

Feeding ecology of marine fish larvae across the Great Whale River plume in seasonally ice-covered southeastern Hudson Bay*

Michel Gilbert**, Louis Fortier, Dominique Ponton, René Drolet

Département de biologie, Université Laval, Ste-Foy, Québec, Canada G1K 7P4

ABSTRACT: In ice-covered southeastern Hudson Bay (northern Québec, Canada), the foraging of first-feeding Arctic cod *Boreogadus saida* and sand lance *Ammodytes* sp. was adversely affected by the plume of the Great Whale River. Before the freshet, marine fish larvae and their potential prey were marginally more abundant offshore where porous sea ice supported the development of ice algae than inshore where freshwater ice prevented algal growth. Larval fish foraging under the ice appeared limited by prey availability in the diluted ($S < 5\text{‰}$), 5 m thick, surface layer and by light availability in the underlying marine waters. Arctic cod larvae which avoided the freshwater surface layer did not feed. The more euryhaline sand lance were present in the surface layer and fed to some limited extent until the freshet when further light attenuation by the turbid waters of the expanding plume completely halted their foraging activity. Feeding resumed in sand lance and started in Arctic cod at the ice break-up when the fragmentation of the ice cover and the vertical mixing of the plume allowed light to penetrate at depth. An anthropogenic reduction of the Great Whale River discharge in spring would generally improve local feeding conditions for marine fish larvae that occur under the ice. The impacts of such a reduction on the productivity of the coastal zone in summer remain to be assessed.

INTRODUCTION

According to the transport hypothesis, circulation may determine the early survival of marine fish by dispersing their planktonic larvae towards hydrographic areas where feeding conditions are unsuitable for survival (Hjort 1926, Harden Jones 1968). The hypothesis assumes: (1) that regions of either high or low productivity exist within the potential area of dispersion of the larval population, and (2) that feeding, growth and survival are better in areas where production of suitable prey is higher.

In seasonally ice-covered southeastern Hudson Bay, the grazing of ice algae triggers the early reproduc-

tion of calanoid copepods (Runge & Ingram 1991, Tourangeau & Runge 1991) and the production of copepod eggs and nauplii which are the main prey of first-feeding fish larvae (Drolet et al. 1991). The inshore production and distribution of ice algae is strongly influenced by the outflow of the Great Whale River (Poulin et al. 1983, Gosselin et al. 1986). Inside the area covered by the river plume in winter the freezing of freshwater results in crystal ice at the bottom of which little or no algal biomass develops. Outside this area, porous sea ice supports the vernal development of a dense algal mat (e.g. Tremblay et al. 1989). Thus the areas of crystal ice associated with river plumes could be less suitable for copepod reproduction and larval fish feeding than areas of sea ice. If this is so, the transport hypothesis (Hjort 1926) predicts that larval fish survival in the coastal zone of Hudson Bay will be inversely proportional to the fraction of the dispersal area of first-feeding larvae that is covered by crystal ice.

Fish larvae are visual predators and feeding depends not only on prey density but also on the amount of light

* Contribution to the research programs of GIROQ (Groupe interuniversitaire de recherches océanographiques du Québec) and Institut Maurice-Lamontagne (Ministère des Pêches et des Océans)

** Present address: Institut Maurice-Lamontagne, Ministère des Pêches et des Océans, C.P. 1000, Mont-Joli, Québec, Canada G5H 3Z4

available to perceive prey (Blaxter 1975a, Theilacker & Dorsey 1980, Munk et al. 1989). In lakes, the attenuation of light by an ice cover narrows the depth range over which fish larvae can forage (Dabrowski 1985). Daytime intensities of less than $100 \mu\text{Ein m}^{-2} \text{s}^{-1}$ have been measured under the ice cover of southeastern Hudson Bay in spring (Gosselin et al. 1985, 1986). These values compare with the thresholds at which the foraging of fish larvae becomes limited (Theilacker & Dorsey 1980, Dabrowski 1982). Thus, the further attenuation of light by the turbid waters of a river plume expanding immediately under the ice cover could represent an additional constraint for first-feeding fish larvae transported to or retained in coastal areas influenced by the freshwater outflow of rivers.

In the present study we describe the distribution and foraging of marine fish larvae in the area of southeastern Hudson Bay influenced by the plume of the Great Whale River. In particular, we test the hypotheses that the local abundance of copepod eggs and nauplii depends on ice type, and that the foraging of first-feeding fish larvae is affected by light availability as well as prey abundance.

MATERIALS AND METHODS

Study area. With a drainage basin of 41800 km^2 , the Great Whale River is one of the most important rivers of northern Québec. The river flows into southeastern Hudson Bay near Kuujjuarapik (Fig. 1). In summer, the plume of the river is 1 to 2 m thick and covers less than 100 km^2 (Ingram 1981). In spring, the plume expands immediately under the 1.5 m thick first-year ice cover and may exceed 1000 km^2 in area as a result of increased river runoff and lack of wind mixing (Ingram & Larouche 1987).

Sampling. Sampling was carried out from 24 April to 14 June 1988. Four stations 5 km apart along a south-north transect covering the salinity gradient of the plume were sampled in daylight of the same day, at intervals ranging from 2 to 4 d depending on weather conditions (Fig. 1). Stn A was located in the inshore region of crystal ice, while Stns B, C and D were positioned in the region of porous ice, beyond the offshore limit of the winter plume.

Two different but comparable methods were used to sample fish larvae and zooplankton before and after the break-up of the ice in the Bay (Drolet et al. 1991). Before the break-up, plankton nets were towed with a heavy-duty snowmobile between 2 holes 200 m apart. At each station, 2 tows were made using a rectangular metal frame, supporting two 1 m^2 $500 \mu\text{m}$ mesh plankton nets fitted with $80 \mu\text{m}$ mesh live-capture cod-ends and TSK flowmeters. A first tow was carried out with

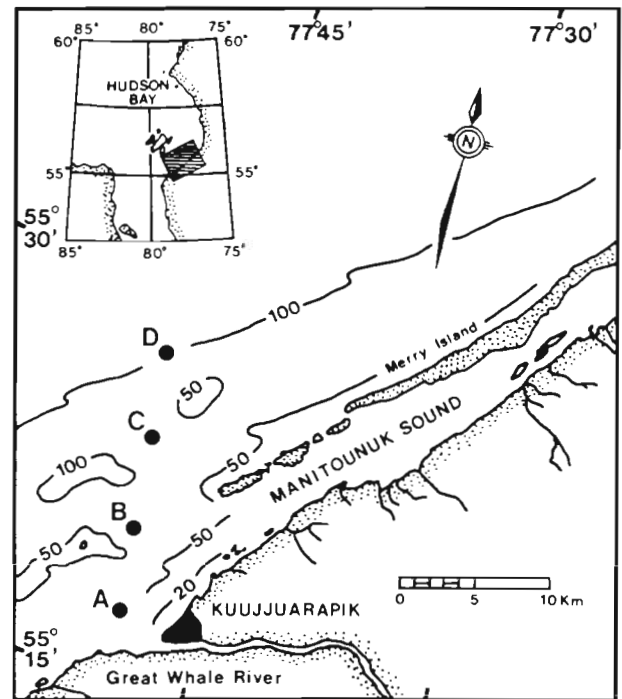


Fig. 1. Southeastern Hudson Bay (northern Québec) showing the position of Stns A to D, off the Great Whale River mouth. Isobaths are in meters

spherical buoys attached to the frame, to sample the 0.5 to 1.5 m depth interval immediately under the ice, this layer corresponding to the freshwater plume when the latter was present. To sample the marine waters below the plume, the buoys were removed and a time-depth recorder (TDR) was attached to the frame. Sampling depth was around 8 m and varied little along the tow.

After ice break-up (18 May), a helicopter was used for transportation between the stations and to deploy the plankton nets. The helicopter, mounted on floats, alighted on the water in ice-free areas and was used like a boat to tow a $500 \mu\text{m}$ mesh 1 m diameter conical net (with a TSK flowmeter and a $80 \mu\text{m}$ mesh cod-end). A spherical buoy was attached to the net for the surface tow and a 20 kg depressor for the deep tow. The speed of the helicopter was adjusted to keep the net at 8 m during the deep tow and thus provide samples comparable to those obtained before ice break-up.

Microzooplankton was sampled at each station with a vertical haul from bottom to surface, using a $64 \mu\text{m}$ mesh net mounted on a 0.5 m diameter ring. To limit gut content regurgitation by fish larvae, all samples were immersed in a MS-222 solution immediately after collection (Lyczkowski Laroche 1982). All samples were preserved in 4% neutralized formalin.

Analysis. In the laboratory, all fish larvae were identified and measured to the nearest 0.1 mm. Gut contents of the most abundant larval fish species were identified and quantified. Larval fish prey were enumerated in the microzooplankton collections. The food resource of larval fish was then estimated following Fortier & Harris (1989):

$$R = \sum_{i=1}^n A_i W_i F_i$$

where R = potential food resource of a given species; A_i = abundance of the i th prey item in the water column; W_i = average weight (mg) of the i th prey item in the diet; and F_i = frequency of the i th prey item in gut contents. This equation yields an estimation of the potential resource available for a given species over the entire water column. Average weights used in the calculations were estimated from width and length of prey found in the gut of the larvae.

Irradiance measurements. Coefficients of light attenuation across the ice cover and in the water column were measured with a Biospherical quantum scalar irradiance meter. A reference sensor measured the photosynthetically available radiation above the ice cover (incident PAR, 400 to 700 nm) while PAR in the water column was given by an integrating sounding line. Before ice break-up in 1988, measurements were taken at the edge of large holes in the ice, a procedure that clearly underestimated light attenuation by the ice cover. More reliable estimates of percent transmission across the ice cover were obtained from data collected in spring 1989 under comparable conditions of ice and snow cover, by SCUBA divers using the same instrument away from any apertures in the ice. A correction factor, derived from the 1989 estimates of percent light transmission across the ice cover, was applied to measurements of light attenuation at depth made in 1988 at the edge of large holes in the ice:

$$CLA_z = LA_z \times \frac{\%LT_{ice,1989}}{\%LT_{ice,1988}}$$

where CLA_z = corrected value of light attenuation at depth z ; LA_z = measured value of light attenuation at depth z ; $\%LT_{ice,1989}$ = percent light transmission across the ice, as measured in 1989; and $\%LT_{ice,1988}$ = percent light transmission across the ice, as measured in 1988.

Daily variations of incident PAR above the ice cover and at the ice-water interface were obtained from continuous light measurements made between 11 April and 20 May 1986 using a Biospherical MER-1010 spectroradiometer and surface sensor, 25 km north of Kuujuarapik (Legendre & Gosselin 1991). For ice cover conditions, daily variations in absolute irradiance at depth z were estimated by multiplying incident PAR at the ice-water interface by the coefficient of

light attenuation at depth z . Time-depth variations in light intensity for open water conditions were estimated in the same way, using daily variations of incident PAR above the ice cover.

RESULTS

River plume, ice-cover dynamics and light availability at depth

In spring, the expansion of the Great Whale River plume generated important spatial and temporal variations in the physical characteristics of the water column. Three periods were distinguished on the basis of surface salinities, plume thickness and ice cover conditions (Fig. 2). These periods were separated by 2 major events: the river freshet (8 May) and the break-up of the landfast sea ice cover in Hudson Bay (18 May). Period I corresponded to the spatial expansion of the river plume under complete ice cover: surface salinities decreased regularly at all stations (except Stn A where surface salinity was always ca 0 ‰) while plume thickness increased. Hydrographic conditions remained relatively stable during Period II, all stations being characterized by low surface salinities and a relatively thick plume (2 to 5 m). Period III saw the disruption and gradual melting of the ice cover in the bay. With increasing wind mixing, surface salinity rose progressively at Stns B, C, and D and the thickness of the plume decreased sharply. At Stn A, salinity remained low because of the continued input of freshwater, and plume thickness remained high following the break-up of the ice cover.

Light intensities in the water column were closely related to ice conditions (Fig. 3). Less than 0.1 % of light in the 400 to 700 nm spectrum reached the water column before ice break-up (Periods I and II), compared to 50 % after (Period III). During Periods I and II, an additional fraction of incident PAR was absorbed by the turbid waters of the river plume immediately under the ice. During Period III, the coefficient of light attenuation remained relatively constant over the water column (Fig. 3).

Our reconstruction of the daily light regime in the upper part of the water column (0 to 12 m) indicated that apart from the diel cycle, several factors affected light availability at depth (Fig. 4). First, days of high and low underice irradiance may have occurred as a result of changes in cloudiness or changes in the nature of the upper surface of the ice cover (Maykut & Grenfell 1975). Second, irradiance at depth increased with distance from the river mouth, as the turbid waters of the Great Whale River plume were progressively diluted with clear marine waters. As a result of

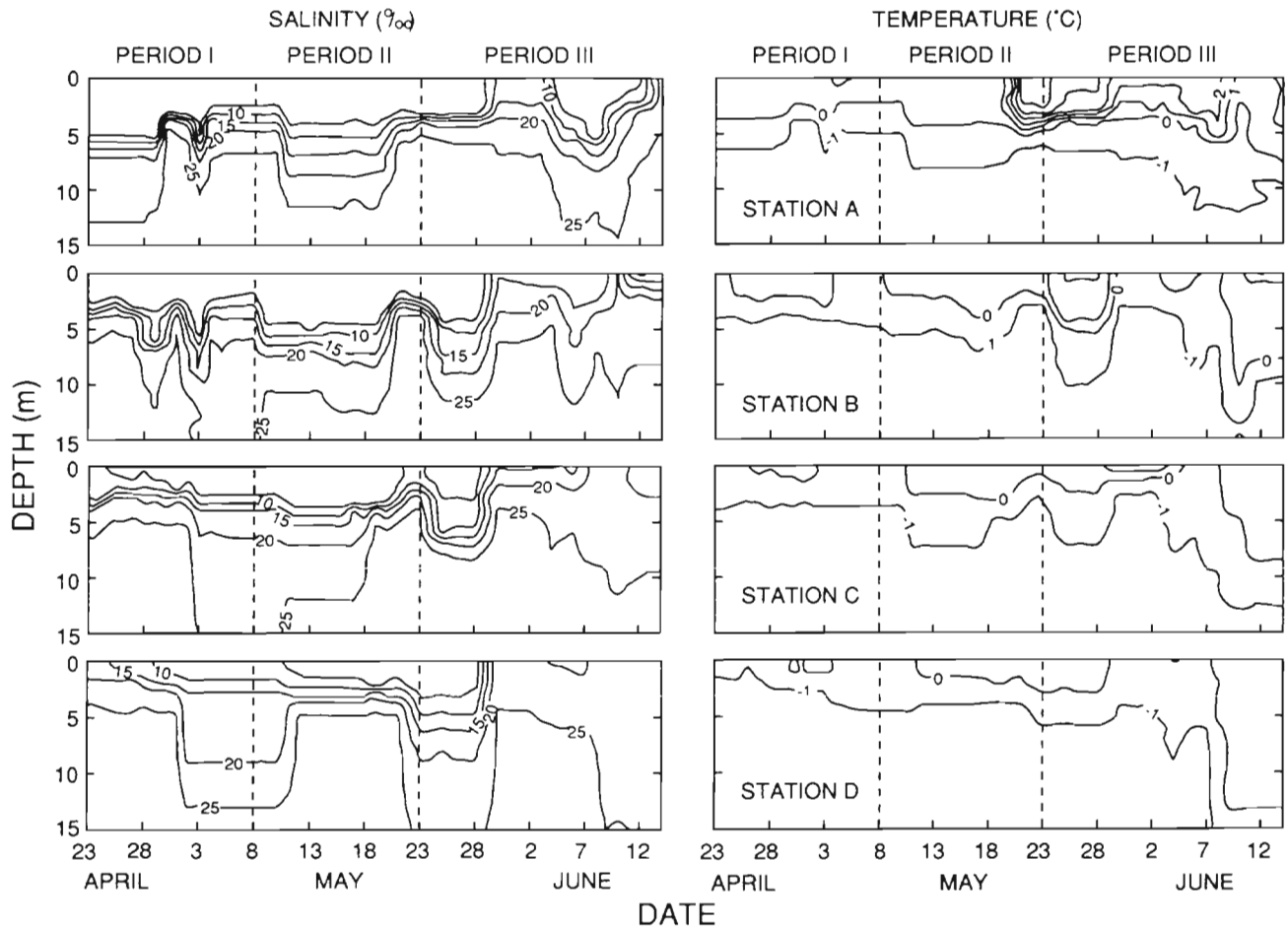


Fig. 2. Time-depth section of salinity and temperature at Stns A (inshore) to D (offshore), off the Great Whale River mouth in coastal Hudson Bay from 23 April to 14 June 1988. The periods correspond to different hydrographic regimes (I: before the river freshet, II: after the freshet, III: after the ice break-up); Hatching indicates the river plume with salinities $< 5\text{‰}$.

the combined effects of these factors, the daily maximum in absolute irradiance immediately beneath the plume (ca 3 m) varied approximately from 0.1 to $1.0 \mu\text{Ein m}^{-2} \text{s}^{-1}$ in Periods I and II (Fig. 4). Light levels at depth were ca 100 times higher in Period III in the absence of an ice cover (Fig. 4).

Larval fish distribution and apparent growth

Sand lance *Ammodytes* sp. and Arctic cod *Boreogadus saida* numerically dominated the ichthyoplankton assemblage (Table 1). Yolk-sac larvae of the burbot *Lota lota* originated from the river and were abundant in Periods I and II. The spatial distribution of burbot larvae, which never fed and apparently did not survive their dispersion in marine waters (Drolet et al. 1991), will not be considered here. Other species that were found regularly in the samples after the ice break-up included Arctic shanny *Stichaeus punctatus*,

slender eelblenny *Lumpenus fabricii*, gelatinous snailfish *Liparis fabricii*, and 3 species of cottids: Arctic staghorn sculpin *Gymnocanthus tricuspis*, fourhorn sculpin *Myoxocephalus quadricornis* and Arctic sculpin *Myoxocephalus scorpioides*. The abundance of these species before the ice break-up was too low to warrant a detailed study of their under-ice distribution and feeding ecology.

Significant numbers of sand lance and Arctic cod larvae were captured at all 4 stations in the 3 sampling periods (Fig. 5). The average density of both species varied little between periods (ANOVA, sand lance: $F = 0.90$, $p = 0.408$; Arctic cod: $F = 1.73$, $p = 0.183$) but differed significantly among stations (sand lance: $F = 4.56$, $p = 0.005$; Arctic cod: $F = 3.45$, $p = 0.019$) and sampling layers (sand lance: $F = 11.62$, $p < 0.001$; Arctic cod: $F = 11.04$, $p = 0.001$). Both species were generally less abundant at Stn A than at the other stations (Fig. 5). Density tended to increase with distance offshore (A to D) during Periods I and II, but less so during Period III.

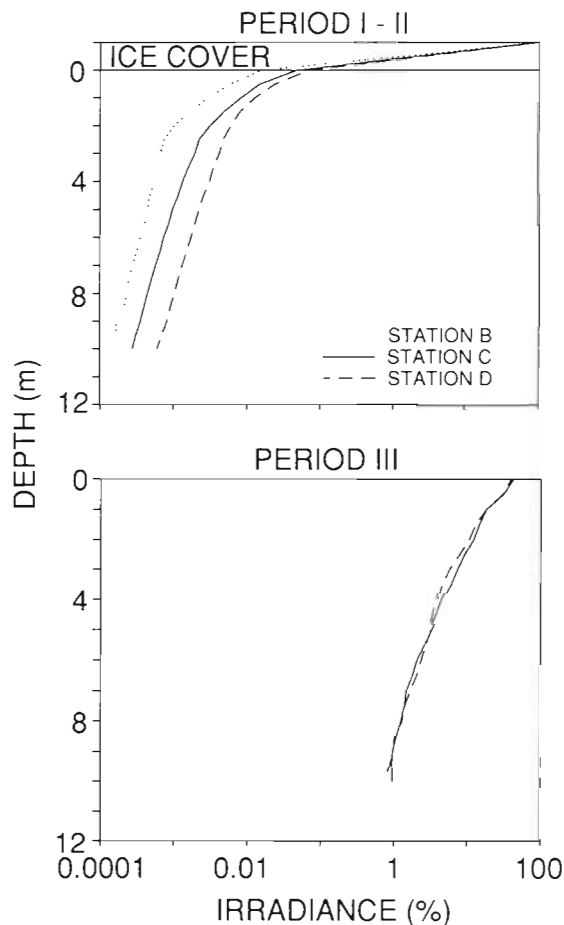


Fig. 3. Vertical profiles of light intensity (percent of incident irradiance in the 400 to 700 nm range) at Stns B (inshore) to D (offshore) before (Periods I and II) and after (Period III) the break-up of the ice cover in coastal Hudson Bay

The vertical distribution of sand lance and Arctic cod larvae (Fig. 5) reflected the different affinity of each species to the low salinities of the plume. During Periods I and II, sand lance larvae were less abundant in the low-salinity plume than in the deeper marine layer, especially at inshore stations where surface salinities were much lower (Fig. 2). Arctic cod larvae clearly avoided the plume (Fig. 5). During Period III, wind mixing eroded the vertical gradient of salinity and both species were captured in roughly equal numbers in the 2 layers.

Based on changes in length, the apparent growth of larval sand lance and Arctic cod was slow (Table 2). Differences in mean lengths between periods were statistically significant (ANOVA, sand lance: $F = 24.6$, $p < 0.0001$; Arctic cod: $F = 40.5$, $p < 0.0001$) but never exceeded 0.5 mm (Table 2). For sand lance, the apparent growth rate did not vary between periods. Arctic cod length increased faster from Period II to III than from Period I to II. Spatially, both species presented slight but significant differences in length (sand lance: $F =$

5.05, $p = 0.0018$; Arctic cod: $F = 4.99$, $p = 0.0018$). Larvae were invariably larger at Stn A in all 3 sampling periods. Marine fish larvae exposed to low salinity tend to absorb water (e.g. Aronovitch et al. 1975). Slightly longer lengths at Stn A may have reflected an osmotic response of the larvae to the salinity of the surface water which was used to preserve samples from both the surface and deep layer. Average apparent growth rates for sand lance and Arctic cod at Stn A did not differ much from those at stations offshore.

Yolk-sac resorption

In both sand lance and Arctic cod, yolk-sac frequency gradually decreased over the 3 periods (Fig. 6). Fifty percent yolk resorption occurred during Period II for Arctic cod and Period III for sand lance. Twenty percent of Arctic cod larvae still had yolk reserves in Period III.

For sand lance, differences in the percentage of yolk-sac larvae between stations were significant for Periods II and III (frequency test; Period II: $\chi^2 = 3.99$, $p < 0.05$; Period III: $\chi^2 = 7.03$, $p < 0.05$). Yolk-sac larvae were slightly (<20 %) more frequent at Stn A than at the more offshore stations. For Arctic cod, no significant difference in yolk sac frequency was found among stations for any of the 3 periods.

Larval fish feeding and potential food resource

The diet of sand lance and Arctic cod larvae comprised the same food items, but in different proportions (Table 3). Sand lance fed primarily on algal cells, tintinids and copepod eggs, and marginally on copepod nauplii. Arctic cod larvae fed primarily on copepod eggs and nauplii, which were the largest items in the diet of the 2 species.

Mean food size and the frequency of each item in the diet of each species varied little between stations (Table 3). Differences in frequencies were statistically significant for Arctic cod only (contingency table analysis; sand lance: $\chi^2 = 9.08$, $p > 0.05$; Arctic cod: $\chi^2 = 30.3$, $p < 0.05$) which tended to capture copepod nauplii slightly less frequently inshore (Stns A and B) than offshore (Stns C and D).

Sand lance larvae fed during Periods I and III but not during Period II (Table 3). Arctic cod larvae started to feed in Period III only. For both species, the percentage of feeding larvae (i.e. larvae with at least one prey in the gut) varied significantly between stations (frequency tests: $\chi^2 > 13.8$, $p < 0.001$) and was lower at Stn A for all periods when feeding took place (Fig. 7).

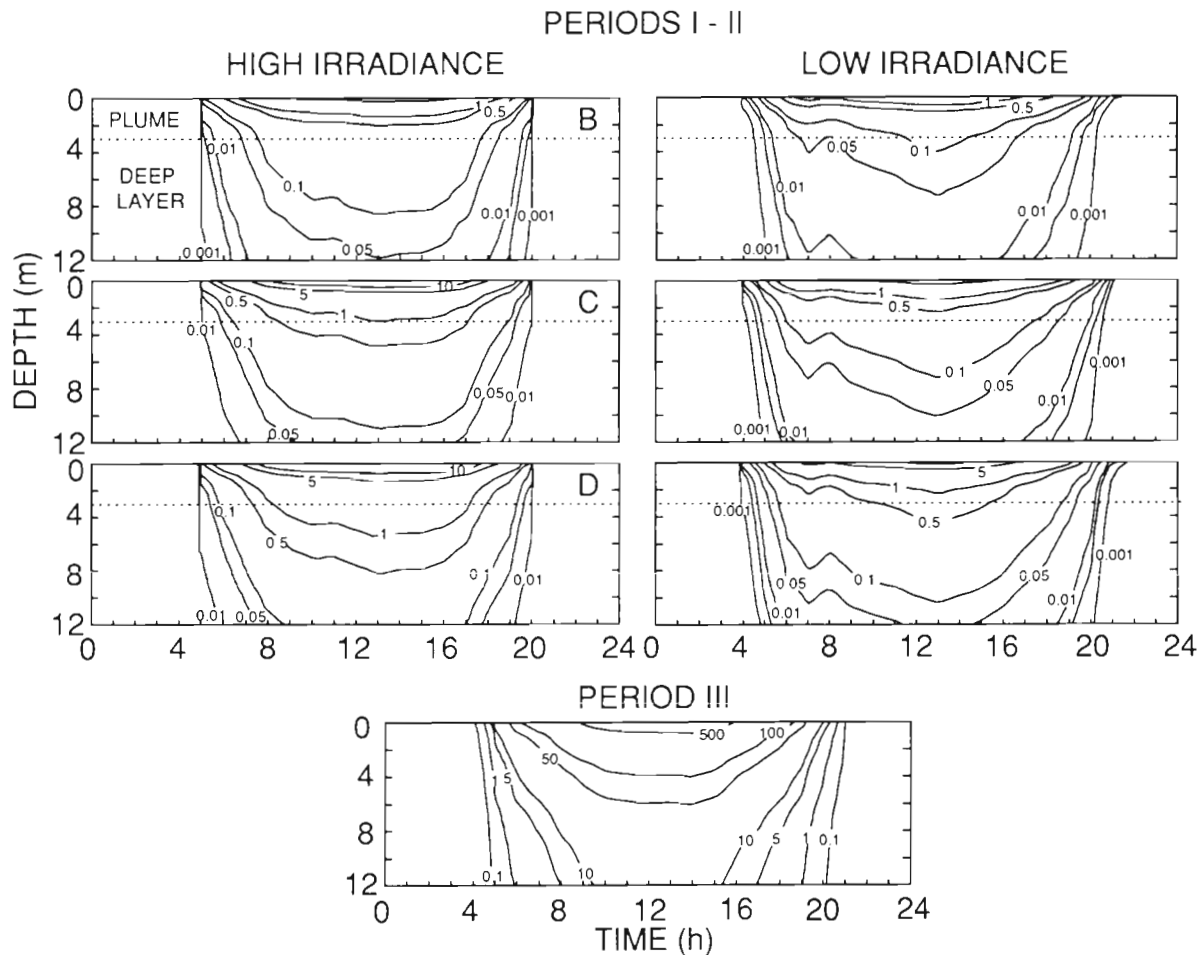


Fig. 4. Diel variations in the depth of isolumes (in $\mu\text{Ein m}^{-2} \text{s}^{-1}$, 400 to 700 nm range) for Stns B (inshore) to D (offshore) before (Periods I and II) and after (Period III) the break-up of the ice cover in coastal Hudson Bay. For Periods I and II, variations are presented for days of high and low irradiance

The relative frequency of the various food items in the plankton differed from that in the diet of the fish larvae (Table 4). Algal cells were the most abundant food item by at least one order of magnitude, followed by copepod nauplii, copepod eggs and tintinids. All items showed an increase in abundance from one period to the next. Food organisms were generally less abundant at Stns A and D in Period I, but this pattern gradually disappeared with time and no clear differences were observed between stations during Period III.

The potential food resource of sand lance larvae (Fig. 8) increased significantly with time, but no significant difference was found between stations (ANOVA, periods: $F = 10.51$, $p < 0.01$; stations: $F = 1.79$, $p > 0.05$). The average density of potential food resource varied from $0.02\text{--}0.04 \text{ mg m}^{-3}$ in Period I to $0.1\text{--}0.2 \text{ mg m}^{-3}$ in Period III. For Arctic cod, potential food resource did not vary significantly in time or space (ANOVA, periods: $F = 0.83$, $p > 0.05$;

Stations: $F = 1.18$, $p > 0.05$). Food resource was always more abundant for Arctic cod (average of 0.3 mg m^{-3}) than for sand lance.

DISCUSSION

Larval fish distribution and growth in relation to hydrography

The variations in ice cover conditions and the dynamics of the Great Whale River plume reported here are consistent with the observations and conclusions of Ingram & Larouche (1987) and Lepage & Ingram (1991). Before the break-up, the ice cover prevents wind mixing and significantly attenuates tidal mixing in the upper layer (Lepage & Ingram 1991). Under these conditions, increased river runoff and the melting of the ice pack at the time of the freshet lead to a quick expansion of the plume over the study area.

Table 1. Total number of individuals (n), number of samples (N), mean density (ind. 100m⁻³) and standard deviation for each larval fish species by sampling period

Species	Period	n	N	Mean	SD
Sand lance	I	284	64	2.42	4.07
<i>Ammodytes</i> sp.	II	194	54	1.88	1.88
	III	906	74	2.77	4.69
Arctic cod	I	144	64	1.55	3.29
<i>Boreogadus saida</i>	II	224	54	2.23	3.77
	III	687	74	1.89	2.88
Burbot	I	52	64	0.45	1.26
<i>Lota lota</i>	II	51	54	0.51	0.78
	III	3	74	0.01	0.09
Arctic shanny	I	0	64	0.00	0.00
<i>Stichaeus punctatus</i>	II	7	54	0.07	0.18
	III	381	74	0.85	1.89
Slender eelblenny	I	1	64	0.01	0.04
<i>Lumpenus fabricii</i>	II	5	54	0.05	0.12
	III	41	74	0.11	0.22
Arctic staghorn sculpin	I	1	64	0.01	0.04
<i>Gymnocanthus</i>	II	3	54	0.03	0.09
<i>tricuspis</i>	III	70	74	0.15	0.30
Fourhorn sculpin ^a	I	0	64	0.00	0.00
<i>Myoxocephalus</i>	II	1	54	0.01	0.06
<i>quadricornis</i>	III	73	74	0.15	0.34
Arctic sculpin ^a	I	0	64	0.00	0.00
<i>Myoxocephalus</i>	II	0	54	0.00	0.00
<i>scorpioides</i>	III	18	74	0.05	0.14
Gelatinous snailfish	I	0	64	0.00	0.00
<i>Liparis fabricii</i>	II	7	54	0.07	0.12
	III	5	74	0.03	0.08

^aIdentification uncertain (see Drolet et al. 1991)

After the break-up, increased wind stress and larger tidal flow rapidly mix the freshwater of the plume with deeper saline water (Lepage & Ingram 1991). Offshore, the plume is quickly eroded by this process and may totally disappear within a few days, depending on floe density and wind direction. Because of continued freshwater input, the plume persists near the river mouth where vertical mixing by winds increases its thickness.

The vertical distribution of sand lance and Arctic cod larvae varied with spatio-temporal changes in the horizontal extent and thickness of the river plume. Both species tended to avoid the brackish waters of the plume, but sand lance larvae were apparently more tolerant to low salinities than Arctic cod larvae. Densities of sand lance larvae in the surface layer varied little between periods whereas Arctic cod larvae remained virtually absent from the surface layer until the ice break-up, when surface salinities increased. Recent studies of the fine-scale vertical dis-

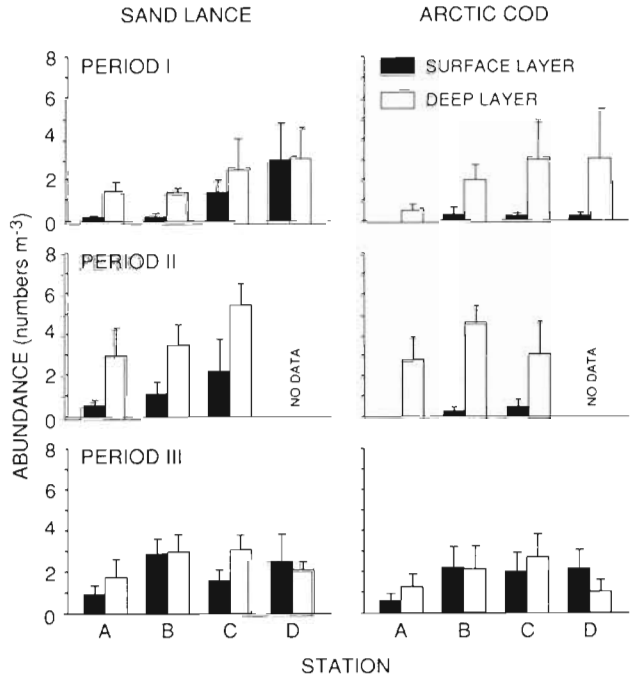


Fig. 5. *Ammodytes* sp., *Boreogadus saida*. Average densities (with standard error) of sand lance and Arctic cod larvae by hydrographic period in the surface (1 m) and deep layer (8 m) at Stns A (inshore) to D (offshore) off the Great Whale River mouth in coastal Hudson Bay

tribution of fish larvae under the ice of the bay indicate that sand lance and Arctic cod are concentrated immediately below the river plume, within 5 to 10 m of the surface (Ponton & Fortier 1992). Thus, densities measured at 8 m in the present study are probably a fair indicator of actual densities of larvae in the deep layer.

The horizontal distribution of sand lance and Arctic cod was little affected by the expansion or mixing of the river plume. The larvae were present over the entire sampling area, and their distribution varied little between sampling periods. The abundance of both species was generally higher at stations characterized by productive porous ice (B, C and D) than at Stn A, where crystal ice was found. The concentration of fish larvae under porous ice could result either from more intense spawning, advection, higher mortality under non-productive crystal ice or a combination of these factors.

Growth based on average length at date may be underestimated if several cohorts of young fish hatch or are advected in succession in the sampling area. In the spring of 1988, the length frequency distributions of sand lance and Arctic cod larvae presented a single mode, indicating that only one cohort of each species occurred in the area (Drolet et al. 1991). Thus, the un-

Table 2. *Ammodytes* sp., *Boreogadus saida*. Average total length (mm), standard deviation and number of larvae measured by period, and apparent growth rates (mm d^{-1}) between periods for sand lance and Arctic cod larvae at each station

	Period I			Period II			Period III			Apparent growth rate	
	Mean	SD	n	Mean	SD	n	Mean	SD	n	I–II	II–III
Sand lance											
Stn A	8.17	0.50	21	8.30	0.45	44	8.57	0.80	107	0.009	0.015
Stn B	7.99	0.48	15	8.19	0.64	52	8.42	0.76	236	0.014	0.012
Stn C	7.96	0.46	120	8.20	0.52	63	8.22	0.65	254	0.017	0.001
Stn D	7.90	0.48	117	–	–	–	8.38	0.74	141	–	–
Arctic cod											
Stn A	7.48	0.45	6	7.30	0.64	36	7.68	0.75	83	–0.012	0.021
Stn B	6.92	0.55	45	7.10	0.53	79	7.58	0.73	179	0.012	0.026
Stn C	7.07	0.52	100	7.00	0.54	91	7.42	0.73	180	–0.005	0.023
Stn D	6.96	0.44	19	–	–	–	7.36	0.78	91	–	–

usually low growth rates reported here are more likely to reflect reduced metabolism at low temperature than the continuous influx of small, newly-hatched larvae in the sampling area. Apparent growth rates between periods did not exceed 0.030 mm d^{-1} on average for either species. For sand lance, these values are lower than those reported for the genus in the literature. For *Ammodytes americanus* in Long Island Sound, eastern USA, Monteleone & Peterson (1986) report average growth rates of 0.08 mm d^{-1} at temperatures ranging from 1 to 5°C , and similar values were observed at 2°C in the laboratory (Smigielski et al. 1984). For Arctic cod in Lancaster Sound, northern Canada, Sekerak (1982) reports an average growth rate of 0.25 mm d^{-1} between July and October 1978 but does not provide temperature data.

His results show no significant growth during the first 2 wk after hatching, which is consistent with our observations. In the present study, low growth rates are unlikely to be an artifact resulting from net avoidance by the larger larvae, given the low irradiances under the ice and the fact that not a single larva significantly larger than the mean was captured during any of the periods sampled.

Table 3. *Ammodytes* sp., *Boreogadus saida*. Percent composition of diet and feeding statistics by station or period for sand lance and Arctic cod larvae

Food type	Station ^d				Period ^b		
	A	B	C	D	I	II	III
Sand lance							
Algal cells	50.0	33.3	25.0	32.1	50.0	0	27.6
Tintinids	0	36.7	30.4	34.0	43.8	0	30.7
Copepod eggs	25.0	26.7	39.3	22.6	6.2	0	33.1
Copepod nauplii	25.0	3.3	5.3	11.3	0	0	8.6
Mean prey width (μm)	45	74	67	50	50	–	64
No. of larvae	186	333	586	320	420	194	811
Total no. of prey	9	62	109	89	20	0	249
Prey/feeding larv.	1.29	1.35	1.47	1.71	1.18	–	1.54
Arctic cod							
Algal cells	11.8	26.4	3.3	14.8	0	0	10.9
Tintinids	11.8	5.7	11.4	7.4	0	0	9.6
Copepod eggs	29.3	41.5	27.6	25.9	0	0	30.9
Copepod nauplii	47.1	26.4	57.7	51.9	0	0	48.6
Mean prey width (μm)	100	92	97	107	–	–	96
No. of larvae	134	348	460	153	257	225	613
Total no. of prey	17	53	123	27	0	0	22
Prey/feeding larv.	2.57	1.87	2.98	1.71	–	–	2.35

^aPeriods combined; ^bstations combined

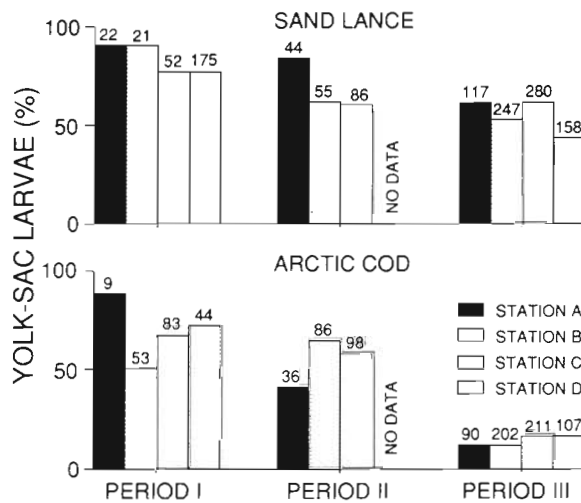


Fig. 6. *Ammodytes* sp., *Boreogadus saida*. Percentage of sand lance and Arctic cod larvae with yolk reserves by hydrographic period at Stns A (inshore) to D (offshore) off the Great Whale River mouth in coastal Hudson Bay

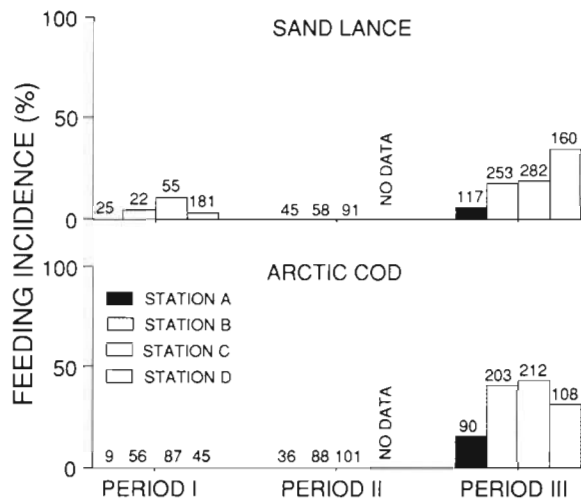


Fig. 7. *Ammodytes* sp., *Boreogadus saida*. Percent feeding incidence in sand lance and Arctic cod larvae by hydrographic period at Stns A (inshore) to D (offshore) off the Great Whale River mouth in coastal Hudson Bay

Variations between periods in the average growth rates of sand lance and Arctic cod were closely associated with yolk sac resorption and feeding incidence. Growth was slow for both species between Periods I and II, when feeding activity was low or null and larvae still had their vitelline reserves. In Period III, most Arctic cod larvae had lost their yolk sac and feeding was intense, which resulted in higher growth rates between Periods II and III than between the first 2 periods. Sand lance yolk-sac larvae were still abundant in Period III, and this explains that feeding was not as intense as in Arctic cod and that growth remained slow.

The transport hypothesis

The transport hypothesis (Hjort 1926) assumes that first-feeding fish larvae can be dispersed in areas where different feeding conditions prevail. The horizontal distribution of the different food items of sand lance and Arctic cod during Period I generally supports the hypothesis of marginally better feeding conditions in the area covered by porous ice where ice algae are known to develop. Before the freshet of the river, the abundance of copepod eggs and nauplii was higher offshore than inshore. This is consistent with the results of Tourangeau & Runge (1991) who found that the availability of ice algae hastened the reproduction of *Calanus glacialis*. Differences in the biomass of sea-ice meiofauna, in and outside of the Great Whale River plume, have also been reported by Grainger (1988). Compared to Stns B and C, the lower abundances of prey at Stn D in Period I may have reflected a delay in the release of algae from the ice which in turn could

Table 4. *Ammodytes* sp., *Boreogadus saida*. Average density ($N\ m^{-3}$) of the prey of sand lance and Arctic cod larvae in bottom to surface net tows (64 μm mesh) by station and period

	Stn	Period I		Period II		Period III	
		Mean	SE	Mean	SE	Mean	SE
Algal cells	A	881	372	1720	251	2088	810
	B	2564	1319	1921	404	1469	244
	C	1854	456	2046	310	3207	1128
	D	1183	204	-	-	1381	406
Tintinids	A	0	0	0	0	27	22
	B	12	5	11	3	47	17
	C	0	0	6	4	24	11
	D	13	6	-	-	34	12
Copepod eggs	A	15	1	46	23	159	21
	B	47	16	87	16	124	22
	C	36	8	71	18	237	62
	D	18	4	-	-	107	20
Copepod nauplii	A	69	33	179	42	309	65
	B	277	163	224	61	341	53
	C	149	40	262	70	612	310
	D	134	21	-	-	280	66

have retarded copepod reproduction (Tourangeau & Runge 1991). The river plume, which contributes to the initiation of the sedimentation of sea-ice microalgae (Tremblay et al. 1989) did not reach Stn D until Period II.

Several lines of evidence indicate that sand lance larvae may have actually exploited the community associated with the ice-water interface during Period I. First, sand lance larvae were present in the brackish waters of the plume and fed before the freshet of the river. Second, algal cells were major food items of sand lance in Period I and were mainly present at or near the ice-water interface at that time (Drolet et al. 1991). Finally, sand lance did not feed at Stn A where crystal ice did not support the development of ice algae and the associated meiofauna.

After the river freshet, food availability to planktonic fish larvae became roughly the same over the entire study area. The spatial gradient in food abundance between Stn A and stations offshore was strong in Period I, decreased sharply in Period II and disappeared in Period III probably in response to a combination of several factors. The expansion of the river plume was followed by algal sedimentation (Drolet et al. 1991) and the horizontal gradient in the biomass of sedimenting algae, phytoplankton and zooplankton was gradually destroyed by tidal currents, advection and wind-induced mixing following the break-up of the ice cover.

Spatial variations in feeding incidence of sand lance and Arctic cod during Periods II and III were consequently not related to spatial differences in the abun-

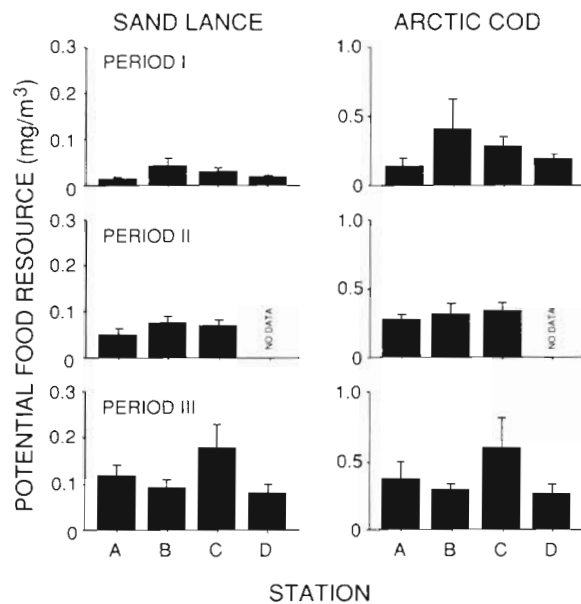


Fig. 8. *Ammodytes* sp., *Boreogadus saida*. Average density of potential food resource (with standard error) available to sand lance and Arctic cod larvae by hydrographic period at Stns A (inshore) to D (offshore) off the Great Whale River mouth in coastal Hudson Bay

dance of their potential food resource. Neither species fed during Period II in spite of the fact that resource was available and a substantial proportion of both populations had used up its yolk reserves. Intensive feeding began only in Period III, when food conditions were comparable to Period II, and spatial variations in feeding frequency did not correlate with food availability. Thus, at the scale of the area studied, the existence of a spatial gradient in prey abundance, which is assumed in Hjort's second hypothesis, was verified only for sand lance prior to the river freshet. Spatial variations in food availability to fish larvae may exist at larger scales. Rochet & Grainger (1987) identified 4 geographical regions in eastern Hudson Bay between which total zooplankton abundances varied. The area covered by the 4 stations sampled in 1988 was located within one of these geographical region, the coastal current that flows counterclockwise from James Bay (Prinsenbergh 1986). In Hudson Bay, Hjort's transport hypothesis might be more relevant at the scale of these different geographical regions.

Irradiance, ice cover and larval fish foraging

The eye of fish larvae is most sensitive in the blue-green region (400 to 600 nm) of the light spectrum (Blaxter 1968, 1975b). Transmission of visible light through first-year ice is also maximum within that range (Maykutt & Grenfell 1975). Thus, irradiance

measurements in the PAR range (400 to 700 nm) are probably good estimators of the actual light available to fish larvae foraging under the ice.

Feeding occurrence in sand lance and Arctic cod larvae was related to light availability in the water column which varied both with ice conditions and the dynamics of the Great Whale River plume. In Periods I and II, the incident PAR reaching the water column was drastically reduced by the ice cover. At that time, a significant fraction (20 to 40 %) of the population of both species had lost their yolk reserves and should have been feeding. Yet Arctic cod larvae did not feed in Periods I and II. Marginal feeding activity occurred in sand lance prior to the horizontal expansion of the plume (Period I), probably within a few metres of the ice-water interface where light intensity was maximum. Dabrowski (1985) also reported that light attenuation by the ice cover narrows the foraging depth range of coregonid larvae in lakes.

Sand lance larvae stopped feeding in Period II as the turbid waters of the Great Whale River plume expanded over the sampling area and further reduced the light available to perceive prey. We conclude that the expansion and thickening of the river plume in Period II with the associated decrease in light availability stopped sand lance foraging and prevented Arctic cod larvae from initiating feeding. Intense feeding by both species began only in Period III when the fragmentation of the ice cover and the vertical mixing of the plume allowed light to penetrate at depth. In Period III, the influence of the river plume was felt mainly at Stn A where the thickness of the brackish turbid layer sometimes reached 6 m. Again, light limitation probably explains the low feeding activity of sand lance and Arctic cod at this station after the ice break-up.

Assuming that foraging in the deep layer was limited by light during Periods I and II, the irradiances found immediately below the river plume (ca 0.1 to 1.0 $\mu\text{Ein m}^{-2} \text{s}^{-1}$) would represent the thresholds at which sand lance and Arctic cod larvae could no more perceive their prey. These values are slightly higher than feeding thresholds reported for other species (Table 5). High feeding thresholds in the present study could be linked to low prey density which is known to affect feeding efficiency at a given irradiance (Paul 1983, Batty 1987, Munk et al. 1989). For example, Fortier & Harris (1989) estimated that the density of food available to fish larvae off Plymouth (Western English Channel) in May ranged from 5.85 to 10.67 $\text{mm}^3 \text{m}^{-3}$ with depth (ca 6 to 11 mg m^{-3}). In comparison, the potential food resource available to sand lance and Arctic cod larvae during Periods I and II never exceeded 0.5 mg m^{-3} .

Table 5. Minimum (0 %) and optimum (100 %) feeding irradiance thresholds ($\mu\text{Ein m}^{-2} \text{s}^{-1}$) for larvae of various fish species. Conversion factors: 1 fc (footcandle) = 10.8 lux = 0.216 $\mu\text{Ein m}^{-2} \text{s}^{-1}$

Species	Minimum threshold	Optimum threshold	Source
<i>Clupea harengus</i>	0.07	70	Blaxter (1968)
<i>Pleuronectes platessa</i>	0.007	70	Blaxter (1969)
<i>Coregonus autumnalis migratorius</i>	0.20	–	Volkova (1973) ^b
<i>Cottomephorus grewingki</i>	0.10	–	Volkova (1973) ^o
<i>Rutilus rutilus caspicus</i>	0.02	–	Sbikin (1974) ^b
<i>Theragra chalcogramma</i>	0.004	59	Paul (1983)
<i>Coregonus pollan</i> ^a	0.21	0.45	Dabrowski (1982)
<i>Esox lucius</i> ^a	0.014	0.33	Dabrowski (1982)
<i>Ammodytes</i> sp.	0.1–1.0	–	Present study
<i>Boreogadus saida</i>	0.1–1.0	–	Present study

^a Values obtained in the blue range (400 to 490 nm); ^b in Blaxter (1975a)

The irradiance levels beneath the pycnocline were comparable to the thresholds at which most species of fish larvae begin to perceive prey and feed, but much lower than optimal levels for feeding (Table 5). Thus, there is little doubt that the foraging of sand lance and Arctic cod larvae in the deep layer was limited by light during Periods I and II. Low density of prey combined to low irradiances resulted in poor feeding conditions for first-feeding fish larvae that occurred before the ice break-up in the zone influenced by the Great Whale River outflow. These conditions improved drastically at ice break-up when light penetrated between the floes and the turbid waters of the plume were progressively mixed by wind.

Projected hydroelectric developments in southeastern Hudson Bay involve a drastic reduction of the freshwater discharge of the Great Whale River (Hydro-Québec 1991). The results presented in this study suggest that natural or anthropogenic modifications of river runoff would affect local trophic conditions for first-feeding marine fish larvae emerging under fast ice. A significant reduction in the extent of the Great Whale River plume in early spring would increase surface salinities, ice algal production and underice light intensity, all of which would improve feeding conditions for fish larvae that occur in the coastal zone before the break-up.

The impact of an eventual reduction of the Great Whale River spring discharge on the coastal planktonic food web that supports larval fish growth in summer remains conjectural. At the time of the freshet, the diluted waters of the plume contain relatively high concentrations of phytoplankton (0.2 to 0.8 mg m^{-3}) made up primarily of the centric diatoms *Thalassiosira* spp., *Chaetoceros* spp. and the pennate diatom *Fragilaria* spp. (Ponton & Fortier 1992). Much lower algal densities (<0.03 mg m^{-3}) are found in marine waters where the

algal community is dominated by Dynophyceae and *Fragilaria* spp. (Ponton & Fortier 1992). Thus, the different phytoplankton community associated with the plume could favor an early summer bloom of centric diatoms in coastal waters. Given that copepod reproduction is often linked to the production of centric diatoms (e.g. Fortier et al. in press), coastal areas influenced by river plumes in southeastern Hudson Bay could represent important nursery grounds for the early stages of marine fish which feed primarily on copepod nauplii and copepodites. The existence of such an inshore-offshore gradient in the timing of the diatom bloom needs to be verified before the impact of eventual hydroelectric developments of the Great Whale River on the early dynamics of coastal marine fish can be fully assessed.

Acknowledgements. This study was part of a collaborative project between GIROQ and the Department of Fisheries and Oceans (Institut Maurice-Lamontagne). Field and laboratory work was funded by grants to L.F. from NSERC and DFO, and by grants to GIROQ from NSERC and the Fonds FCAR of Québec. M.G. and R.D. were supported by scholarships from the Department of Indian and Northern Affairs. Helicopter time was supplied by DFO. The Centre d'études nordiques (Université Laval) provided accommodation at its field station in Kuujuaupik where we benefited from the assistance of the superintendent C. Côté. Special thanks to C. Dutil for her contribution to this study. G. Bergeron, M. Frenette, N. Hamel, R. Labbé, M.-A. Rémillard, M. Salathé, S. Tourangeau, and J. Vaillancourt helped in the field or the laboratory. L. Legendre (GIROQ) kindly provided data on the daily cycle of under-ice PAR.

LITERATURE CITED

- Aronovich, T. M., Doroshev, S. I., Spectorova, L. V., Makhotin, V. M. (1975). Egg incubation and larval rearing of navaga (*Eleginus navaga*), polar cod (*Boreogadus saida* Lepechin) and Arctic flounder (*Liopsetta glacialis* Pall.) in the laboratory. *Aquaculture* 6: 233–242

- Batty, R. S. (1987). Effect of light intensity on activity and food-searching of larval herring, *Clupea harengus*: a laboratory study. *Mar. Biol.* 94: 323–327
- Blaxter, J. H. S. (1968). Visual thresholds and spectral sensitivity of herring larvae. *J. exp. Biol.* 48: 39–53
- Blaxter, J. H. S. (1969). Visual thresholds and spectral sensitivity of flatfish larvae. *J. exp. Biol.* 51: 221–230
- Blaxter, J. H. S. (1975a). Fish vision and applied research. In: Ali, M. A. (ed.) *Vision in fishes*. Plenum Publishing Corp., New York, p. 757–773
- Blaxter, J. H. S. (1975b). The eyes of larval fish. In: Ali, M. A. (ed.) *Vision in fishes*. Plenum Publishing Corp., New York, p. 427–443
- Dabrowski, K. R. (1982). The influence of light intensity on feeding of fish larvae and fry. I. *Coregonus pollan* (Thompson) and *Esox lucius* (L.). *Zool. Jb. Physiol.* 86: 341–351
- Dabrowski, K. R. (1985). Can coregonid fish larvae feed under the ice? *Arch. Hydrobiol.* 104: 427–432
- Drolet, R., Fortier, L., Ponton, D., Gilbert, M. (1991). The production of fish larvae and their prey in subarctic south-eastern Hudson Bay. *Mar. Ecol. Prog. Ser.* 77: 105–118
- Fortier, L., Harris, R. P. (1989). Optimal foraging and density dependent competition in marine fish larvae. *Mar. Ecol. Prog. Ser.* 51: 19–33
- Fortier, L., Levasseur, M. E., Drolet, R., Therriault, J.-C. (in press). Export production and the distribution of fish larvae and their prey in a coastal jet frontal region. *Mar. Ecol. Prog. Ser.*
- Gosselin, M., Legendre, L., Demers, S., Ingram, R. G. (1985). Response of sea-ice microalgae to climatic and fortnightly tidal energy inputs (Manitounuk Sound, Hudson Bay). *Can. J. Fish. Aquat. Sci.* 42: 999–1006
- Gosselin, M., Legendre, L., Therriault, J. C., Demers, S., Rochet, M. (1986). Physical control of the horizontal patchiness of sea-ice micro-algae. *Mar. Ecol. Prog. Ser.* 29: 289–298
- Grainger, E. H. (1988). The influence of a river plume on the sea-ice meiofauna in southeastern Hudson Bay. *Estuar. coast. Shelf Sci.* 27: 131–141
- Harden Jones, F. R. (1968). *Fish migration*. Edward Arnold, London
- Hjort, J. (1926). Fluctuations in the year classes of important food fishes. *J. Cons. perm. int. Explor. Mer* 1: 5–38
- Hydro-Québec (1991). Grande Baleine complex. *Hydro-Québec, Bulletin* 4:1–24
- Ingram, R. G. (1981). Characteristics of the Great Whale River plume. *J. geophys. Res.* 86(C3): 2017–2023
- Ingram, R. G., Larouche, P. (1987). Variability of an under-ice river plume in Hudson Bay. *J. geophys. Res.* 92(C9): 9541–9547
- Legendre, L., Gosselin, M. (1991). In situ spectroradiometric estimation of microalgal biomass in first-year sea ice. *Polar Biol.* 11: 113–115
- Lepage, S., Ingram, R. G. (1991). Variation of upper layer dynamics during breakup of the seasonal ice cover in Hudson Bay. *J. geophys. Res.* 96(C7): 12711–12724
- Lyczkowski Laroche, J. (1982). Trophic patterns among larvae of five species of sculpin (family: cottidae) in a Maine estuary. *Fish. Bull. U.S.* 80: 827–840
- Maykut, G. A., Grenfell, T. C. (1975). The spectral distribution of light beneath first-year ice in the Arctic ocean. *Limnol. Oceanogr.* 20: 554–563
- Monteleone, D. M., Peterson, W. T. (1986). Feeding ecology of American sand lance *Ammodytes americanus* larvae from Long Island Sound. *Mar. Ecol. Prog. Ser.* 30: 133–143
- Munk, P., Kiørboe, T., Christensen, V. (1989). Vertical migrations of herring, *Clupea harengus*, larvae in relation to light and prey distribution. *Environ. Biol. Fishes* 26: 87–96
- Paul, A. J. (1983). Light, temperature, nauplii concentrations, and prey capture by first feeding pollock larvae *Theragra chalcogramma*. *Mar. Ecol. Prog. Ser.* 13: 175–179
- Ponton, D., Fortier, L. (1992). Vertical distribution and foraging of marine fish larvae under the ice cover of south-eastern Hudson Bay. *Mar. Ecol. Prog. Ser.* 81: 215–227
- Poulin, M., Cardinal, A., Legendre, L. (1983). Réponse d'une communauté de diatomées de glace à un gradient de salinité (Baie d'Hudson). *Mar. Biol.* 76: 191–202
- Prinsenberg, S. J. (1986). The circulation pattern and current structure of Hudson Bay. In: Martini, I. P. (ed.) *Canadian inland seas*. Elsevier, Amsterdam, p. 187–204
- Rochet, M., Grainger, E. H. (1988). Community structure of zooplankton in eastern Hudson Bay. *Can. J. Zool.* 66: 1626–1630
- Runge, J. A., Ingram, R. G. (1991). Under-ice feeding and diel migration by the planktonic copepods *Calanus glacialis* and *Pseudocalanus minutus* in relation to the ice algal production cycle in southeastern Hudson Bay, Canada. *Mar. Biol.* 108: 217–225
- Sbikin, Yu. N. (1974). Age-related changes in the role of vision in feeding of various fishes. *J. Ichthyol.* 14: 133–138
- Sekerak, A. D. (1982). Young-of-the-year cod (*Boreogadus*) in Lancaster Sound and western Baffin Bay. *Arctic* 35: 75–87
- Smigielski, A. S., Halavik, T. A., Buckley, L. J., Drew, S. M., Laurence, G. C. (1984). Spawning, embryo development and growth of the american sand lance *Ammodytes americanus* in the laboratory. *Mar. Ecol. Prog. Ser.* 14: 287–292
- Theilacker, G. H., Dorsey, K. (1980). Larval fish diversity, a summary of laboratory and field research. Intergovernmental Oceanographic Commission, Workshop Rep. no. 28, p. 105–142
- Tourangeau, S., Runge, J. A. (1991). Reproduction of *Calanus glacialis* under ice in spring in southeastern Hudson Bay. *Mar. Biol.* 108: 227–233
- Tremblay, C., Runge, J. A., Legendre, L. (1989). Grazing and sedimentation of ice algae during and immediately after a bloom at the ice-water interface. *Mar. Ecol. Prog. Ser.* 56: 291–300
- Volkova, L. A. (1973). The effect of light intensity on the availability of food organisms to some fishes of Lake Baikal. *J. Ichthyol.* 13: 591–602

This article was submitted to the editor

Manuscript first received: November 12, 1991

Revised version accepted: May 4, 1992