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### Impact of freshwater on a subarctic coastal ecosystem under seasonal sea ice (southeastern Hudson Bay, Canada). III. Feeding success of marine fish larvae \*

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#### Abstract

We monitored the feeding success (percent feeding incidence at length and mean feeding ratio at length) of Arctic cod (*Boreogadus saida*) and sand lance (*Ammodytes* sp.) larvae in relation to prey density, light, temperature and potential predator density under the ice cover of southeastern Hudson Bay in the spring of 1988, 1989 and 1990. Both prey density and light limited larval fish feeding. The relationship between feeding success and actual food availability (nauplii density  $\times$  irradiance) was adequately described by an Ivlev function which explained 64 and 76% of the variance in Arctic cod and sand lance feeding success respectively. By affecting both prey density and irradiance, the thickness of the Great Whale River plume (as defined by the depth of the 25 isohaline) was the main determinant of prey availability. Arctic cod and sand lance larvae stopped feeding when the depth of the 25 isohaline exceeded 9 m. Limitation of feeding success attributable to freshwater inputs occurred exclusively in 1988, the only time when the depth of the 25 isohaline exceeded the 9 m threshold. The close dependence of larval fish feeding success on the timing of the freshet and plume dynamics suggests a direct link between climate and survival of Arctic cod and sand lance larvae. The actual impact of climate fluctuations and/or hydro-electric developments on recruitment will depend on the fraction of the larval dispersal area of the two species that is affected by river plumes.

### 1. Introduction

Vulnerability to predators being size dependent, fast initial growth may reduce cumulative

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mortality during the first months of life of marine fishes by shortening the period during which the larvae are vulnerable to predators (Cushing, 1974, 1990; Ware, 1975; Shepherd and Cushing, 1980; Anderson, 1988). At a given temperature, energy intake determines the growth rate of young fish. Thus, feeding success of the planktonic larvae and postlarvae may determine total cumulative mortality in the first year of life.

Fish larvae are visual predators and, in some

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situations, feeding success may depend not only on the availability of prey but also on the availability of sufficient light to perceive prey (Chesney, 1989; Munk et al., 1989; Gilbert et al., 1992; Ponton and Fortier, 1992; Miner and Stein, 1993; Ponton et al., 1994). Light is unlikely to limit the feeding of epipelagic fish larvae in temperate and tropical open waters, at least during daytime. Yet, the larvae of several species occur in Arctic and subarctic seas in early spring (e.g. Drolet et al., 1991; Ponton et al., 1993; Fortier and Fortier, 1995), when over 99.9% of the incident light is blocked by the snow and ice covers. The irradiance then available in the water column is often lower than typical thresholds below which the feeding of fish larvae is limited (Gilbert et al., 1992).

In southeastern Hudson Bay (northern Quebec, Canada), the planktonic larvae of Arctic cod, Boreogadus saida and sand lance, Ammodytes sp. initiate feeding in mid May, several weeks before the breakup of the ice cover in late May or early June (Drolet et al., 1991; Ponton et al., 1993; Fortier et al., 1995). At that time, the areal extent of several river plumes increases rapidly under the ice cover of the bay in response to the spring freshet. With the ice cover reducing friction and preventing wind mixing, river plumes may extend over thousands of km<sup>2</sup> in the coastal zone of Hudson, Bay, forming a thin layer of brackish turbid waters immediately under the ice. The plume of the Great Whale River, for example, reaches between 1000 and 2000 km<sup>2</sup> in area at the time of the spring freshet (Ingram, 1981; Ingram and Larouche, 1987). After the freshet, the light that reaches the ice-water interface is rapidly attenuated in the first meters of the water column by the turbid waters of the plume. Hence, whatever light is available to foraging fish larvae before the spring freshet will be severely reduced in the area affected by expanding river plumes.

In the present study, we analyse how interannual variations in the thickness of the Great Whale River plume contributed to interannual variations in the feeding success of Arctic cod and sand lance larvae from 1988 to 1990 in southeastern Hudson Bay. Feeding success is related to light and prey availability at the halocline where the larvae feed (Ponton and Fortier, 1992), in order to define the threshold plume thickness at which feeding becomes impossible. Predictions of global climate change models (Ingram et al., 1995) are used to speculate on the impact of climate warming on the feeding of fish larvae in coastal Hudson Bay.

#### 2. Materials and methods

Study area. Hudson Bay is a large shallow subarctic inland sea covered with annual ice from December to early June (Fig. 1). Residual circulation in the bay is cyclonic and slow  $(3-5 \text{ cm s}^{-1})$ (Prinsenberg, 1986; Lepage and Ingram, 1991). Biological production starts in early April when light becomes sufficient for algal biomass (mostly diatoms) to develop in the bottom few centimetres of the ice cover and at the ice-water interface (e.g. Gosselin et al., 1985; Michel et al.,



Fig. 1. Location of the sampling stations (A-E) off the mouth of the Great Whale River in southeastern Hudson Bay, Canada. Depth at stations A to E was 35, 65, 70, 100 and 140 m respectively. Isobaths are in metres.

1993). Some calanoid copepods emerge from winter diapause, mature and start reproducing as soon as ice algae develop (Drolet et al., 1991; Runge and Ingram, 1991; Runge et al., 1991). The phytoplankton bloom is triggered shortly after the breakup of the ice cover in early June (Drolet et al., 1991; Michel et al., 1993).

The study was conducted off the mouth of the Great Whale River in southeastern Hudson Bay (Fig. 1). In winter and spring, a 5-m thick brackish plume is formed under the ice-cover of the bay by the freshwater outflow of the river. River discharge, which averages ca. 170  $m^3 s^{-1}$  from February to April, increases to >1000 m<sup>3</sup> s<sup>-1</sup> during the freshet in May. At that time, the plume rapidly expands in a NNE direction from the mouth of the river and its surface increases to over 1000 km<sup>2</sup> (Ingram and Larouche, 1987). To cover the salinity and turbidity gradients associated with the Great Whale River plume, sampling stations ranging in depth from 35 to 140 m were positioned at intervals of about 5 km along a northward transect starting from the mouth of the river (Fig. 1). Four stations were occupied regularly in 1988 (A, B, C and D), 2 in 1989 (B and E) and 3 in 1990 (A, B and E) (Fig. 1).

Sampling. Details of the sampling methodology are given in Drolet et al. (1991), Gilbert et al. (1992) and Ponton et al. (1993). In summary, ice stations were reached by snowmobile every 2nd or 3rd day from mid April until the ice breakup in late May or early June. Vertical profiles of salinity and temperature were recorded at each station with a CTD. To estimate microzooplankton abundance, a 64- $\mu$ m mesh plankton net was towed from the bottom to the surface. To capture fish larvae, a sampler consisting of two plankton nets (500  $\mu$ m mesh, 1 m<sup>2</sup> mouth aperture, TSK flowmeters) mounted on a metal frame was towed horizontally at an average speed of 1.3 m s<sup>-1</sup>, over a distance of 200 m (1988, 1989) or 150 m (1990) between two apertures in the ice cover, using a heavy-duty snowmobile. Two free-wheeling spherical buoys mounted on the frame kept the sampler immediately under the ice cover to sample the 0.5-1.5 m depth interval in the brackish river plume. Removing the buoys allowed us to sample at 8-10 m. Both depth intervals (0.5-1.5

and 8-10 m) were sampled in succession at each station.

After the ice breakup, a helicopter mounted on floats or a small boat were used to reach ice-free areas in the vicinity of the original stations. Sampling was pursued at intervals of 2 days until mid June, except in 1989 when operations were terminated on 31 May. Temperature, salinity and microzooplankton were sampled as described above. Fish larvae and zooplankton were collected with a 1 m diameter conical net (500- $\mu$ m mesh) towed with the helicopter or the boat (first at 1 m and then at 8 m). All ice and open water stations were visited in daylight, between 09:00 and 19:00 h.

Zooplankton samples were preserved in 4% buffered formalin in seawater. To attenuate gut content evacuation, fish larvae were anaesthetized with MS-222 prior to fixation. All fish larvae were sorted from the 500-µm mesh samples. A subset of Arctic cod and sand lance larvae were taken at random from each sample for the determination of standard length and gut content. Prey were excised, measured (width and length) and identified whenever possible. Copepods and the microzooplankton prey of fish larvae were identified and enumerated in the  $64-\mu m$ mesh samples. Potential predators of fish larvae (large copepods such as Calanus glacialis and Metridia longa, chaetognaths, medusae and amphipods) were enumerated in both the 64- and 500-µm mesh collections. Potential predator densities in the 64- $\mu$ m (D64) and the 500- $\mu$ m (D500) were similar (D64 = 2.3 + 0.81 D500,  $r^2 = 0.61$ ) and the values for the  $64-\mu m$  mesh collections were used in the analysis.

The efficiency of fish larvae at capturing prey increases with their size, and body length is the first determinant of feeding incidence (percent larvae with food in gut) or feeding ratio (number of prey per gut) in Arctic cod and sand lance larvae (Fortier et al., 1995). Thus, the feeding of larvae of different lengths captured at different times in the season cannot be directly compared. In the present study, two length-independent indices of feeding success were calculated. First, feeding incidence (percentage of larvae with at least one prey in gut) was divided by the average length of the larvae in a tow. Second, the number of prey in the gut of a larva was divided by its length and this feeding ratio at length was averaged for a given tow. The two indices were strongly correlated (Arctic cod:  $r^2 = 0.738$ ; sand lance:  $r^2 = 0.906$ ) and represented essentially the same information. Accordingly, only the results of feeding incidence at length (henceforth termed feeding success) are presented.

Irradiance (PAR: 400-700 nm) at the snow surface, at the ice-water interface and at different depths down to 10 m in the water column was measured at different times in 1990. The reference probe of a Biospherical quantum meter was located at the surface of the snow while the underwater probe was positioned in the water column by a SCUBA diver. Light profiles were made away from the diving hole to avoid bias. Snow depth and ice thickness were recorded. Hourly values of sunshine and air temperature at Kuujjuarapik airport were supplied by the Atmospheric Environment Service of the Department of Environment Canada, and daily outflow data at the mouth of the Great Whale River (station 093801) by the Division des Réseaux Hydriques, Ministère de l'Environnement du Québec.

### 3. Results

3.1. Interannual variations in river discharge and plume dynamics

In response to unusually warm air temperatures in that year, the spring freshet of the Great Whale River and the break-up of the ice cover



Fig. 2. Southeastern Hudson Bay in spring. Time series of cumulated mean air temperature (sum of daily averages since 10 April divided by number of day) (a-c), time series of the Great Whale River (GWR) discharge (d-f), time-depth sections of temperature (g-i) and salinity (j-l) at station B, for 1988, 1989 and 1990.

occurred earlier in 1988 than in either 1989 or 1990 (Fig. 2). Cumulated mean air temperature (sum of average daily air temperature starting on 10 April divided by number of days) climbed above zero as early as mid April in 1988, but remained below freezing point until 20 June in 1989 and 1990 (Fig. 2a-c). Accordingly, the Great Whale River outflow started to swell around 20 April and reached its maximum on 12 May in 1988, ca. 11 days earlier than in 1989 (23 May) or 1990 (23 May) (Fig. 2d-f). The break-up of the ice cover on the bay started on 20 May in 1988, compared to 7 June and 5 June in 1989 and 1990 respectively.

Time-depth sections of salinity and temperature at station B illustrate the build-up and erosion of the Great Whale River plume in the surface layer of southeastern Hudson Bay during the spring and early summer of the three years (Fig. 2g-1). The brackish plume was separated from the deep marine layer (salinity > 25) by a steep halocline. Water temperature varied little as long as the ice cover persisted, with values of  $0^{\circ}$  C in the brackish river plume and  $-1^{\circ}$  C in the underlying marine layer (Fig. 2d-f). The influence of freshwater reached deeper in the water column in 1988 than in 1989 and 1990. For example, the depth of the 25 isohaline reached down to 10-15 m starting on 1 May 1988, but not below 8 m at any time in 1989 or 1990 (Fig. 2j-l).

A question that arises is whether the observed interannual differences in air temperature, discharge timing and discharge volume between 1988, 1989 and 1990 were typical of the long term record. Records of air temperature at Kuujiuarapik and Great Whale River discharge are available for the period 1976-1991. Over these 16 years, the average spring discharge of the Great Whale River from 1 April to 30 June was fairly well correlated with average air temperature for the same period, the scatter around the relationship being attributable to interannual differences in winter/spring precipitations (Fig. 3a). The timing of maximum swell in discharge was linked to average air temperature from 1 April to 15 May (Fig. 3b). With respect to average air temperature, 1988 was a record year (highest temperature) for the period 1976–1991 and, accordingly,



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83

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function of average air temperature from 1 April to 31 May, for the years 1976-1991 (a). Time of maximum swell in river discharge (calendar day for which the increase in discharge compared to the previous day was maximum) as a function of average air temperature from 1 April to 15 May, for the years 1976-1991 (b).

the volume and timing of the discharge were among the 3 largest and earliest on record respectively (Fig. 3). Average air temperature in 1990 was the lowest on record. Discharge in that year was intermediate in volume but among the latest in timing. In general, conditions were intermediate in 1989.

### 3.2. River freshet and turbidity in coastal Hudson Bay

The vernal increase in the Great Whale River discharge was accompanied by a sharp increase in the turbidity of the brackish plume immediately

600

500

а

under the ice cover of the bay. In 1990 for example, the coefficient of diffuse light attenuation at 2 m below the ice-water interface increased three-fold during the period from 16 to 23 May, when river discharge increased from 373 to 1620 m<sup>3</sup> s<sup>-1</sup> (Fig. 4). The extinction coefficient in the plume declined towards pre-freshet values by mid June despite continuing high discharges.

### 3.3. Predicting light available to fish larvae in the water column

Direct measurements of light in the water column were available for several dates from 20 April to 12 June 1990. Unfortunately, light measurements were not available for 1988 and 1989, and were not always simultaneous with the sampling of fish larvae in 1990. To palliate this, an empirical model based on sunshine at Kuujjuarapik airport (continuously recorded) and salinity (an index of turbidity) was developed to estimate the irradiance available in the water column at the time fish larvae were sampled. For the 0 to 10 m depth interval under the ice cover, the average coefficient of diffuse light attenuation prevailing



Fig. 4. Time series of the Great Whale River discharge and the coefficient of diffuse light attenuation (R) at 2 m under the ice-water interface at station B in southeastern Hudson Bay in the spring of 1990.



Fig. 5. (a) relationship between the coefficient of diffuse light attenuation (k) and salinity (S) in the 0–10 m depth interval (k = 0.53 - 0.0103S + 0.945/S, r = 0.92, n = 91, F = 290, P < 0.001) and (b) predicted irradiance at depth, based on sunshine at Kuujjuarapik airport and salinity at depth, versus observed irradiance in southeastern Hudson Bay in the spring of 1990.

above a given depth  $(k_w)$  was predictable from salinity at that depth (Fig. 5a). Using salinity at depth z to estimate  $k_w$ , the following equation was used to model  $I_z$ , the irradiance observed in 1990 at depth z under the ice-water interface:

$$I_z = 60.3(\text{SUN} + 1)e^{-k_W t}$$

where SUN is sunshine (in tenth of hour) at Kuujjuarapik airport. Irradiance at depth predicted by the model was well correlated to observed irradiance (Fig. 5b).

### 3.4. Turbidity and availability of prey to fish larvae

Arctic cod and sand lance larvae feed almost exclusively on copepod nauplii (Drolet et al., 1991; Gilbert et al., 1992; Ponton and Fortier, 1992; Fortier et al., 1995). Ponton et al. (1994) reported that the sharp increase in turbidity linked to the freshet in 1990 (Fig. 4) brought a 75% reduction in the density of copepod nauplii in the water column. In the present study, the availability of prey to fish larvae in spring over the three years of sampling was also linked to plume dynamics. For example, the density of copepod nauplii integrated over the entire water column was positively correlated to the irradiance at the base of the plume, an index of the turbidity and thickness of the plume (Fig. 6).

# 3.5. Feeding success of fish larvae in relation to prey and light availability

The standard length of Arctic cod and sand lance larvae sampled over the three years ranged from 4.3 to 9.8 and 4.6 to 12.3 mm respectively. For either species, average standard length varied by  $\leq 0.6$  mm among years (Fortier et al., 1995). The feeding success at length of Arctic cod larvae



Fig. 6. Density of copepod nauplii (N) as a function of predicted irradiance (I) at the base of the Great Whale River plume ( $N = 1.41 \times 10^6 + 2887I$ , r = 0.59, n = 61, F = 18.2, P = 0.0001). Data for the three sampling years (1988, 1989, 1990) were pooled.



Fig. 7. Boreogadus saida. (a) the Ivlev function relating feeding success of Arctic cod larvae (FS, feeding incidence in sample divided by average standard length of larvae) to nauplii density (N, integrated from bottom to surface) (FS =  $-3.3+20.4(1-e^{-0.000032N})$ , r=0.73, n=44, F=38.4, P <0.0001). (b) linear regression between the residuals of the Ivlev function (R) and predicted irradiance (I) at the base of the Great Whale River plume (R = -2.5 + 0.49I, r = 0.41, n=44, F=8.6, P = 0.0055). Data from 1988, 1989 and 1990 were pooled. Only those collections representing five larvae or more were considered in the analysis.

in relation to prey density was adequately described by an Ivlev function (Ivlev, 1961) (Fig. 7a). Feeding success tended towards zero at densities of nauplii  $< 15 \times 10^3$  m<sup>-2</sup> and reached a plateau at nauplii densities  $> 40 \times 10^3$  m<sup>-2</sup>. Yet, there was much scatter around the Ivlev function which explained 53% of the variability in feeding suc-

cess. Arctic cod and sand lance larvae feed in the sharp halocline that separates the plume of the Great Whale River from the underlying marine layer (Ponton and Fortier, 1992). Thus, irradiance at the depth of the 25 isohaline can be used as an index of the light available to fish larvae feeding at the base of the plume. The residuals of the Ivlev function linking the feeding success of Arctic cod larvae to nauplii density (Fig. 7a) were linearly correlated with irradiance at the base of the plume (Fig. 7b). Similar results were obtained for sand lance larvae (Fig. 8).

Thus, both the density of nauplii in the water column and the light available at the base of the plume contributed to determine the feeding success of Arctic cod and sand lance larvae. For both species, the relation between feeding success and the product of nauplii density by irradiance was well described by an Ivlev function (Fig. 9). The model explained 64 and 76% of the variance in the feeding success of Arctic cod and sand lance larvae respectively.

### 3.6. Sampling depth, time of day, temperature and potential predators

Few Arctic cod and sand lance larvae were captured in the surface brackish layer. On nine occasions, sufficient numbers of sand lance larvae (i.e.  $\geq 5$  larvae) were captured to calculate reliable feeding indices at both sampling depths at the same station on the same day. On these nine occasions, there was no significant difference in feeding incidence or feeding ratio between the 0.5–1.5 m and the 8–10 m layers (paired comparison, n = 9,  $t \leq 1.3$ ,  $P \geq 0.23$ ). Sufficient numbers of Arctic cod larvae were captured at both depths on four occasions only, too few to conduct the same analysis for this species.

There was no relationship between feeding success or the residuals of the above Ivlev model and hour of the day for Arctic cod or sand lance (linear or hyperbolic regression:  $P \ge 0.53$ ). The regression between the residuals of the Ivlev model and temperature at the base of the plume was not significant for either species ( $P \ge 0.110$ ). None of the twelve regressions calculated between the residuals of the Ivlev model and indi-



Fig. 8. Ammodytes sp. (a) the Ivlev function relating feeding success of sand lance larvae (FS, feeding incidence in sample divided by average standard length of larvae) to nauplii density (N, integrated from bottom to surface) ( $FS = -0.5 + 12.7(1 - e^{-0.000073N})$ , r = 0.76, n = 44, F = 35.2, P < 0.0001). (b) linear regression between the residuals of the Ivlev function (R) and predicted irradiance (I) at the base of the Great Whale River plume (R = -0.7 + 0.128I, r = 0.44, n = 44, F = 10.0, P = 0.0029). Data from 1988, 1989 and 1990 were pooled. Only those collections representing five larvae or more were considered in the analysis.

vidual predator density or total predator density was significant, except that between the residuals for Arctic cod and the density of the large copepod *Metridia longa*, which was marginally significant (P = 0.02). The slope of the regression was negative as expected under the hypothesis that



Fig. 9. Boreogadus saida and Ammodytes sp. The Ivlev function relating feeding success (FS, feeding incidence in sample divided by average standard length of larvae) to actual prey availability (NxI, density of nauplii × irradiance) in Arctic cod (FS =  $18.4(1 - e^{-0.0039N \times I})$ , r = 0.80, n = 44, F = 85.2, P < 0.0001) and sand lance larvae (FS =  $7.1(1 - e^{-0.00175N \times I})$ , r = 0.87, n = 44, F = 111.8, P < 0.0001). Data from 1988, 1989 and 1990 were pooled. Only those collections representing five larvae or more were considered in the analysis.

avoidance of *Metridia longa* interfered with the foraging of Arctic cod larvae.

### 3.7. Feeding success of fish larvae and plume thickness

The thickness of the Great Whale River plume, as measured by the depth of the 25 isohaline, influenced the availability of both light and prey to foraging fish larvae (Fig. 10a, b). The product of nauplii density by irradiance dropped abruptly when the depth of the 25 isohaline exceeded the threshold value of ca. 9 m (Fig. 10c) and, accordingly, the feeding success of Arctic cod and sand



Fig. 10. Density of nauplii (a), predicted irradiance at base of plume (b), actual prey availability (density of nauplii  $\times$  irradiance) (c), and feeding success of Arctic cod *Boreogadus saida* (d) and sand lance *Ammodytes* sp. larvae (e) in function of the depth of the 25 isohaline. Only those collections representing five larvae or more were considered in (d) and (e).

lance larvae then dropped to zero (Fig. 10d, e). Low values of irradiance, density of nauplii, and larval fish feeding success occurred when the depth of the 25 isohaline was less than the 9 m threshold in all three sampling years. Limitation of feeding success attributable to unusually large plume thickness occurred in 1988 exclusively, the only one of the three years sampled when the depth of the 25 isohaline exceeded the 9 m threshold (Fig. 2j).

### 4. Discussion

### 4.1. Biotic and abiotic control of larval fish feeding success in ice-covered seas

Prey density (Crecco and Savoy, 1984; Gadomski and Boehlert, 1984; Fortier et al., 1995), light (Dabrowski, 1985; Gilbert et al., 1992; Ponton and Fortier, 1992; Miner and Stein, 1993), turbulence (Rothschild and Osborn, 1988; Sundby and Fossum, 1990; MacKenzie and Leggett, 1991), temperature (e.g. Paul, 1983), and the presence of predators (Mathias and Li, 1982; Fortier and Harris, 1989; Brown et al., 1994) can potentially affect the feeding success of competent fish larvae.

In the present study, plume thickness reduced not only the light available to fish larvae at the base of the plume but also the density of nauplii in the water column. At the time of the freshet in 1990, the expansion of the plume drastically decreased the concentration of chlorophyll a in the brackish plume (Ponton et al., 1994). This decrease in chlorophyll a coincided with a three-fold decrease in the density of small cyclopoid copepods in the surface layer. These cyclopoid copepods are the main producers of nauplii in spring under the ice cover of Hudson Bay (Fortier et al., 1995). Thus, the reduction of chlorophyll a at the time of the freshet was associated with a > 5-fold decline in prey availability to fish larvae (Ponton et al., 1994). On a seasonal scale, chlorophyll a concentration in the surface layer is best correlated with air temperature, an index of the vernal increase in incident light and the decline in ice

cover thickness (Legendre et al., 1996). Our results lead to the hypothesis that, in addition to incident light and ice cover thickness, plume dynamics also affect phytoplankton abundance and, hence, prey availability to fish larvae at the seasonal and interannual scales.

Previous studies have emphasized the role of light (in complement to prey density) in determining the feeding success of fish larvae in spring in southeastern Hudson Bay. Gilbert et al. (1992) reported that light attenuation following the expansion of the Great Whale River plume completely halted the feeding activity of sand lance larvae under the ice cover. Feeding resumed in sand lance — and started in Arctic cod — at the ice breakup when the fragmentation of the ice cover allowed for the direct penetration of light at depth. Under the ice cover, Arctic cod larvae were shown to concentrate at the sharp halocline separating the river plume from the underlying marine layer (Ponton and Fortier, 1992). Maximum feeding ratio coincided with maximum prey availability (i.e. prey density x irradiance) immediately under the halocline (Ponton and Fortier, 1992).

In the present study, the Ivlev model relating feeding success to actual prev availability (prev density  $\times$  irradiance) explained the greater part of the variance in the feeding success of Arctic cod and sand lance larvae (64 and 76% respectively). Given that irradiance at the base of the plume was not directly measured but rather derived from sunshine at Kuujjuarapik airport and salinity (an index of turbidity), the model performed remarkably well in explaining larval fish feeding success under the ice. Although variable among species and developmental stages, the threshold value at which light begins to limit larval fish feeding and growth probably lies in the range 50-1000 lux (e.g. Blaxter, 1986; Chesney, 1989; Huang and Hu, 1989; Miner and Stein, 1993), corresponding roughly to 1–20  $\mu$ mole photons  $m^{-2}$  s<sup>-1</sup> for the 400–700 nm wavelength range (Thimijan and Heins, 1983) to that the eye of fish larvae is sensitive (Blaxter, 1975). Consistent with these values, our results indicate that the feeding of Arctic cod and sand lance larvae was limited by light over the range  $0-16 \mu$  mole

photons  $m^{-2} s^{-1}$  that prevailed under the ice cover of Hudson Bay (Figs. 7 and 8).

Turbulence may increase the encounter rate between fish larvae and their prey (Rothschild and Osborn, 1988; Sundby and Fossum, 1990; MacKenzie and Leggett, 1991). In the Norwegian Sea, the relationship between the feeding ratio of Atlantic cod larvae (Gadus morhua) and prey density was adequately described by an Ivlev function (Ellertsen et al., 1989; Sundby and Fossum, 1990). The variance in feeding ratio that was not accounted for by prey density was considerably reduced when the level of wind-generated turbulence was introduced in the model (Sundby and Fossum, 1990). Because the ice cover prevents any mixing of the surface layer by wind (Lepage and Ingram, 1991), wind-generated turbulence is unlikely to play a major role in determining the feeding success of fish larvae dispersed in ice-covered seas. Similarly, by isolating the surface layer from atmospheric influence, the ice cover prevents any substantial interannual variations in the thermal regime of the water column in winter and spring. In the present study, the low water temperature  $(-1^{\circ} C)$  prevailing at and below the base of the plume where fish larvae feed, varied little ( $< 0.4^{\circ}$  C) between years (Fig. 2). Accordingly, temperature did not contribute significantly towards explaining variations in feeding success.

Finally, field and laboratory studies suggest that a trade-off between predator avoidance and foraging could decrease the rate of capture of prey by first-feeding fish larvae (e.g. Mathias and Li, 1982; Fortier and Harris, 1989; Brown et al., 1994). Potential planktonic predators of fish larvae such as large copepods, chaetognaths, medusae and amphipods (see Bailey and Houde, 1989, for a review) were relatively scarce under the ice cover of Hudson Bay (on average 14.1  $m^{-3}$ , sum of all taxa; see also Ponton and Fortier, 1992). Low abundance of predators in spring contrasts with the summer months, which are characterized by swarms of medusae and other gelatinous zooplankton (D. Ponton, pers. obs.) Matching the production of the larvae with this reduced abundance of planktonic predators could be a major selective pressure driving some fish species

to reproduce early in subarctic seas (Bollens et al., 1992; Fortier et al., 1995). In the present study, we found little evidence that predator avoidance reduced the feeding success of fish larvae. Once the effect of prey density and light on feeding success was removed, predator density appeared significant in explaining the residual variation in feeding in only one of the twelve cases examined.

### 4.2. Freshwater inputs and interannual fluctuations in the feeding success of fish larvae under the ice cover of Hudson Bay

By affecting both prey density and light, the thickness of the Great Whale River plume was the main determinant of larval fish feeding success under the ice cover of southeastern Hudson Bay. Low values of feeding success were not distributed at random among the three years of sampling but occurred primarily in 1988, the only year when the thickness of the plume exceeded the 9 m threshold above which fish larvae stopped feeding. By comparison to 1990, fish larvae experienced particularly harsh feeding conditions in 1988. In that year, an interruption of feeding in sand lance larvae coincided with the expansion of the plume, and Arctic cod larvae did not initiate feeding until the ice breakup (Gilbert et al., 1992). Feeding incidence and mean feeding ratio at length were four- and two-fold lower in 1988 than in 1990 for Arctic cod and sand lance larvae respectively (Fortier et al., 1995). The postlarvae of both species became emaciated in the days that preceded the ice breakup in 1988 (Drolet et al., 1991) and, based on average length at date, growth was significantly reduced in both species relative to 1990 (Fortier et al., 1995). We conclude that unusually high river plume thickness associated with warm air temperature can have a major detrimental impact on the early feeding, growth, and survival of Arctic cod and sand lance larvae by reducing light and prey availability in the coastal zone. The importance of turbidity in controlling light and the distribution and/or feeding success of fish larvae has been well documented for freshwater and estuarine systems (e.g. Crecco and Savoy, 1984; Matthews, 1984; Crecco and Savoy, 1985; Chesney, 1993). In the Connecticut River, enhanced early growth and survival as well as strong year classes of American shad (*Alosa sapidissima*) have been related to low river discharge, reduced turbidity and increased zooplankton densities (Crecco and Savoy, 1984, Crecco and Savoy, 1985), a situation very similar to that found in southeastern Hudson Bay.

Thanks to Serendipity, the range of climatic conditions observed from 1988 to 1990 in the present study spanned the extremes observed over the period for which records are available (1976–1991, Fig. 3). Thus, the feeding conditions experienced by fish larvae in 1988 and 1990 can be expected to be among the worst and the best possible respectively, under the present climatic regime.

# 4.3. Global warming and the feeding success of fish larvae in coastal Hudson Bay

Our results underscore the importance of air temperature in determining the timing and intensity of the spring freshet and the feeding conditions experienced by fish larvae under the ice cover of coastal Hudson Bay. Models of global climate change forecast substantial increases in winter/spring air temperature over Hudson Bay in response to a doubling of atmospheric carbon dioxide  $(2 \times CO_2)$ . For example, the Global Circulation Model of the Canadian Climate Centre predicts an increase in air temperature of 9° C in winter (Dec, Jan, Feb) and 4°C in spring (Mar, Apr, May) (Ingram et al., 1995). This warming of the atmosphere will hasten both the freshet of rivers and the breakup of the sea ice cover by 3-4weeks, so that the bay would still break about 2-3weeks after the rivers (Ingram et al., 1996). The model also predicts an increase in precipitation of 15 and 20% in winter and spring respectively, but errors associated with these predictions are of the same order of magnitude than the predictions themselves. Finally, based on the ice model of Wang et al. (1994) for Hudson Bay, Ingram et al. (1995) calculated that a doubling of atmospheric CO<sub>2</sub> will result in a 35% reduction of ice thickness in Hudson Bay.

Assuming that thick river plumes under the ice cover of coastal Hudson Bay are a correlate of warm air temperature and early freshet (as suggested by our results), the predicted increase in air temperature under a  $2 \times CO_2$  scenario would result in poor feeding conditions for fish larvae. Conditions comparable to, or worse than, those of 1988 (when the freshet occurred eleven days earlier than average), could be expected if the freshet was hastened by 3–4 weeks.

Could the modification of the light regime at depth due to changes in snow depth and ice cover thickness compensate for the increase in plume thickness? To assess the potential impact of an increase in precipitations and/or a decrease in ice thickness, we modelled the contribution of snow and ice to the attenuation of light at depth. The following equation was used to model  $I_z$ , the observed irradiance at depth z under the ice-water interface as a function of snow depth (SD), ice thickness (IT) and depth under the ice cover (Z):

### $\operatorname{Ln}(I_z/I_0) = -k_{\rm S}SD - k_{\rm I}IT - k_{\rm W}Z$

where  $I_0$  is the irradiance at the surface of the snow and  $k_s$ ,  $k_I$  and  $k_W$  are the coefficients of diffuse light attenuation prevailing in the snow, the ice and the water respectively. Fitting the model to the observed data (Ln observed  $I_z = 0.96$ Ln predicted  $I_z$ ,  $r^2 = 0.66$ , n = 76) yielded values of 10.7, 3.3 and 0.26 m<sup>-1</sup> for  $k_s$ ,  $k_I$  and  $k_W$ respectively. Average (±standard deviation) snow depth and ice thickness in the sampling area over the three years were 0.035 (±0.04) and 1.31 (±0.074) m respectively (n = 76). Based on the above equation, the predicted increase of 20% in snow depth would result in a 7% decrease in irradiance at a given depth, while a 35% decrease in ice thickness would result in a 354% increase.

Assuming that Arctic cod and sand lance adapt to an earlier breakup and modify their spawning season in such a way that the larvae start feeding in the second half of April instead of the second half of May, the above equation enables us to estimate the light available to the larvae under new climatic conditions. Let us first examine the scenario in which plume thickness does not increase with a doubling of atmospheric  $CO_2$ . Based on the average incident irradiance observed in the second half of both April and May over the three years (2131 and 2061  $\mu$  mole photons m<sup>-2</sup>  $s^{-1}$  respectively), irradiance at the base of the standard plume (5.6 m, i.e. the average depth of the 25 isohaline in 1989 and 1990) would increase from 4.4 (in the second half of May with normal ice thickness) to 20.6  $\mu$  mole photons m<sup>-2</sup> s<sup>-1</sup> (in the second half of April with 35% reduction of ice thickness). The maximum estimate of the threshold at which larval fish feeding becomes limited is ca. 20  $\mu$  mole photons m<sup>-2</sup> s<sup>-1</sup> (see above). Assuming that neither incident light nor plume thickness will be affected by the predicted increase in air temperature, we conclude that the feeding of Arctic cod and sand lance larvae in coastal Hudson Bay would no longer be limited by light in the event of a 35% reduction in ice thickness due to global warming. Now let us assume that plume thickness would increase with a doubling of atmospheric CO<sub>2</sub>. If the average depth of the 25 isohaline increased to 12 m (the average for 1988), predicted average irradiance at the base of the plume under the reduced ice cover would be 3.9  $\mu$  mole photons m<sup>-2</sup> s<sup>-1</sup>, a level that would clearly limit larval fish feeding. Thus, the reduced ice cover in the second half of April would not compensate for a deepening of the 25 isohaline from 5.6 to 12 m.

#### 5. Conclusions

Our analysis of the impact of freshwater inputs on the feeding of marine fish larvae in the coastal zone of southeastern Hudson Bay revealed a potentially strong link between climate and recruitment in Arctic cod and sand lance. Given the central importance of the two species in the Arctic and subarctic marine food web (Bradstreet et al., 1986; Ponton et al., 1993), interannual variations in the pattern of freshwater inputs to Hudson Bay could significantly affect the transfer of energy from the plankton to the upper trophic levels (including man). Note, however, that the actual impact of freshwater inputs on the early survival and recruitment of the two species will be proportional to the fraction of the larval dispersal area that is affected by river plumes (Ponton et al., 1993). The actual dispersal area of Arctic cod and sand lance larvae under the ice cover of Hudson Bay in spring remains to be assessed. If most of it is affected by river plumes, we would predict that, by affecting the feeding success and early survival of the two species, natural and/or anthropogenic modifications of the river flow regime in spring will have a significant impact on the global productivity of Hudson Bay. This impact will not necessarily be negative, in particular if it involves a reduction in ice cover or plume thickness.

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### Impact of freshwater on a subarctic coastal ecosystem under seasonal sea ice (southeastern Hudson Bay, Canada). III. Feeding success of marine fish larvae \*

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