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Vertical distribution and foraging of marine fish larvae under the ice cover of southeastern Hudson Bay*

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ABSTRACT: In ice-covered southeastern Hudson Bay (northern Québec, Canada), the production of suitable zooplankton prey for marine fish larvae was similar within and outside the area covered by the Great Whale River plume. Within the plume however, light attenuation by the turbid surface layer reduced the foraging efficiency of first-feeding Arctic cod *Boreogadus saida* and sand lance *Ammodytes* sp. larvae. In daytime, first-feeding larvae accumulated at the pycnocline where food availability (i.e. light × prey density) was maximum. Below the pycnocline, the average number of prey ingested by individual larvae (foraging gain) declined with depth. At night, fish larvae and their prey redistributed more uniformly over the water column, suggesting a similar passive response to the turbulence field in the absence of a light gradient. The observed ideal free distributions (IFDs) were better explained by unequal foraging abilities of the larvae than by density-dependent interactions among the assemblage of planktonic predators.

INTRODUCTION

In seasonally ice-covered arctic and subarctic waters, the phytoplankton bloom is usually preceded by the development of ice algae which colonize the bottom few centimetres of the sea ice (e.g. Apollonio 1961, Horner 1976, Alexander 1980). Ice algae are grazed by a so-called 'under-the-ice benthos' (George 1977) and by pelagic herbivore copepods which migrate at night towards the ice-water interface to feed (Conover et al. 1986, Runge & Ingram 1988, 1991). Grazing of ice algae has been shown to trigger the early reproduction of calanoid copepods such as *Calanus glacialis* (Hirche & Bohrer 1987, Tourangeau & Runge 1991).

In Hudson Bay (northern Québec, Canada), the pelagic larvae of Arctic cod *Boreogadus saida* and sand lance *Ammodytes* spp. hatch several weeks before the ice break-up (Drolet et al. 1991). First-feeding Arctic cod and sand lance prey on copepod eggs and nauplii (Ponomarenko 1967, Monteleone & Peterson 1986, Drolet et al. 1991). By fuelling the early reproduction of copepods, the ice-algal bloom provides whatever food is available to the larvae before the ice break-up and the development of the phytoplankton bloom (Drolet et al. 1991).

With an average annual discharge of 700 $m^3 s^{-1}$, the Great Whale River is one of the major rivers entering Hudson Bay (Ingram & Larouche 1987). In late spring, the plume of the river under the ice of Hudson Bay extends dramatically with the freshet (Ingram & Larouche 1987) and flushes away the community that has developed at the ice-water interface in April and early May (Grainger 1988). Ice melt also contributes to the formation of the 3 to 5 m thick brackish surface layer from mid to late spring (Lepage & Ingram 1991). Gilbert et al. (in press) suggested that sub-optimal light intensities due to plume turbidity combined with low food availability limited the feeding of fish larvae in the underlying marine layer.

In this study we describe and compare the vertical distribution of phytoplankton, zooplankton and fish larvae within and outside the area of southeastern Hudson Bay influenced by the vernal expansion of the Great Whale River plume. In particular, we address the hypothesis that the plume impairs the feeding of

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marine fish larvae by reducing prey- and light availability.

MATERIALS AND METHODS

Study area. The study was conducted in southeastern Hudson Bay at 2 stations on first-year landfast ice off Kuujjuarapik, Québec (Fig.1). Station D (55° 28′ 80″ N, 77° 49′ 01″ W, 140 m depth) was located offshore, outside the area influenced by the Great Whale River plume. Station B (55° 20′ 95″ N, 77° 47′ 94″ W, 65 m depth) was situated nearshore within the plume.

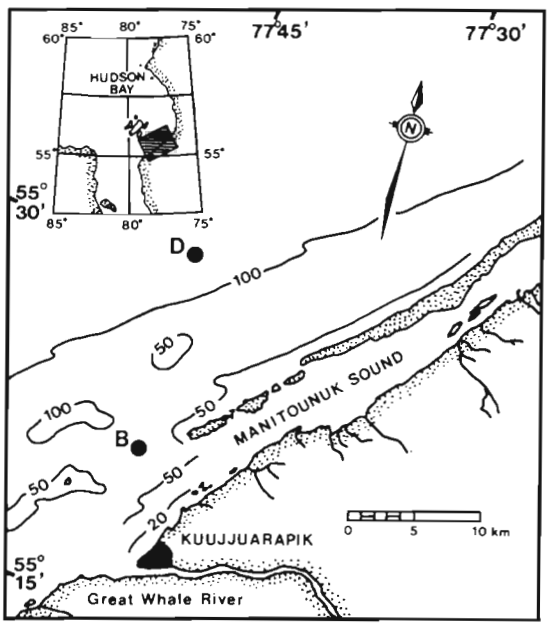

Fig. 1. Location of sampling stations off Kuujjuarapik, Northern Québec, Canada. Isobaths in metres

Sampling. The large volume pump system described by Harris et al. (1986) was adapted for deployment from the ice. The submersible pump (Flygt C-3102) delivered 2.8 m^3 min^{-1} of water which was filtered in standard 64 µm mesh plankton nets. The intake of the 25 m long sampling hose was lowered to discrete depths from the bottom of the ice to 20 m.

Vertical profiling of plankton abundance was carried out at intervals of 3 h during two 48 h periods from 13:00 h EST 8 May 1989 at Stn D and 13:00 h 16 May 1989 at Stn B. Each profile consisted of 7 samples collected at 0 (bottom of the ice), 1, 3, 5, 10, 15 and 20 m under the ice. Every 10 min, the pump intake was lowered from one discrete depth to the next and the outflow was switched from one 64 µm net to the other. This procedure introduced a slight bias in the origin of the plankton sampled since <2 % of the volume of water strained for a given sample actually came from above the desired depth of sampling. Zooplankton samples were preserved in 5 % formalin.

Water samples, collected from each sampling depth at the pump output, were filtered on Whatman GF/F filters for the determination of chlorophyll *a* and phaeopigment concentration by a fluorometric method (Holm-Hansen & Riemann 1978). Once a day, 200 ml water samples from each depth of the midday profile were preserved in acid Lugol solution for phytoplankton enumeration.

Half an hour before each plankton profile, salinity, temperature, and *in vivo* fluorescence were recorded from the surface to 50 m using a portable CTD profiler equipped with an *in situ* fluorometer. Chlorophyll *a* (chl *a*) concentrations from the water samples were regressed against the mean *in situ* fluorescence values (F) over a 50 cm layer centred on the depth of sampling. The fluorescence signal was then transformed into chl *a* concentration using the resulting relationship: chl $a = \exp(-5.0480 + 0.1992F)$, $n = 119$, $r^2 = 0.6774$, $p < 0.001$

Light extinction coefficients were derived from values recorded with a Quantum scalar irradiance meter operated by scuba divers on 27 April 1990 at Stn D, and on 1 May 1990 at Stn B. The hydrographic conditions (extent of the plume, temperature and salinity profiles) at these dates in 1990 were similar to those prevailing during our sampling, and the coefficients measured in 1990 were assumed to represent rough estimates of the extinction coefficients prevailing at the time of the present study. Daily variations in light intensity (400 to 700 nm range) under the ice were obtained from data collected between 11 April and 20 May 1986, 25 km off Kuujjuarapik, using a MER-1010 spectro-radiometer. Examples of time-depth variations of irradiance in the water column were then estimated following Gilbert et al. (in press). The irradiance threshold for feeding of Arctic cod and sand lance was hypothetically set to 0.1 µE m^{-2} s^{-1} (400 to 700 nm waveband) following the same authors.

Analysis. Plankton profiles beginning at 22:00 h, 01:00 h and 04:00 h EST were grouped as 'night profiles' while the other were classified as 'day profiles'. Macro- and microzooplankton taxa were enumerated in samples fractionated on 1000, 250, and 63 µm mesh sieves. The relative abundance of copepod species was assessed for the 0, 5, and 20 m depth samples collected on the midday and midnight profiles at each station. Two cohorts of the chaetognath *Sagitta elegans* occur in southeastern Hudson Bay (Dunbar 1962, Drolet 1990). Chaetognaths longer than 20 mm were considered mature, smaller ones were classified as juveniles.

All fish larvae were sorted and their standard length (SL) was measured to the nearest 0.1 mm. Up to 30

specimens of the most abundant species were selected from each of the 238 samples for gut content analysis. Following Govoni et al. (1986), only prey items contributing more than 2 % in number to the diet were considered in the analysis.

Food resource available at a given depth to the larvae of each length category was calculated from the frequency of occurrence of each prey item in the gut, its average weight and its abundance at that depth (Fortier & Harris 1989). Weights of copepod nauplii and copepod eggs were estimated from their volume, assuming a specific gravity of 1.028 and a half-cylinder shape for copepod nauplii.

A regression analysis was used to quantify the relationship between the vertical distribution of fish larvae (dependent variable) and that of their food resource or light (independent variables). To test the hypothesis that fish larvae were distributed in direct proportion to their food, the slope of the regression (b) was compared to a value of 1. Because plankton samples were not independently collected in time or space, and the abundances of the taxa were estimated from the same collection, parametric tests are inappropriate (Fortier & Harris 1989). The F value of the regression was tested for significance by a non-parametric randomization procedure ('bootstrap' approach with 3000 iterations, see Fortier & Harris 1989 for details), and the value $|1-b|$ was tested against 0 by the same method.

RESULTS

Water column stratification and phytoplankton vertical distribution

The structure of the water column varied very little over the 48 h sampling periods but differed considerably between the 2 stations. There was no evidence for ice melt or plume dilution at Stn D. The water column was nearly isothermal with temperatures from −1 to −1.5 °C. Salinity varied from 28 ‰ near the ice-water interface to 30 ‰ at 50 m (Fig. 2). In contrast the water column was well stratified at Stn B with a steep pycnocline (16.0 σ_t units m^{-1}) around 5 m (Fig. 2). With the input of freshwater from the river and local ice melt, salinity above the pycnocline did not exceed 6 ‰. Temperature oscillated between 0 and −0.2 °C. Below the pycnocline, temperature and salinity were similar to those found at Stn D (Fig. 2).

Vertical distribution of chl *a* reflected the structure of the water column. At Stn D, the concentration of chl *a* was low and varied little with depth, from 0.03 mg m^{-3} at the ice-water interface to 0.02 mg m^{-3} at 50 m (Fig. 2). At Stn B, values were relatively high in the brackish surface layer (0.2 to 0.8 mg m^{-3}). Below the pycnocline,

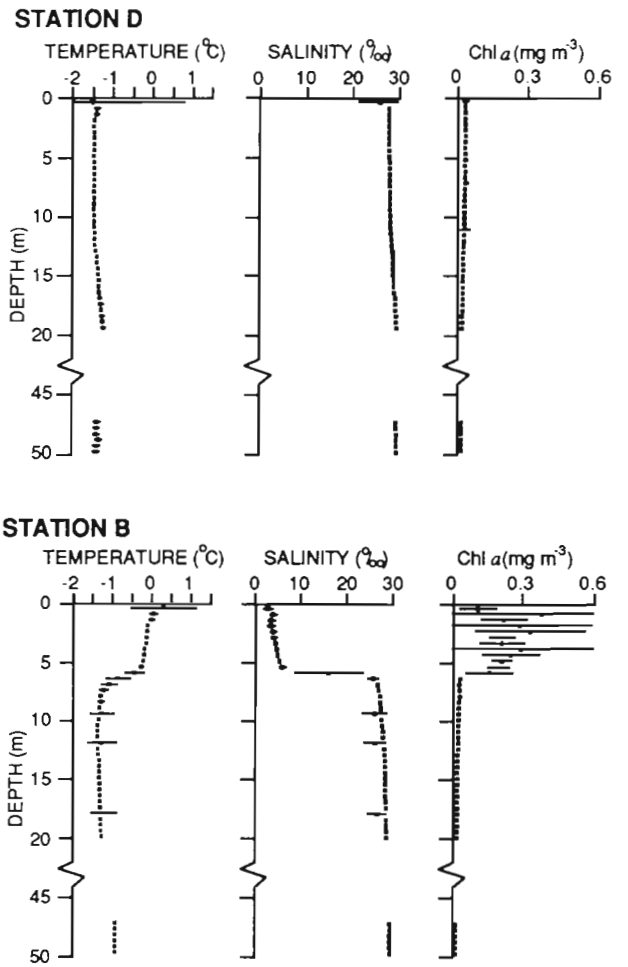

Fig. 2. Average profile (with standard deviation) of temperature (°C), salinity (‰) and chl *a* concentration at Stns D & B (n = 17 profiles at each station)

concentrations were low and similar to those found at Stn D (0.02 to 0.03 mg m^{-3}) (Fig. 2). The phaeopigments/chl *a* ratio was relatively constant over the depth range sampled at Stn D (Table 1). At Stn B, the ratio was higher below the pycnocline than in the brackish plume. At both stations, pennate diatoms outnumbered centric diatoms in the phytoplankton (Table 2). The under-ice plume was abundantly colonized by *Fragilaria* spp., *Thalassiosira* spp. and *Chaetoceros* spp. The 2 genera *Nitzschia* and *Navicula* were relatively scarce.

Zooplankton abundance, composition and vertical distribution

High densities of rotifers and tintinnids were found in the brackish waters of the river plume (Table 2). Other zooplankton taxa were from 1 to 2 orders of magnitude

Table 1. Average phaeopigments/chl *a* ratio by depth at each station

Depth (m)	Phaeopigments/chl *a*	
	Stn D	Stn B
0	0.60	0.15
1	0.18	0.08
3	0.73	0.34
5	0.65	0.42
10	0.50	1.03
15	0.77	1.35
20	0.44	1.63

less abundant in the plume than below the pycnocline. Mean densities of copepod nauplii, the main prey of fish larvae, were similar at Stn D and beneath the pycnocline at Stn B (2710 versus 3396 ind. m^{-3}), but much lower in the plume (88 ind. m^{-3}) (Table 2).

The copepod assemblage was similar to that previously reported for southeastern Hudson Bay (Rochet & Grainger 1988), where arctic species (*Calanus glacialis, Oncea borealis* and *Microcalanus pygmaeus*) mix with species associated with less saline conditions (*Acartia longiremis* and *Pseudocalanus* spp.). The copepods *Oithona similis* and *Pseudocalanus* spp. dominated the zooplankton community of the marine layer (Table 2). The relative abundance of the different species was similar at the 2 stations except for *Oncea borealis* which was more abundant at Stn B (Table 2). At both stations, the fraction >1000 µm consisted mainly of female *Pseudocalanus* spp. (66.6 % by numbers) in daytime, female *Calanus glacialis* (68.4 %) and adult *Metridia longa* (26.0 %) at night. *Oithona similis* dominated (76.9 %) the 2 other size-fractions. Planktonic predators were principally represented by juveniles of the chaetognath *Sagitta elegans*.

Vertical distribution of copepod eggs, copepod nauplii, and small copepods (Fractions 63–250 µm and 250–1000 µm) differed little between day and night (Fig. 3). Larger copepods (Fraction >1000 µm), *Sagitta elegans*, and jellyfish presumably distributed at a greater depth than the lower limit of our sampling (20 m) in daytime and were captured primarily at night in the 0 to 20 m depth interval. At Stn B, the pycnocline acted as a sharp boundary to the distribution of marine taxa which were virtually excluded from the brackish waters of the plume (Fig. 3). *Sagitta elegans* tended to accumulate at the pycnocline at night.

Ichthyoplankton composition and length distribution

Two species of fish larvae were captured in significant numbers: Arctic cod *Boreogadus saida* (Lepechin) and sand lance *Ammodytes* sp. (Table 2). Both *A. americanus* and *A. dubius* are likely to occur in Hudson Bay (Scott & Scott 1988), but sand lance larvae were identified to genus only as recommended by Fahay (1983). Seasnail *Liparis* sp. (n = 9, SL = 6.5 to 7.5 mm) and capelin *Mallotus villosus* (n = 11, SL = 4.5 to 6.3 mm) were also caught at Stn B, but their low abundance precluded the analysis of their vertical distribution.

Table 2. Average density of the dominant phytoplankton, zooplankton and ichthyoplankton taxa at Stn D (all depths, n = 119 samples) and Stn B (brackish surface layer, n = 51 samples; deep marine layer, n = 68 samples)

Taxon	Stn D	Stn B	
	0–20 m	0–3 m	5–20 m
Phytoplankton (no. l^{-1})			
Centric diatoms			
Melosira spp.	0	279	0
Thalassiosira spp.	928	12497	366
Chaetoceros spp.	60	4189	157
Other	389	0	1326
Pennate diatoms			
Nitzschia spp.	209	209	262
Navicula spp.	299	0	0
Synedra spp.	1646	0	140
Amphora spp.	120	70	0
Fragilaria spp.	5206	37001	1518
Other	509	0	0
Dinophyceae	2035	140	2409
Flagellates	1765	1676	70
Zooplankton			
Copepods (no. m^{-3})			
Calanus glacialis	2	<1	1
Metridia longa	<1	<1	<1
Pseudocalanus spp.	968	13	883
Microcalanus pygmaeus	45	2	148
Oithona similis	4152	68	3844
Acartia longiremis	54	<1	56
Oncea borealis	7	9	263
Copepod spp.	57	4	128
Copepod eggs	86	5	291
Copepod nauplii	2710	88	3396
Other			
Oïkopleura sp. (no. m^{-3})	<1	<1	14
Gasteropod larvae (no. m^{-3})	28	2	62
Rotifers (no. m^{-3})	0	1328	0
Tintinnids (no. l^{-1})	120	1396	471
Planktonic predators (no. 100 m^{-3})			
Sagitta elegans adults	19	<1	12
S. elegans juveniles	728	53	1198
Cnidaria – Ctenophora	26	12	78
Ichthyoplankton (no. 100 m^{-3})			
Boreogadus saida	7	9	92
Ammodytes sp.	2	3	7
Liparis sp.	0	0	<1
Mallotus villosus	0	0	<1

Arctic cod and sand lance were represented in our collections by yolk-sac larvae and first-feeding post

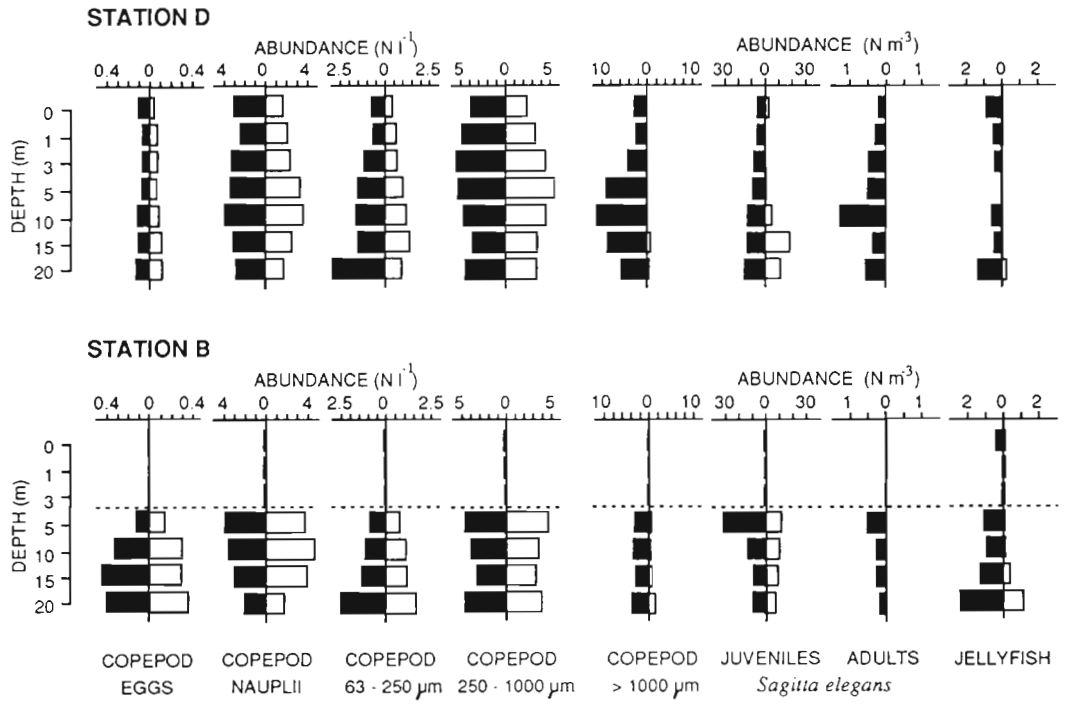

Fig. 3. Vertical distribution of different zooplankton taxa by night (black histograms, n = 6 profiles) and by day (open histograms, n = 11 profiles) at Stns D & B. Dotted line for Stn B indicates depth of the sharp pycnocline between brackish surface layer and deep marine layer Note the compressed vertical scale

yolk-sac larvae. Yolk-sac frequency in Arctic cod was low at both stations (Stn D: 32 %; Stn B: 10 %). A comparison of yolk-sac frequency at length for larvae sampled in the same area at the same time with nets towed horizontally (Ponton & Fortier unpubl.) suggests that some Arctic cod larvae (ca 22 %) lost their yolk sac when captured with the pump. The majority (89 %) of sand lance captured at Stn D were yolk-sac larvae. Yolk-sac frequency was lower (63 %) 9 d later at Stn B. At both stations, Arctic cod and sand lance larvae were slightly larger in night samples than in daytime samples (Stn D: Mann-Whitney test, $Z = -3.070$, $p < 0.01$; Stn B: $Z = 2.309$, $P = 0.021$), suggesting some avoidance of the pump intake in daytime (Fig. 4).

Diet and feeding rhythms of fish larvae

Feeding incidence (the percentage of larvae with at least 1 prey in the gut) increased with larval length and was much higher in Arctic cod than in sand lance (Table 3). The 2 species fed primarily on copepod nauplii. The frequency of copepod eggs in the diet tended to decline as length increased. At Stn B, Arctic cod larvae fed almost exclusively on nauplii. For this species, diet composition, feeding incidence and the

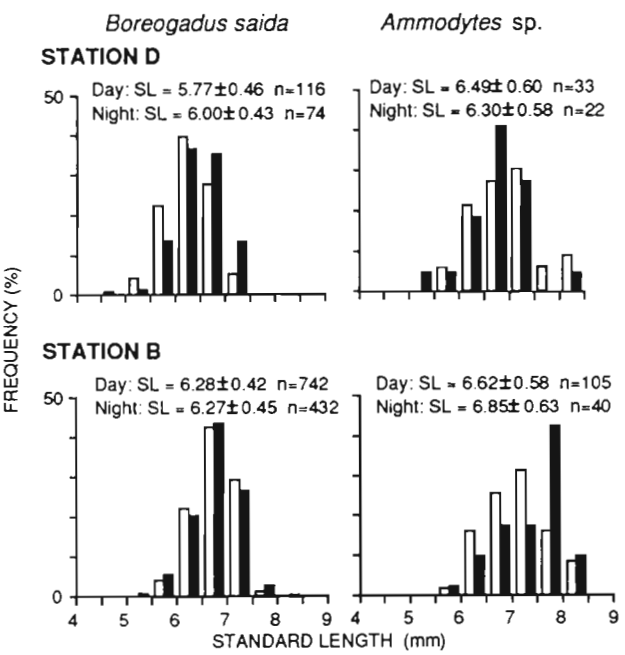

Fig. 4. *Boreogadus saida, Ammodytes* sp. Length-frequency distribution of Arctic cod and sand lance larvae by night (black histograms) and by day (open histograms) at Stns D & B. Average standard length in mm (SL ± SD) and sample size given for day and night

Table 3. *Boreogadus saida, Ammodytes* sp. Percent diet and feeding statistics for Arctic cod and sand lance larvae by length-class and station

		Boreogadus saida					*Ammodytes* sp.				
		Stn D		Stn B			Stn D		Stn B		
		<6 mm	≥6mm	<6 mm	6–7 mm	≥7 mm	<6 mm	≥6 mm	<6 mm	6–7 mm	≥7 mm
Copepod eggs	Day	33.3	14.3	0	0.4	0	0	33.3	0	20.0	0
	Night	0	0	2.9	1.2	0	0	0	0	0	0
Copepod nauplii	Day	33.3	85.7	96.7	97.8	94.1	0	66.6	0	60.0	75.0
	Night	0	100	94.1	97.0	100	0	0	0	0	100
Unidentified	Day	33.3	14.3	1.7	1.8	5.9	0	0	0	20.0	25.0
	Night	0	0	2.9	1.8	0	0	0	0	0	0
Number examined	Day	68	39	153	536	24	5	27	9	63	29
	Night	31	41	84	304	22	6	16	4	112	23
Percent with prey	Day	4.4	17.9	39.2	51.9	70.8	0	11.1	0	7.9	13.8
	Night	0	7.3	40.5	55.3	81.8	0	0	0	0	13.0
Mean no. of prey in positive gut content	Day	1.0	1.7	3.5	3.9	5.5	0	1.0	0	1.0	1.7
	Night	0	2.7	2.8	4.4	5.3	0	0	0	0	1.0

mean number of prey in gut contents varied little between day and night.

Low feeding incidence in both species impeded the study of feeding rhythms at Stn D. At Stn B, Arctic cod displayed a diel feeding rhythm which was most evident in larvae ≥6 mm (Fig. 5). The number of prey in the gut of Arctic cod ≥6 mm increased significantly with time in daytime (linear regression, $F = 18.9$, n = 11, $P = 0.002$) and decreased at night from the evening maximum to the early morning minimum ($F = 15.3$, n = 10, $P = 0.006$). Sand lance with prey were too scarce to detect any rhythm in foraging activity.

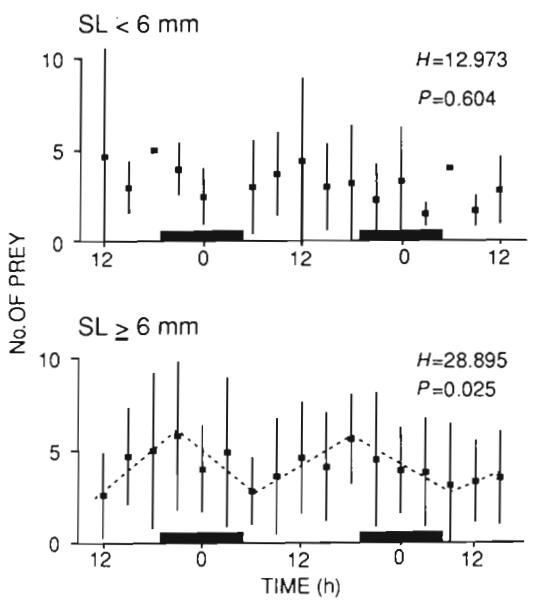

Fig. 5. *Boreogadus saida*. Time series of the average no. of prey (±SD) in the gut of Arctic cod <6 mm and ≥6 mm at Stn B. Black horizontal bars correspond to night. Dotted lines fitted by hand. *H*-statistic for the Kruskal-Wallis 1-way ANOVA over the entire period of time and the associated probability *P* are given

Vertical distribution of fish larvae

Variations in the vertical distribution of fish larvae were related primarily to stratification and food availability. At Stn D where stratification was weak, Arctic cod larvae and their food resource were rather evenly distributed over the 0 to 20 m depth interval (Fig. 6). Because of this lack of variance over depth, the regression between the distributions was either non-significant or marginally significant (Fig. 6). At Stn B, stratification strongly affected the distribution of the larvae and their prey which were nearly excluded from the brackish waters of the plume (Fig. 6). At night, Arctic cod were distributed in direct proportion to food abundance. In daytime, this pattern was distorted as the larvae (especially the larger post yolk-sac larvae) aggregated at the pycnocline (5 m).

Few sand lance larvae were captured at either of the 2 stations and feeding incidence was always very low (Table 3). Therefore, statistical inferences regarding their vertical distribution in relation to that of their potential food resource should be interpreted with caution. At Stn D, sand lance larvae were found deeper in the water column than their future prey which were distributed evenly over depth (Fig. 7). At Stn B, few larvae were found in the plume where little food resource was available. Larvae <7 mm which hardly

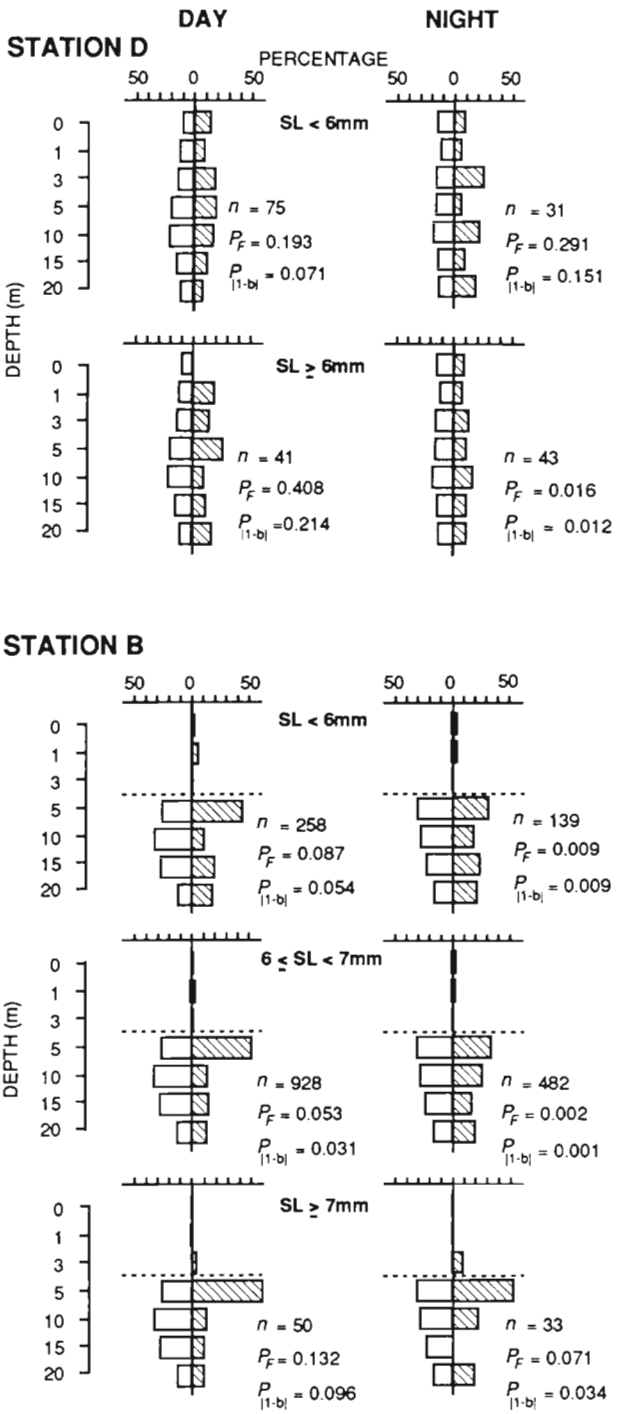

Fig. 6. *Boreogadus saida*. Percent vertical distribution of Arctic cod larvae (hatched histograms) and their food resource (open histograms) by day (average of 11 profiles) and by night (average of 6 profiles) for different length-classes at Stns D & B. Note the compressed vertical scale. n: no. of larvae. P_F and $P_{|1-b|}$ are respectively the probability of a larger F and a lesser value of |1-slope| for the regression of larval abundance on resource abundance. Tested by randomization (see 'Materials and Methods')

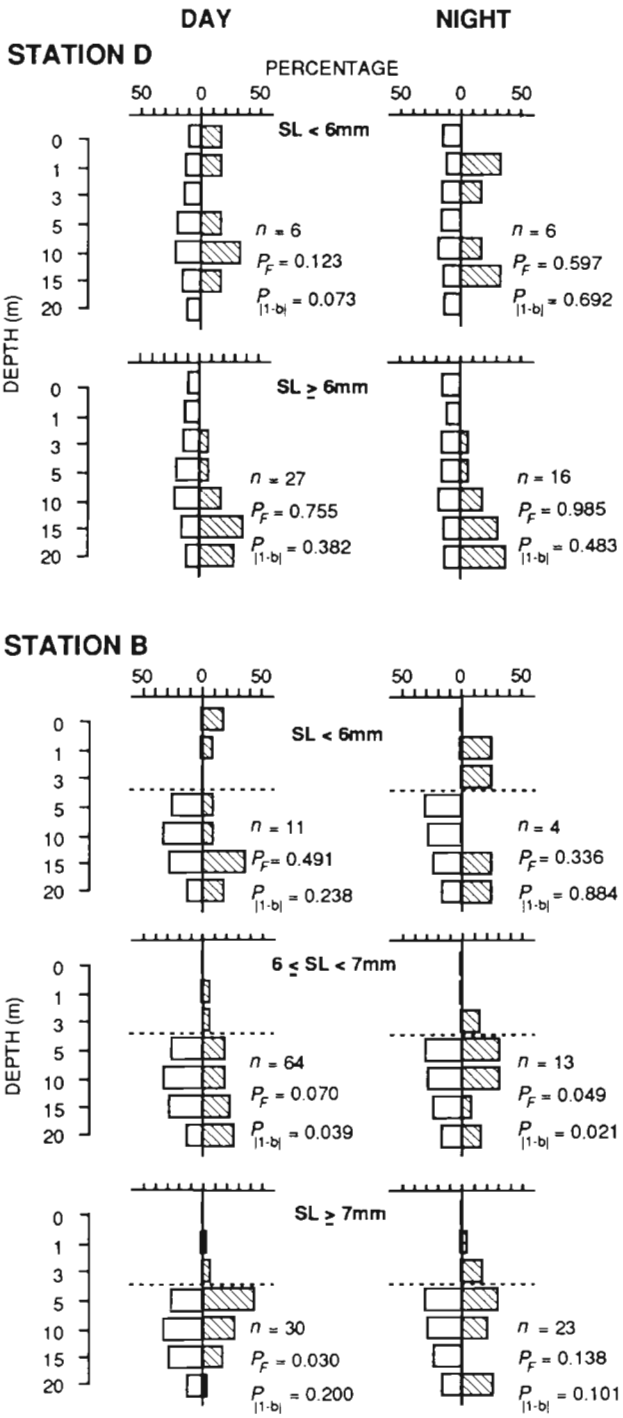

Fig. 7. *Ammodytes* sp. Percent vertical distribution of sand lance larvae (hatched histograms) and their food resource (open histograms) by day (average of 11 profiles) and by night (average of 6 profiles) for different length-classes at Stns D & B. Note the compressed vertical scale. n = no. of larvae. P_F and $P_{|1-b|}$ as in Fig. 6

fed (0 to 8 % feeding incidence) were again found deeper than their future prey in daytime. Larvae ≥ 7 mm which fed slightly more frequently (14 %) were distributed roughly in proportion to their food resource by day, with a tendency like Arctic cod to accumulate at the pycnocline (Fig. 7).

At Stn B, feeding incidence and the mean number of prey captured by the larvae of both species were not evenly distributed over depth (Fig. 8). In Arctic cod larvae, feeding incidence and the average number of prey were often as high or higher at night than in daytime (Fig. 8). Feeding incidence was maximum at the pycnocline and decreased significantly at greater depth for larvae < 6 mm SL but not for larvae ≥ 6 mm SL. Feeding incidence in the few larvae that were captured in the plume was relatively high. The mean number of prey ingested by both length classes was maximum near the pycnocline and tended to decline with depth especially in larger larvae (Fig. 8).

Sand lance larvae captured in the plume did not feed (Fig. 8). In daytime, feeding incidence and the number of prey ingested by this species were maximum between 5 and 10 m, i.e. within or immediately below the pycnocline. The tendency for these 2 variables to decrease with greater depth was not statistically significant. At night, only 3 larvae with prey were sampled (2 at 5 m and 1 at 20 m), and no clear pattern could be ascertained.

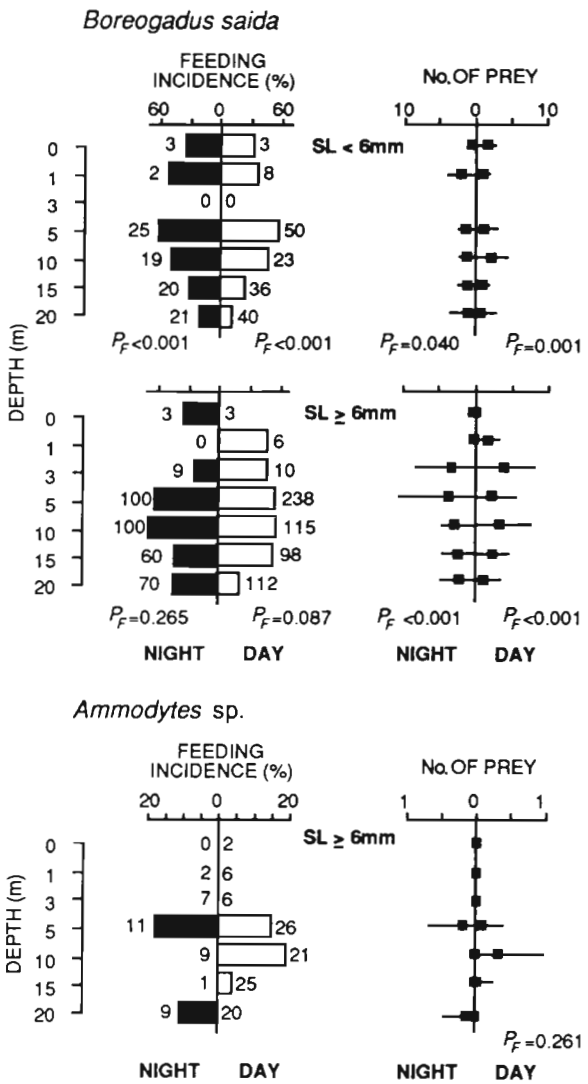

Fig. 8. *Boreogadus saida*, *Ammodytes* sp. Vertical distribution of feeding incidence (% with at least 1 prey) and no. of prey in gut (±SD) for Arctic cod and sand lance larvae at Stn B by night (black histograms, average of 6 profiles) and by day (open histograms, average of 11 profiles). No. of larvae is given near each histogram. Note the compressed vertical scale. P_F is the probability of a larger F for the regression of feeding incidence or number of prey on depth. Tested by randomization (see 'Materials and Methods')

Irradiance and food availability

At Stn B in daytime, foraging fish larvae tended to accumulate at the pycnocline rather than distribute in proportion to prey density (Figs. 7 & 8). This suggested that the suitability of a given depth for foraging was a function of both prey density and the amount of light available to detect and capture prey. To test this hypothesis, food availability below the pycnocline was redefined as the percentage of the total food resource found at a given depth times the percentage of incident light remaining at that depth. At Stn B, calculated irradiances above the pycnocline were substantially higher than the hypothetical feeding threshold (0.1 μE m^{-2} s^{-1} in the 400 to 700 nm waveband) for Arctic cod and sand lance larvae (Fig. 9). Below the pycnocline irradiance values were close to or lower than this threshold. Thus, the correction for light was applied below the pycnocline (5 m) where light was potentially limiting but not above it where light was assumed to be sufficient for feeding. At Stn D, irradiances were higher than the feeding threshold over the 0 to 20 m depth range sampled (Fig. 9).

Once the correction for light was applied at depths below the pycnocline, foraging fish larvae sampled in daytime at Stn B were distributed in direct proportion to food availability. For example, the vertical distribution of Arctic cod larvae ≥ 7 mm SL was not significantly correlated to either light (Fig. 10a), or food density (Fig. 10b) but was significantly correlated to the product of food density by light availability (Fig. 10c). The slope of the latter regression was not significantly different from 1, indicating that the larvae distributed themselves in direct proportion to the product of food

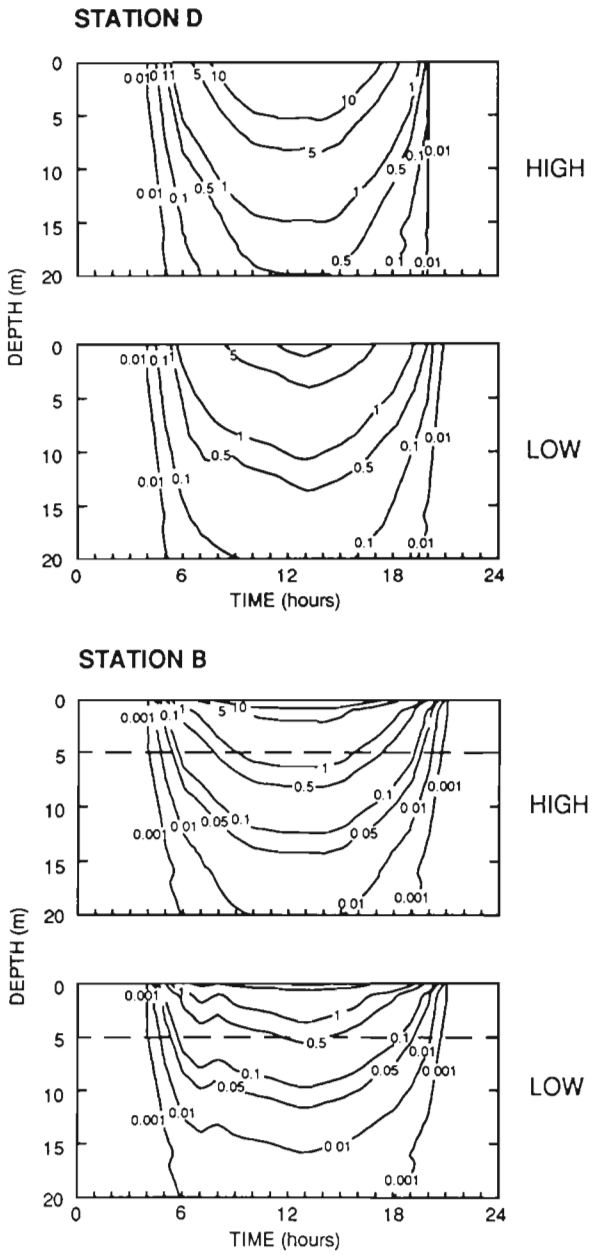

Fig. 9. Time-depth distribution of light intensity in $\mu E\ m^{-2}\ s^{-1}$ (400 to 700 nm waveband) for low and high incident irradiance at Stns D & B. Broken line indicates pycnocline at Stn B

density by light availability (Fig. 10). Similar results were obtained for other lengths classes of Arctic cod and for sand lance ≥ 7mm (Table 4). In both species, the correlation between the vertical distribution of the larvae and that of corrected food availability tended to increase with larval fish length (Table 4).

DISCUSSION

Effect of the freshwater plume on phytoplankton production and copepod reproduction

In ice-covered southeastern Hudson Bay, the vernal expansion of the Great Whale River plume washes away the under-ice algal mat (Poulin et al. 1983) and drastically reduces the associated ice meiofauna (Grainger 1988). The loss of meiofaunal biomass within the 2000 km^2 area of the plume in 1983 was estimated at 250 t by Grainger (1988). Assuming a significant coupling between the ice biota and the pelagic ecosystem (Grainger 1988, Runge & Ingram 1991, Runge et al. in press), it can be hypothesized that this reduction of primary and secondary production at the ice-water interface could slow down the reproduction of pelagic

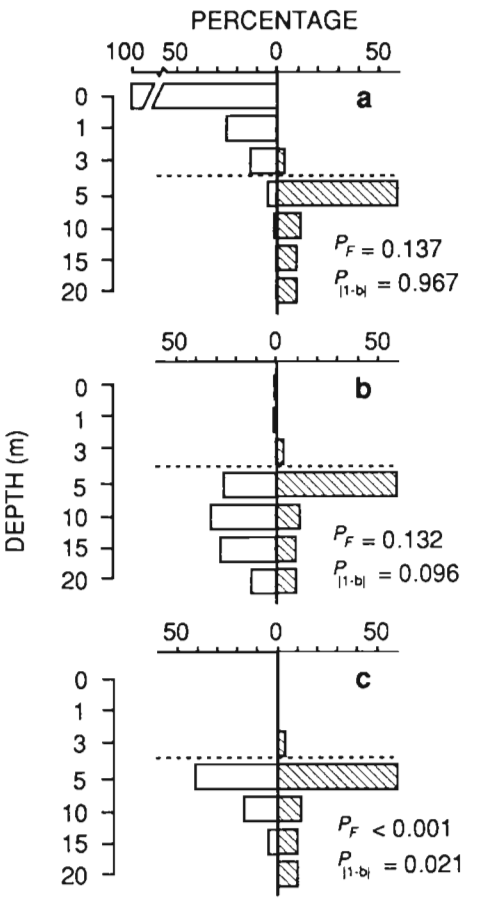

Fig. 10. *Boreogadus saida*. Percent vertical distribution of Arctic cod larvae ≥ 7 mm (hatched histograms) at Stn B compared to (a) percent irradiance at depth, (b) percent food density at depth, and (c) percent food availability at depth (i. e. % food density × % irradiance, see text). Dotted line indicates pycnocline. Note the compressed vertical scale. P_F and $P_{|1-b|}$ as in Fig. 6

Table 4. *Boreogadus saida, Ammodytes* sp. Statistics of the regression between vertical distribution of fish larvae and food availability (i.e. % food density × % irradiance, see text) for Arctic cod and sand lance by length-class at Stn B. P_F and $P_{|1-b|}$ are respectively the probability of a larger F and a lesser value of $|1-\text{slope}|$ for the regression of larval abundance on resource abundance. Tested by randomization (see 'Materials and Methods')

Species	Length (mm)	F	P_F	$\|1-b\|$	$P_{\|1-b\|}$	r^2
Boreogadus saida	<6	13.8	0.045	0.477	0.048	0.734
	6–7	42.2	0.010	0.317	0.023	0.894
	≥7	53.2	<0.001	0.119	0.021	0.914
Ammodytes sp.	<6	0.17	0.485	1.086	0.623	0.033
	6–7	0.63	0.476	0.862	0.271	0.112
	≥7	58.7	0.004	0.376	0.005	0.921

copepods and, hence, the production of larval fish food in the area covered by the plume (Gilbert et al. in press).

In this study, the low phytoplankton biomass (<0.04 mg chl *a* m^{-3}) outside the plume can be attributed to the absence of the stratification necessary to maintain the cells in the very shallow photic layer that characterizes ice-covered seas. Within the plume, some biomass (0.2 to 0.8 mg chl *a* m^{-3}) accumulated in the brackish layer above the pycnocline, where light intensity was maximum. Except for *Chaetoceros*, the abundant diatoms in the brackish layer (*Fragilaria* and *Thalassiosira*) were not representative of the assemblage found at the ice-water interface in spring (Poulin et al. 1983, Gosselin et al. 1985, Tremblay et al. 1989). The 2 genera *Nitzschia* and *Navicula* which usually dominate the assemblage of ice algae were relatively scarce in the brackish layer. This suggests that the dominant diatoms in the brackish plume originated primarily from the river and not from the ice-water interface.

Within the area covered by the plume the phytoplankton of the brackish surface layer could be exploited directly by rotifers and tintinids, but not by large copepods which were stopped at the pycnocline in their nycthemeral migrations. Yet, the relatively high phaeopigments/chl *a* ratios found below the pycnocline suggest that herbivore grazing and excretion in the marine layer was more intense at Stn B than Stn D (Shuman & Lorenzen 1975). Since the concentration of chl *a* in the marine waters of both stations was similar, one may speculate that within the area covered by the plume, copepods had some indirect access to the higher phytoplankton biomass of the brackish layer. Outside the plume of the Great Whale River, females of the dominant copepods *Calanus glacialis* and *Pseudocalanus minutus* migrate to within 0.2 m of the ice at night to feed at the basis of the diluted interfacial layer that contains high concentrations of ice algae (Runge & Ingram 1991). We propose that within the area covered by the plume a similar behaviour enables copepods to exploit the phytoplankton of the surface brackish layer.

Density of copepod eggs and nauplii in the marine layer was similar inside and outside the area covered by the Great Whale River plume. Comparing the same regions before the river freshet in 1988 (24 April to 8 May), Gilbert et al. (in press) found marginally lower abundances of suitable prey for larval fish inside the area covered by the plume, and no significant difference after the freshet (8 May to 14 June). This suggests that within the area covered by the plume, the phytoplankton available at the pycnocline to fuel copepod reproduction (and the production of larval fish food) probably compensates for the unavailability of ice algae at the ice-water interface.

Salinity, light intensity and the under-ice foraging of fish larvae

Although some were found in the surface layer, Arctic cod and sand lance larvae generally avoided the brackish waters of the plume (see also Gilbert et al. in press). In the laboratory, exposure to a salinity of 5 ‰ for a period of 5 d did not affect the survival or activity of young Arctic cod larvae, but resulted in slower growth and minor morphological aberrations such as hydropsy (Doroshev & Aronovich 1974). Consistent with these results, the apparent condition of the few larvae sampled in the brackish (3 to 6 ‰) surface layer did not differ from that of larvae sampled beneath the pycnocline except for signs of a slight hydropsy. This indicates that despite the observed distributions, Arctic cod and the more euryhaline sand lance (Gilbert et al. in press) were physiologically able to tolerate incursions in the brackish surface layer.

Tintinids which are often found in the gut of first-

feeding fish larvae (e.g. Last 1980) and rotifers which are suitable prey to larval Arctic shanny *Stichaeus punctatus* (Drolet et al. 1991) were abundant in the Great Whale River plume. Yet, rotifers and tintinids were never found in the gut of first-feeding Arctic cod or sand lance even in larvae captured above the pycnocline. It is thus likely that a lack of suitable prey rather than low salinity kept the larvae of these species out of the diluted surface layer.

Light attenuation by the ice cover is another factor that can narrow the feeding depth range of fish larvae (Dabrowski 1985). Gilbert et al. (in press) hypothesized that the feeding of Arctic cod and sand lance larvae was limited at irradiances less than 0.1 to 1 $\mu E\ m^{-2}\ s^{-1}$ (400 to 700 nm waveband). According to their calculations, illumination would have been sufficient for these species to feed over most of the 0 to 20 m depth range sampled at Stn D, but would have been suboptimal below 10 m at Stn B because of the additional light extinction due to plume turbidity.

These predictions are confirmed to some extent by our results. Feeding incidence and the number of larvae sampled at Stn D were too low to verify that feeding was not limited by light at any depth. As predicted for Stn B however, feeding incidence and/or the mean number of prey captured by Arctic cod larvae declined beyond 10 m (Fig. 8). The same conclusion can tentatively be drawn for sand lance despite the low sample size and feeding incidence. Paradoxically, foraging success also declined with depth at night when no light gradient existed. This can probably be attributed to slow digestion at low temperature (−1.0 to −1.5 °C), the nighttime depth distribution of feeding incidence and gut content reflecting the daytime distribution.

Thus, turbid plume waters constrained foraging post yolk-sac larvae to a narrow layer immediately beneath the pycnocline. By further narrowing this layer, any natural or anthropogenic increase in the turbidity and/or thickness of the surface layer could threaten the success of Arctic cod and sand lance first feeding within the area covered by the plume of the Great Whale River.

The vertical co-distribution of fish larvae and their prey

In daytime, Arctic cod larvae and sand lance ≥ 7 mm were not distributed in exact proportion to food density but rather aggregated at the pycnocline where the product of resource density and light intensity, which determined food availability, was maximum. The same behaviour was demonstrated by Munk et al. (1989) for Atlantic herring *Clupea harengus* and suggested by Yamashita et al. (1985) for Japanese sand-eel *Ammodytes personatus*. Thus the suitability of a given depth for foraging fish larvae appears to be a function not only of prey density but also of the amount of light available to detect and capture prey.

Larvae of several fish aggregate in a relatively narrow depth range in daytime and spread more evenly over the water column at night (e.g. Boehlert et al. 1985, Brewer & Kleppel 1986, Heath et al. 1988). Redistribution at night has been suggested to result from the relaxation of the daytime aggregation, the larvae sinking passively in the absence of a light gradient (Wood 1971, Munk et al. 1989). Consistent with this hypothesis, the nighttime distribution of Arctic cod was relatively uniform (compared to their daytime distribution) and coincided with the vertical distribution of the small, presumably passive, microplanktonic prey. This result likely reflects a similar and passive response of the larvae and their prey to the turbulence field in the absence of a light gradient.

Density-dependent competition or unequal foraging abilities?

If density-dependent competition for food occurs, the Ideal Free Distribution (IFD) model (Fretwell & Lucas 1970, Fretwell 1972) predicts that fish larvae will distribute in direct proportion to food availability at depth (Fortier & Harris 1989). The model assumes that the larvae select the 'Ideal' or most profitable depth to forage, and that they have 'Free' access to all depths. Under these conditions, Fortier & Harris (1989) have shown that first feeding post yolk-sac larvae of species preying on copepods achieved an IFD over a 60 m water column in the English Channel. Given the small impact of fish larvae on the standing biomass of their prey (Cushing 1983, Dagg et al. 1984, Monteleone & Peterson 1986, Fortier & Harris 1989), they concluded that if density-dependent competition was causing the observed IFD, this competition had to be generated at the level of the entire assemblage of planktonic predators (including fish larvae).

Once a correction was made for light intensity, first-feeding Arctic cod and sand lance larvae were distributed in proportion to prey availability. Yet, evidence suggests that density-dependent competition was not the driving force behind the observed Ideal Free Distribution. Density of fish larvae and invertebrate planktonic predators was low (< 14 ind. m^{-3} on average at Stn B), and interference (i.e. a slowing down of the individual rate of prey capture due to interactions with other predators, Parker & Sutherland 1986) was unlikely. Chaetognaths, the dominant planktonic predator, preyed upon older stages of copepods and

did not share the food resource of first-feeding fish larvae (Drolet 1990). Hydromeduseans remove only a small fraction of the daily production of zooplankton (Purcell 1990) and, given their low abundance, could not reduce the availability of microzooplankton to fish larvae in the present study. Thus, density-dependent interactions between planktonic predators and fish larvae were unlikely to develop in early spring in Hudson Bay.

If density-dependent competition is too weak to force them to spread in proportion to food availability, larvae trying to maximize their energy intake will accumulate in the depth interval where foraging gain is maximum (Fortier & Harris 1989). In the present study, foraging gain (as measured by the average number of prey in the gut) was maximum at the pycnocline where the majority of foraging larvae congregated as predicted. Yet, significant numbers of larvae remained at depths where individual gain was less than maximum. When Arctic cod grow from 6.4 to 7.2 mm, the proportion of larvae with an inflated swim bladder increases from 2 to 65 % (Aronovich et al. 1975). An inflated swim bladder confers motility, better depth control and greater foraging efficiency (Aronovich et al. 1975). Thus, larvae of the same length-class may present significant differences in foraging abilities. These differences, rather than the density-dependent exclusion of some larvae from the most profitable layer at the pycnocline, could explain the presence of larvae at depth in daytime.

In early spring, the larvae of arctic marine fish emerge in a harsh environment: food is scarce (Gilbert et al. in press), temperature is low and the ice cover retain more than 90 % of the incoming light. At that time, river plumes extend under the ice cover over large areas of the coastal region (Ingram & Larouche 1987). Away from direct plume effects, local ice melt also result in strong thermohaline stratification but without the increase in turbidity associated with river plumes. By further attenuating whatever light penetrates the ice cover, river plumes represent a supplementary constraint for the first feeding larvae of neritic spawners. Our results show that the impact of this constraint on the reproduction of coastal species will be a function not only of the fraction of the spawning distribution covered by the plume (Gilbert et al. in press) but also of the thickness of the plume.

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