrates in southern Labrador (summarized in Morin & Dodson 1986); and in Greenland, capelin supplemented by other bottom-dwelling fish and invertebrates (Jensen 1948)). This is very different from *B. saida*, which take mostly copepods, hyperiid amphipods, ice-associated crustacea, and other pelagic prey. It is likely that the food habits of the two cod species are quite different in areas where they overlap.

#### Metabolic rate

We consider our  $O_2$  consumption rates to be equal to standard or basal metabolism rather than routine metabolism (Brett & Groves 1979, Fry 1971), because our fish were constrained from normal swimming activity by the respiration chambers, and allowed to acclimate and respire without feeding.

There has been considerable debate as to whether polar fish compensate by maintaining higher metabolic rates at very low temperatures than would be expected from studies on temperate species. Scholander et al. (1953) and Wohlschlag (1960, 1963) concluded from their own studies that there was polar adaptation. Holeyton (1973, 1974) questioned that work on the basis that the earlier results obtained on polar fish included times of stress and short acclimation times. Brett & Groves (1979) discussed the problem and concluded that Holeyton's own data on *Boreogadus saida* supported the polar adaptation hypothesis, whereas his data for more sluggish Arctic species of cottids, zoarcids and liparids showed lower 'uncompensated' rates. Recent work on the cryopelagic nototheniid *Pagothenia borchgrevinki* in Antarctica showed that Wohlschlag's results probably had been elevated

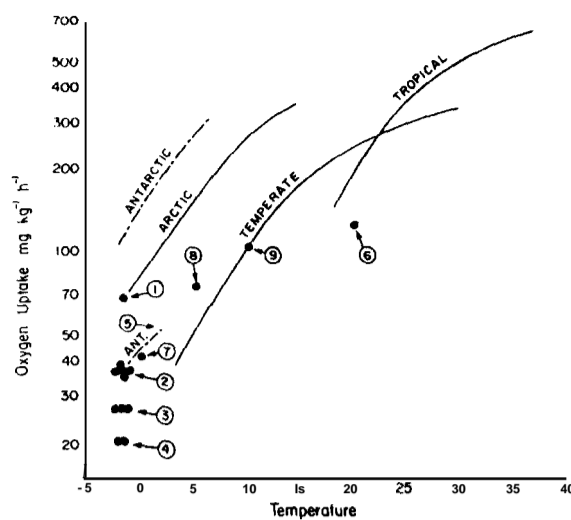


Fig. 10. The relationships between oxygen consumption and temperature for polar, temperate, and tropical fish (solid lines) as commonly accepted in earlier literature (e.g. Scholander et al. 1957; Wohlschlag 1964). Lower broken line applies to data for an Antarctic zoarcid having 'unusually' low metabolism (Wohlschlag 1963). Recent data for Arctic fish (Holeyton 1973, 1974 and present study) have been plotted for comparison. Key to data: 1 = *Boreogadus saida*; 2 = Arctic cottids; 3 = Arctic zoarcids; 4 = Arctic liparids; 5 = *Salvelinus alpinus*; 6 = *Dallia pectoralis*; 7, 8 and 9 = *Gadus ogac* (present study) (redrawn from Holeyton 1974).

by handling stress, but that the species still has a metabolic rate two-fold higher than temperate fish at low temperatures (Forster et al. 1987). The position of *G. ogac* is therefore of theoretical interest because it bridges the gap between temperate species which die at the temperature of freezing seawater, and polar stenotherms which never experience temperatures above 0°C.

Our data show that at -1.5°C, the basal metabolic rate for *G. ogac* (point 7 in Fig. 10) would be about half that for *B. saida*, and intermediate between Arctic and temperate forms. At 5°C *G. ogac* approaches the temperate curve, and at 10°C falls exactly on it. The  $Q_{10}$  is 2.5, reasonably close to the mean of 2.3 used as a general figure for fish (Brett & Groves 1979) and does not imply any sort of cold-adapted compensation. We conclude that *G. ogac* does in fact have a metabolic rate which is intermediate between polar stenothermal and temperate eurythermal, along with the obvious ability to function at the temperature of freezing seawater.

ter,  $-1.8^{\circ}\text{C}$ . In this regard it is interesting that they have a solute in the blood which depresses the freezing point below  $-2^{\circ}\text{C}$  (Van Voorhies et al. 1978). At the same time they have a high tolerance for moderate temperatures and low salinities; Ochman & Dodson (1982) reported *G. ogac* larvae from water as low as 4‰ salinity in SE Hudson Bay.

#### *Position of Gadus ogac in the Arctic food web*

*G. ogac* appear to have few predators in the Saqvaquac Inlet. Ringed seal, *Phoca hispida*, are common outside the inlet but rarely come far inside. Harbor seal, *Phoca vitulina*, occur regularly in the inlet but only several at a time. They are frequently observed to eat anadromous charr at the mouths of both the Saqvaquac and Connery rivers (to the north) (Welch, personal observation) but their potential predation rates on *G. ogac* are unknown. Anadromous charr from the Saqvaquac River have been caught with large numbers of unidentified fish larvae, probably *G. ogac*, in late June in the Camp Basin, but in general they contain capelin and epibenthic crustacea (Welch, unpublished). Johnson (1980) also found that returning anadromous charr on the Kent Peninsula had not fed extensively on *G. ogac*. We found no cod in the stomachs of 50 sculpin (*Myoxocephalus* and others) examined from Saqvaquac Inlet in 1983. Beluga whales, *Delphinapterus leucas*, feed extensively on capelin in the Churchill River estuary (P. Richard, personal communication) and sometimes contain *G. ogac* in the Eskimo Point (SW Hudson Bay) area (R. Walker, personal communication); however, white whales are not common near Saqvaquac and only rarely come inside the inlet.

Approximately two million thick-billed murres feed in Hudson Bay and Hudson Strait, taking 350 g fish d<sup>-1</sup> each (Morrison & Gaston 1986), or 3.5 kg km<sup>-2</sup>, primarily *B. saida* with lesser amounts of benthic fish, but *G. ogac* was not found (Gaston & Noble 1985). Black guillemots in Hudson Bay have similar feeding habits (Cairns 1987). It seems highly unlikely that *G. ogac* would be present at the offshore islands and feeding areas where these

birds were studied, yet not be found at all in stomach contents, suggesting that *G. ogac* is rare away from the mainland coast, bays and estuaries.

McLaren (1958) listed food species for 220 ringed seals from Hudson Bay, Ungava Bay, northern Labrador, and Baffin Island. A variety of fish were eaten, especially *B. saida*, which had been eaten in every locality except Southampton Island (5 stomachs) and Churchill (2 stomachs); *G. ogac* was not listed as prey at any locality.

From this we conclude that, in Hudson Bay at least, and probably throughout its range, *G. ogac* is not a major prey species for marine birds or mammals, or for other common near-shore fish predators. It functions as a carnivorous 'dead-end', rather than as a vital intermediary in Arctic food webs. This is very different from the role played by *B. saida*, whose central importance as whale, seal, bird and charr food is universally recognized.

#### *Summary of life history of Gadus ogac at Saqvaquac*

*G. ogac* are medium-sized fish (35 cm long; 0.3 kg) abundant in Saqvaquac Inlet (jigging CPUE 17 h<sup>-1</sup> in early June). It is demersal and non-schooling, feeding opportunistically on large epibenthic prey (crabs, amphipods, polychaetes and fish) but preferring capelin in those summers when capelin migrate into Saqvaquac Inlet in large numbers. *G. ogac* are slow growing (annual mortality 0.5), maturing at age 2 or 3 y, after which they spawn annually beneath the ice in March and early April. They reach at least 12 y of age. Larvae are pelagic and may pass in and out of the Inlet with the tidal currents, but adult fish exhibit growth rates characteristic of their particular inlet and apparently do not move more than a few kilometers, remaining in their home inlet for life. They are not like Arctic cod, *Boreogadus saidu*, a shorter-lived species which often schools, is often or usually pelagic, feeds primarily on planktonic crustacea, and is a key component of Arctic marine bird and mammal food chains. *G. ogac* appear to have relatively few predators and are not the primary food of any common top predator; instead, they fill the top

predator role in shallow Hudson Bay benthic food chains. Their metabolic rate is slightly lower than that of h'. *suit-la* at similar temperatures, being intermediate between cold stenothermic and temperate eurythermic.

### Acknowledgements

We thank M. Bergmann, K. Martin-Bergmann, K. Mills, D. Bodaly, M. Giles, W. Franzin and R. Lypka for advice and suggestions during the study. K. Martin-Bergmann collected the 1981 data. Field assistance was provided by G. Amarok, M. Kukkiak, M. Curtis, J. Jorgenson, L. Scharf, B. McIntyre and T. Stevenson. D. Glowacki prepared the manuscript. The cooperation of the Chesterfield Inlet people is gratefully acknowledged.

### References cited

- Andriashev, A. P. 1970. Cryopelagic fishes of the Arctic and Antarctic and their significance in polar ecosystems. pp. 297-304. In: M.W. Holdgate (ed.) Antarctic Ecology, vol. 1. Academic Press, London.
- Andriashev, A. P., B.F. Mukhomedgarov & E.A. Pavshikov. 1980. On the mass accumulations of cryopelagic cods (*Boreogadus saida* and *Arctogadus glacialis*) in the circumpolar regions of the Arctic. pp. 196-210. In: M.E. Vinogradov & I.A. Melnikov (ed.) Biology of the Central Arctic Basin. Shirshov Inst. Oceanology Academy of Sciences U.S.S.R. [Transl. from Russian by D.W. Nelson. College of Fisheries, University of Washington, Seattle.]
- Bagenal, T.B. & F.W. Tesch. 1975. Age and growth. pp. 101-136. In: T. B. Bagenal (ed.) Methods for Assessment of Fish Production in Freshwaters, 3rd ed., Blackwell Sci. Publ., Oxford.
- Beamish, R.J. 1972. Design of a trap net for sampling shallow water habitats. Fish. Res. Board Can. Tech. Rep. 305. 1-1 pp.
- Beamish, R.J. & D. Chilton. 1977. Age determination of ling cod (*Ophiodon elongatus*) using dorsal fin rays and scales. J. Fish. Res. Board Can. 34: 1305-1313.
- Beamish, R.J. & I. L. Harvey. 1969. Age determination in white sucker. J. Fish. Res. Board Can. 26: 633-638.
- Bedford, B. C. 1964. Two mechanical aids for otolith reading. Int. Comm. Northwest Atl. Fish. Res. Bull. 1: 79-81.
- Boulva, J. 1970. The systematics of sympatric populations of the Arctic codfishes, *Arctogadus borisovi* Drjagin and *A. g. (ciacila)* (Peters), from Cambridge Bay, N.W.T., Canada. M.Sc. Thesis, Dalhousie University, Halifax. 122 pp.
- Brett, J. I. & "P. L. J. (revs. 1979. Physiological energetics. pp. 279-352. In: W.S. Hoar, D.J. Randall & J.R. Brett (ed.) Fish Physiology, Vol. 9, Academic Press, New York.
- Cairns, D.K. 1977. Diet and foraging ecology of black guillemots in northeastern Hudson Bay. Can. J. Zool. 65: 1257-1263.
- Carpenter, J.H. 1968. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. Limnol. Oceanogr. 10: 141-143.
- Clarke, A. 1933. Life in cold water: the physiological ecology of polar marine ectotherms. Oceanogr. Mar. Biol. Ann. Rev. 21: 341-453.
- Craig, P.C., W.B. Griffiths, L. Halderson & J. McElderry. 1982. Ecological studies of Arctic cod, *Boreogadus saida* in Beaufort Sea coastal waters, Alaska. Can. J. Fish. Aquat. Sci. 39: 395-406.
- Dalton, J.A. 1981. Hydrometeorological data from the Saqvaquac Project, N.W.T., 1977 to 1980. Can. Data Rep. Fish. Aquat. Sci. 273: v+43 pp.
- Elliot, J.M. 1971. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc. Sci. Publ. 25: 1-148.
- Forster, M.E., C.E. Franklin, H.H. Tiryler & W. Davidson. 1977. The aerobic scope of an antarctic fish, *Pagothenia borchgrevinki* and its significance for metabolic cold adaptation. Polar Biol. 8: 155-159.
- Fry, F.E.J. 1971. The effect of environmental factors on the physiology of fish. pp. 1-98. In: W.S. Hoar & W.D. Randall (ed.) Fish Physiology, Vol. 4, Academic Press, New York.
- Gaston, A.J. & D.G. Noble. 1985. The diet of thick-billed murre (*Uria lomvia*) in west Hudson Strait and northeast Hudson Bay. Can. J. Zool. 63: 1148-1160.
- Holcton, G.F. 1973. Respiration of Arctic char, *Salvelinus alpinus* from a high Arctic lake. J. Fish. Res. Board Can. 30: 717-723.
- Holcton, G.F. 1974. Metabolic cold adaptation of polar fish: fact or artifact? Physiol. Zool. 47: 137-152.
- Jensen, Ad. S. 1948. Contributions to the ichthyofauna of Greenland. Skrift. U. Zool. Mus. København 9: 1-182.
- Johnson, L. 19X(). The Arctic charr, *Salvelinus alpinus*. pp. 15-98. In: E.K. Baton (ed.) Charrs: Salmonid Fishes of the Genus *Salvelinus*, Dr W. Junk Publishers, The Hague.
- Kcir, R.S. 196f). Answers to the questionnaire on age reading. Int. Comm. Northwest Atl. Fish. Ann. Meet., Dec. no. 4, Ser. no. 714.67 pp.
- Lambert, Y. & J. Dodson. 1982. Structure et rôle des facteurs physiques dans le maintien des communautés estuariennes de poissons de la Baie James. Naturalist Can. 109: 815-823.
- Lear, W.H. 197J. Distribution, size and sexual maturity of Arctic cod (*Boreogadus saida*) in the northwest Atlantic during 1959-1978. CAFSAC Res. Dec. 79/17. 40 pp.
- Leim, A.H. & W.B. Scott 1966. Fishes of the Atlantic coast of Canada, Fish. Res. Board Can. Bull. 35: 1469-1478.
- Lowry, L.F. & K.J. Frost. 1981. Distribution, growth, and foods of a Arctic cod (*Boreogadus saida*) in the Bering and Beaufort seas. Can. Field. Nat. 95: 186-191,

- McLaren, I.A. 1958. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic. Fish. Res. Board Can. Bull. 118. 77 pp.
- Mikhailii, M.Y. 1985. Respiration, growth, food habits and distribution of Greenland cod, *Gadus ogac* (Richardson), on the northwest coast of Hudson Bay, N.W.T. M. SC. Thesis, University of Manitoba, Winnipeg. 131 pp.
- Morin, R. & J.J. Dodson. 1986. The ecology of fishes in James Bay. Hudson Bay and Hudson Strait. pp. 293-325. /n: [P. Martini (cd.) Canadian Inland Seas, Elsevier, New York.
- Morrison, R. L.G. & A.J. Gaston: 1986. Marine and coastal birds of James Bay. Hudson Bay and Foxe Basin. pp. 355-386. /n: J.P. Martini (cd.) Canadian Inland Seas, Elsevier, New York.
- Ochman, S. & J. Dodson. 1982. Composition and structure of the larval and juvenile fish community of Eastmain River and estuary, James Bay. Naturalist Can. 109: 803-813.
- Robson, D.S. & D.G. Chapman. 1961. Catch curves and mortality rates. Trans. Amer. Fish. Soc. 90: 181-189.
- Scott, D.M. 1952. Greenland cod (*Gadus ogac*) in Cape Breton Island. Nova Scotia. Can. Field Nat. 66: 123-124.
- SAS. 1982a. SAS User's Guide: Basics. SAS Institute Inc. Cary. 921 pp.
- SAS 1982b. SAS Users Guide: Statistics. SAS Institute Inc. Cary. 584 pp.
- Scholander, P. F., W. Ffagg, V. Walters & L. Irvin. 1953. Climatic adaptation in Arctic and tropical poikilotherms. Physiol. Zool. 26: 67-92.
- Van Voorhies, W.V., J.A. Raymond & A.L. De Vries. 1978. Glycoproteins as biological antifreeze agents in the cod, *Gadus ogac* (Richardson). Physiol. Zool. 51: 347-353. ,
- Welch, H.E. 1985. Introduction to limnological research at Saqvaquac, northern Hudson Bay. Can. J. Fish. Aquat. Sci. 42: 494-505.
- Welch, H.E. & M.A. Bergmann. 1985. Winter respiration of lakes at Saqvaquac, N.W.T. Can. J. Fish. Aquat. Sci. 42: 521-528.
- Wohlschlag, D.E. 1960. Metabolism of an antarctic fish and the phenomenon of cold adaptation. Ecology 41: M-292.
- Wohlschlag, D.E. 1963. An antarctic fish with unusually low metabolism. Ecology 44: 557-564.