Polar Biol (1993) 13: 321-331

Polar Biology
© Springer-Verlag 1993

Production and dispersion of freshwater, anadromous, and marine fish larvae in and around a river plume in subarctic Hudson Bay, Canada

D. Ponton[1]*, J.A. Gagné[2], L. Fortier[1]

[1] Département de biologie, Université Laval, Ste-Foy, Québec, Canada G1K 7P4
[2] Ministere des Pêches et des Océans, Institut Maurice Lamontagne, C.P. 1000, Mont-Joli, Québec, Canada G5H 3Z4

Received: 17 July 1992 / Accepted: 30 December 1992

Abstract. From 1988 to 1990, fish larvae were sampled before, during, and after ice breakup within and outside the plume of the Great Whale River off Kuujjuarapik, southeastern Hudson Bay, Canada. Arctic cod (*Boreogadus saida*) and sand lance (*Ammodytes* spp.) were the most abundant larvae. Half of the larval fish taxa emerged before the ice broke up in the Bay. The highest densities of Arctic cod, sand lance, slender eelblenny, and gelatinous snailfish larvae were in salinities exceeding 25 practical salinity units (p.s.u.). Arctic shanny, sculpins, and capelin larvae were more abundant at salinities between 1 and 25 p.s.u.. Burbot and coregonid larvae were clearly associated with fresh or brackish waters even when caught in the Bay. The timing and extent of the Great Whale River freshet influenced the distribution of marine fish larvae in southeastern Hudson Bay and determined the moment when the larvae of anadromous and freshwater species entered the Bay.

Arctic and subarctic seas are characterized by a short season of production which begins with the development of ice algae at the ice bottom (Apollonio 1961; Horner 1976; Alexander 1980). Fish larvae emerging in these environments often present a protracted larval phase due to poor feeding conditions and slow growth (Houde 1989). Because of this slow development and the short production season, fish larvae are presumably more likely to encounter adverse environmental conditions at these high latitudes than at lower latitudes (Houde 1989). Hence, the timing of spawning (Cushing 1975) and the selection of favorable spawning sites by adults (Iles and Sinclair 1982) should be particularly critical for the recruitment success of fish species inhabiting Arctic and subarctic environments.

Hudson Bay is a large subarctic inland sea usually covered by ice from December to early June (Markham 1986; Larouche and Galbraith 1989). Several studies have been conducted on the distribution and basic biology of adult fish in this area (Vladykov 1933; Hunter 1968; Auger and Power 1978; Morin et al. 1980; Morin and Dodson 1986) especially for anadromous coregonids (Dymond 1933; Kemp et al. 1989; Morin et al. 1981). Yet, except for a study of the ichthyoplankton assemblage of the Eastmain River estuary, James Bay (Ochman and Dodson 1982), the early life history of both marine and anadromous species in the general area of Hudson Bay is poorly known.

In southeastern Hudson Bay primary and secondary production dynamics have been intensively studied (Gosselin et al. 1985, 1986, and 1990; Legendre et al. 1981 and 1989; Runge and Ingram 1988; Runge et al. 1991; Tourangeau and Runge 1991). Research on the early life history stages of fish has been initiated only recently and has focused on the survival (Drolet et al. 1991), feeding success (Gilbert et al. 1992), and vertical distribution (Ponton and Fortier 1992) of marine fish larvae in relation to light and food availability under the ice cover.

In this paper we present the seasonal occurrence and general distribution of the larval stages of freshwater, anadromous and marine fish sampled in and around the plume of the Great Whale River in the spring and early summer of 1988, 1989 and 1990. In particular, we relate the timing of the emergence of the different species to the development of the river plume and the breakup of the ice cover in the Bay. Previous information on the spawning strategy and early life history of Arctic and subarctic fish is reviewed and discussed in the light of this new data set.

Materials and methods

Study area

The waters of southeastern Hudson Bay are strongly influenced by freshwater inputs from rivers. The Great Whale River (Fig. 1) is one

Contribution to the research programs of GIROQ (Groupe interuniversitaire de recherches océanographiques du Québec) and Institut Maurice Lamontagne (Department of Fisheries and Oceans, Canada)

**Present address:* ORSTOM, Institut Français de Recherche Scientifique pour le Développement en Coopération, BP 165, 97323 Cayenne-Cedex, Guyane Française, France

Correspondence to: D. Ponton

Fonds Documentaire ORSTOM
010009843

Fonds Documentaire ORSTOM
Cote : B * 9843 Ex : 1

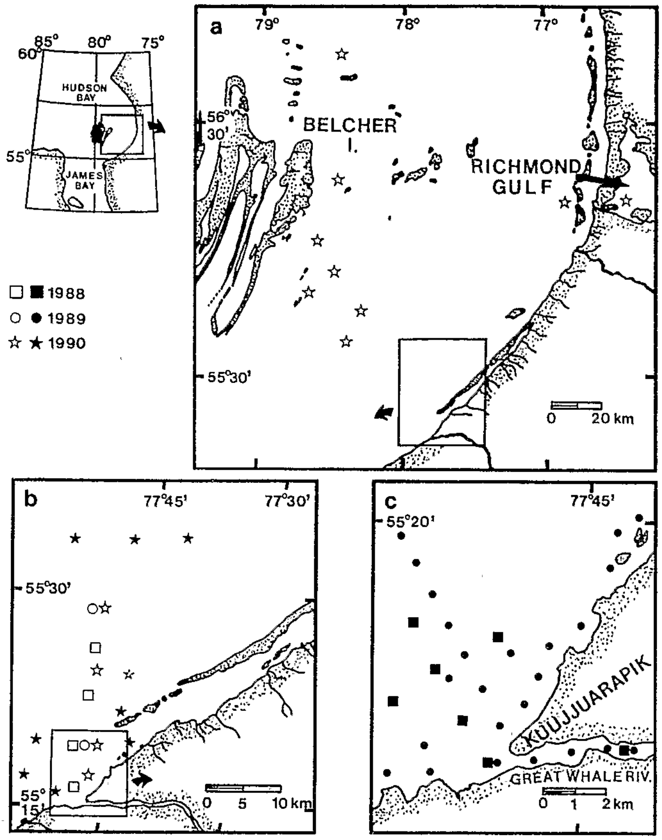

Fig. 1. Sampling stations in southeastern Hudson Bay, Canada. *Open symbols*: location of underice sampling with snowmobiles (UIS) and open-water sampling by helicopter (HS). *Solid symbols*: open water stations sampled from a boat (BS)

of the most important sources of freshwater in the Bay. At the freshet in May, its outflow increases from 135–200 $m^3 \cdot s^{-1}$ to ca. 900 $m^3 \cdot s^{-1}$, forming a plume that extends NNE under the ice of the Bay over a 1000 km^2 area (Ingram 1981; Ingram and Larouche 1987). Ice generally breaks up around May 20 in the Great Whale River (Wilson 1973), i.e., about 10 days earlier than in the Bay itself off Kuujjuarapik. Once the pack-ice has broken up, increased wind stress and larger tidal flow induce rapid mixing of the plume waters with the underlying saline waters, hence reducing stratification in the Bay (Lepage and Ingram 1991).

Sampling techniques and data treatment

Two to four stations located on a 20-km transect heading northward from the mouth of the Great Whale River were sampled before, during and after ice breakup (April to June) in 1988, 1989, and 1990 (Fig. 1b). As ice broke up, open-water stations were added in the lower part of the River and along the Kuujjuarapik coastal area (Fig. 1c). Several ichthyoplankton samples were obtained also in the Richmond Gulf and Belcher Islands areas in June 1990 (Fig. 1a).

Sampling methods were adjusted for changes in ice-cover conditions (Table 1). Under ice cover, two 1 m^2, 500 μm mesh plankton nets fitted side by side on a rectangular metal frame were used to sample horizontally at depths of 0–2 m and ca. 6–8 m (ca. 8–10 m in 1988). These nets were attached to a cable forming a loop between two holes separated by 150 m (200 m in 1988) and towed with a heavy-duty snowmobile. After ice breakup, a 1 m diameter, 500 μm mesh conical net with an 80 μm mesh rigid codend was towed at

Table 1. Characteristics of sampling for each period. UIS: underice sampling, HS: helicopter sampling, and BS: boat sampling (see explanation in text)

Year	1988			1989			1990		
sampling periods	24 Apr to 27 May	23 May to 14 Jun	20 May to 13 Jun	19 Apr to 30 May	31 May to 9 Jun	16 Jul to 20 Jul	21 Apr to 2 Jun	3 Jun to 11 Jun	1 Aug to 7 Aug
type of sampling	UIS	HS	BS	UIS	BS	BS	UIS	HS	BS
number of stations	4	4	3	2	6	28	3	13	22
sampling depth (m)	0–2 and 8–10	0–2 and 8–10	0–2	0–2 and 6–8	0–2	0–2	0–2 and 6–8	0–2 and 6–8	7 to 26
total number of samples	59	74	83	58	41	46	79	46	37
mean sampling speed ($m \cdot sec^{-1}$) ±SD	1.1±0.2	1.0±0.2	1.5±0.1	1.1±0.1	1.0±0.2	1.2±0.3	0.9±0.2	0.6±0.3	0.8±0.2
total effort (min)	187	894	769	127	411	460	235	326	465
mean volume of water filtered per sample (m^3) ±SD	371±29	539±144	653±147	284±28	527±38	496±66	324±37	342±104	356±113

similar depths from a float-mounted helicopter that alighted in ice-free areas near the sampling locations. Details of both underice (UIS) and helicopter (HS) sampling are described in Drolet et al. (1991) and Gilbert et al. (1992). In ice-free conditions, a 1 m diameter, 6 m long and 500 μm mesh size net was pulled by a 35 HP power-boat. Boat sampling (BS) was limited to the surface layer (0–2 m) except in August 1990 when a more powerful boat equipped with a winch allowed sampling between 7 and 26 m depths using the same net. Filtered volume was measured with a calibrated TSK flowmeter installed in the center of the net opening. Depending on the sampling technique, nets were towed from 3 to 15 min and average filtered volumes ranged from 284 m^3 to 653 m^3 (Table 1). All samples were preserved in 4% neutralized formalin.

A CTD profile was obtained with a portable Seacat probe before plankton sampling at each station. Temperature (° C) and salinity (practical salinity units p.s.u.) values were later associated with each ichthyoplankton sample. They were calculated as the arithmetic means of the observations in a 2 m thick water layer corresponding to the plankton sampling depth.

All larvae were sorted, counted and measured to the nearest 0.1 mm. Most of marine fish larvae were identified according to Fahay (1983). Other descriptions used were from Dunn and Vinter (1984) for *Boreogadus saida*, Faber (1976) for Stichaeidae and Lumpenidae, Cucin and Faber (1985) for *Coregonus clupeaformis*, *C. artedii* and *Lota lota*, Auer (1982) for other freshwater species and Khan (1971) for larvae of *Myoxocephalus* spp.

Results

Temperature and salinity

Our sampling design allowed us to cover most of the temperature-salinity conditions existing in spring and summer in the coastal area of southeastern Hudson Bay. Under the ice cover in April–May, the cold (< -1°C) and saline (>25 p.s.u.) marine layer mixed little with the warmer (>0°C) and brackish (<5 p.s.u.) plume of the Great Whale River (Fig. 2a). Mixing increased in June when ice broke up in the Bay (Fig. 2b). The July-August period presented a classical estuarine situation where the warm freshwater progressively mixed with the cold, marine Hudson Bay water (Fig. 2c).

Larval fish community

Individuals from 21 species belonging to 12 families were caught over the three-year period (Table 2). Arctic cod (*Boreogadus saida*) and sand lance (*Ammodytes* spp.) contributed 50.4% and 37.9% of the total respectively. Burbot (*Lota lota*), Stichaeidae (Arctic shanny, *Stichaeus punctatus* and slender eelblenny, *Lumpenus fabricii*), Cottidae (Arctic staghorn sculpin *Gymnocanthus tricuspis* and other sculpins *Myoxocephalus* spp.), Cyclopteridae (gelatinous snailfish, *Liparis fabricii*) and Osmeridae (capelin, *Mallotus villosus*) were one order of magnitude less abundant. Salmonidae represented 0.25% of the larvae with 26 cisco (*Coregonus artedii*) and 6 lake whitefish (*C. clupeaformis*). Other species were scarcer.

Seasonal occurrence and abundance

Larvae from 56% of the fish taxa emerged before the ice breakup in the Bay (Fig. 3). Arctic cod (*Boreogadus saida*) and sand lance (*Ammodytes* spp.) were first to appear at the end of April and persisted throughout each sampling period. Hatching of Arctic cod probably began earlier than our sampling as some individuals were present in the very first collections (Fig. 3). Larvae of burbot (*Lota lota*) and coregonid (*Coregonus* spp.) which hatched in the Great Whale River, first occurred in the Bay in early and late May respectively, i.e. generally just before and after ice breakup in the River. Larvae of two freshwater species, lake chub (*Couesius plumbeus*) and longnose sucker (*Catostomus catostomus*), occurred in July in the lower part of the River. Hatching of Arctic alligator fish eggs (*Aspidophoroides olkiri*) probably began in early June as some yolk-sac larvae were sampled at that time. Capelin (*Mallotus villosus*) and Greenland cod (*Gadus ogac*) larvae did not occur until July.

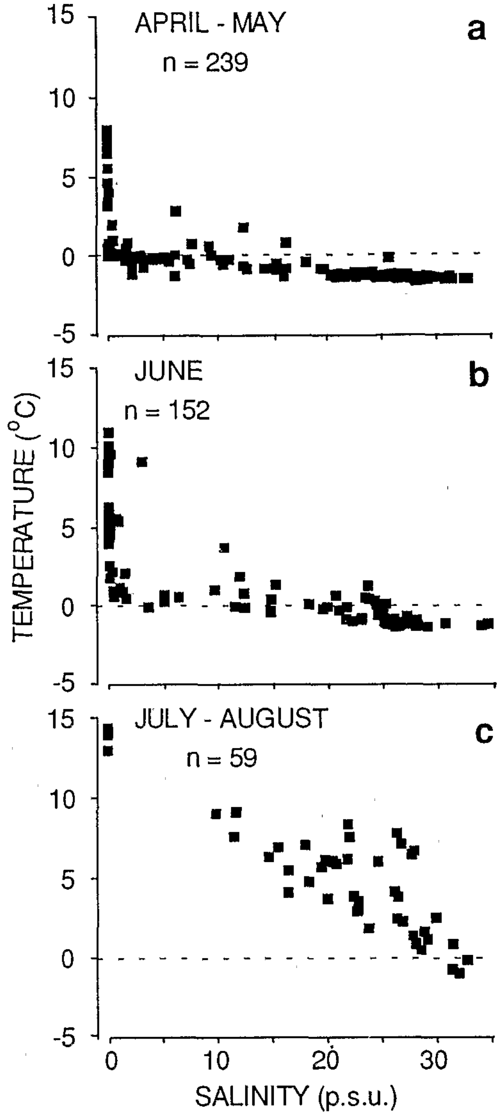

Fig. 2a–c. Temperature-salinity values observed at depths of ichthyoplankton sampling in April–May (**a**), June (**b**), and July–August (**c**)

Arctic cod (*Boreogadus saida*) and sand lance (*Ammodytes* spp.) densities ranged between 5 and 50 larvae per

Table 2. List of the larval fish species caught in the southeastern coastal zone of Hudson Bay and in the Great Whale River. Uncertain identifications are in brackets

Scientific name	Common name	Total number captured
Salmoniformes		
Salmonidae		
Coregoninae		
Coregonus artedii LeSueur, 1818	cisco	26
C. clupeaformis (Mitchill, 1818)	lake whitefish	6
Osmeridae		
Mallotus villosus (Müller, 1777)	capelin	88
Cypriniformes		
Cyprinidae		
[*Couesius plumbeus* (Agassiz, 1850)]	[lake chub]	3
Catostomidae		
Catostomus catostomus (Forster, 1773)	longnose sucker	4
Gadiformes		
Gadidae		
Boreogadus saida (Lepechin, 1774)	Arctic cod	6420
Gadus ogac Richardson, 1836	Greenland cod	5
Lota lota (Linnaeus, 1758)	burbot	334
Perciformes		
Stichaeidae		
Lumpenus [*fabricii*] (Valenciennes, 1836)	[slender eelblenny]	148
Stichaeus punctatus (Fabricius, 1780)	Arctic shanny	498
Pholidae		
Pholis [*fasciata*] (Bloch and Schneider, 1801)	[banded gunnel]	1
Ammodytidae		
Ammodytes spp.		
[*A. americanus* DeKay, 1842 and *A. dubius* Reinhardt, 1838]	[American sand lance and northern sandlance]	4830
Cottidae		
Gymnocanthus tricuspis (Rheinhardt, 1832)	Arctic staghorn sculpin	102
Icelus sp.		
[*I. bicornis* (Reinhardt, 1841) or *I. spatula* Gilbert and Burke, 1912]	[two-horn sculpin or spatulate sculpin]	4
Myoxocephalus quadricornis (Linnaeus, 1758)	fourhorn sculpin	152
M. scorpioides (Fabricius, 1780)	Arctic sculpin	
M. scorpius (Linnaeus, 1758)	shorthorn sculpin	
Triglops sp.		
[*T. murrayi* Günther, 1888 or *T. pingeli* Reinhardt, 1832]	[moustache sculpin or ribbed sculpin]	9
Agonidae		
Aspidophoroides olriki Lütken, 1876	Arctic alligatorfish	6
Cyclopteridae		
Liparis [*fabricii*] Kroyer, 1847	[gelatinous snailfish]	90
Pleuronectiformes		
Pleuronectidae		
Hippoglossoides platessoides (Fabricius, 1780)	American plaice	19

100 m^3 (Fig. 4a and b). Arctic cod densities sometimes exceeded 100 larvae per 100 m^3 (Fig. 4a) and the maximum (470 larvae per 100 m^3) was observed at a station off the Gulf of Richmond. Other species seldom reached densities in excess of $5 \cdot 100\ m^{-3}$. *Coregonus* spp. larvae were always scarce in the Bay or the River where densities never exceeded $1 \cdot 100\ m^{-3}$ (Fig. 4j).

Larval abundance, water salinity and temperature

Larval distribution with respect to salinity and temperature varied between species and over time (Table 3). The highest densities of sand lance (*Ammodytes* spp.) larvae were always found in cold waters of salinity exceeding 25 p.s.u.. Similar trends were observed for gelatinous snailfish (*Liparis fabricii*). Arctic cod (*Boreogadus saida*) and slender eelblenny (*Lumpenus fabricii*) larvae were more abundant in waters of intermediate to high salinity (15–25 p.s.u.) and low temperature (−1.3 to 0.8°C) in April–May (Table 3, Wilcoxon test, $P = 0.049$). In June, both Arctic cod and sand lance larvae were much more abundant at salinities >25 p.s.u. and found only in small numbers, albeit regularly, in warmer waters of low salinity (Table 3). Arctic shanny (*Stichaeus punctatus*), sculpins (*Myoxocephalus* spp. and *Gymnocanthus tricuspis*) and capelin (*Mallotus villosus*) larvae were more abundant in waters of salinity and temperature ranging respectively

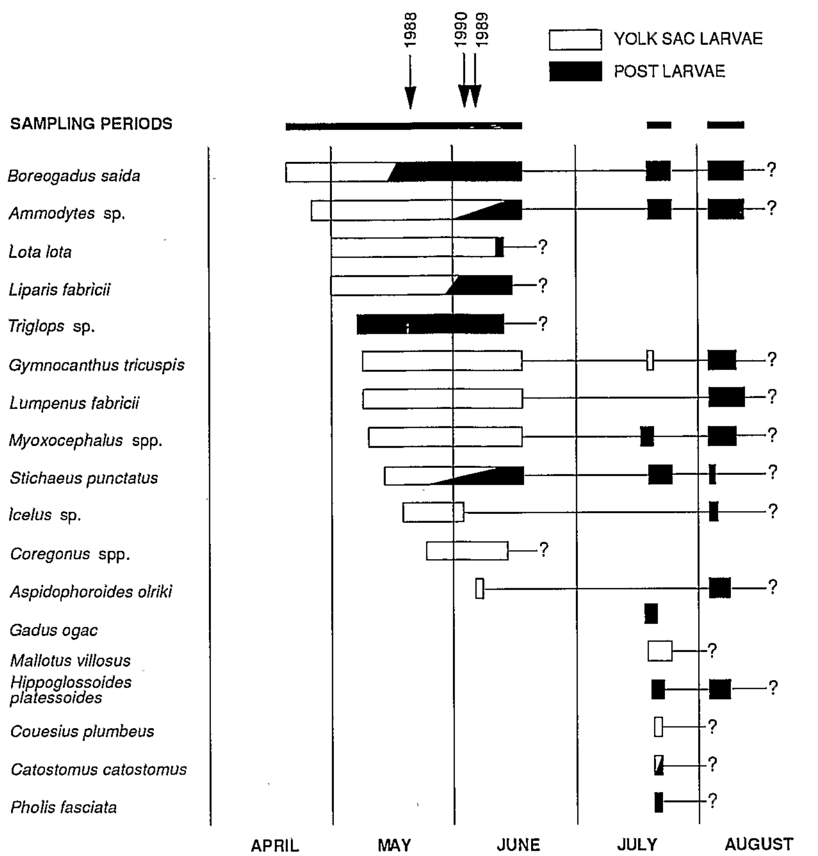

Fig. 3. Seasonal occurrence of all the larval fish species caught during 1988–1990. Arrows indicate the beginning of ice breakup in the Bay off Kuujjuarapik. Note that ice breakup generally occurred ten days earlier within the Great Whale River itself

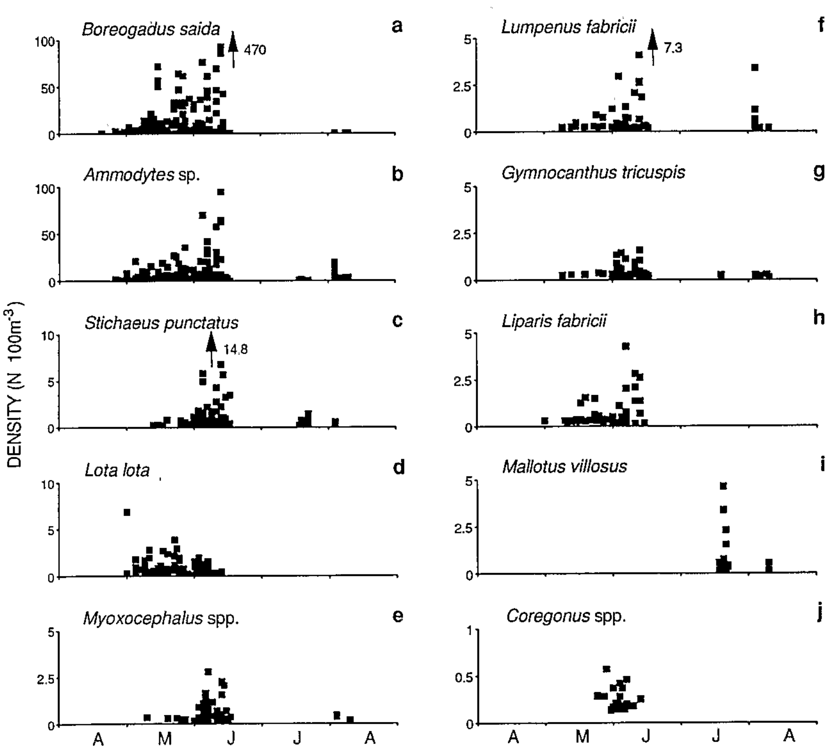

Fig. 4a–j. Densities of the ten most abundant species caught during 1988–1990. Null densities are not represented for clarity

Table 3. Occurrence (percent of samples in which the species was present) and mean densities (N.100m^{-3}) of the ten most abundant species at various salinities (practical salinity units p.s.u.) and corresponding temperature ranges (°C) for the three sampling periods. SD: standard deviation, *P*: associated probability of the Kruskal-Wallis test of differences between mean densities

	APRIL–MAY				JUNE				JULY–AUGUST			
Salinity (p.s.u.)	>1	1–15	15–25	>25	>1	1–15	15–25	>25	>1	1–15	15–25	>25
Temperature ranges (°C)	0 to 8.0	−1.3 to 2.9	−1.3 to 0.8	−1.5 to −0.1	0.6 to 10.8	−0.5 to 9.0	−1.0 to 1.4	−1.3 to 0.2	13.0 to 14.3	6.6 to 9.3	1.9 to 8.4	−1.0 to 8.1
Marine water species												
Boreogadus saida												
Occurrence	24	45	97	78	25	58	67	76	0	0	0	14
Mean Density	0.84	3.40	9.78	8.61	0.65	1.37	0.78	12.55	0	0	0	0.50
SD	3.77	10.43	16.81	17.28	1.99	2.45	1.46	19.94	–	–	–	0.12
P		<0.0001				<0.0001				–		
Ammodytes sp.												
Occurrence	54	59	89	74	35	79	78	82	0	20	55	85
Mean Density	1.18	1.87	3.03	4.02	0.87	1.43	0.67	9.73	0	0.04	0.81	2.21
SD	2.23	5.29	3.05	5.60	1.73	1.84	0.76	14.33	–	0.09	2.23	3.30
P		<0.0001				<0.0001				<0.0001		
Lumpenus fabricii												
Occurrence	0	0	17	11	1	5	27	47	0	0	5	24
Mean Density	0	0	0.07	0.05	<0.01	<0.01	0.07	0.27	0	0	0.06	0.09
SD	–	–	0.18	0.17	0.01	0.02	0.17	0.45	–	–	0.26	0.19
P		<0.0001				<0.0001				<0.0001		
Liparis fabricii												
Occurrence	10	12	22	11	1	10	0	23	0	0	0	0
Mean Density	0.03	0.03	0.06	0.08	<0.01	0.02	0	0.43	0	0	0	0
SD	0.10	0.09	0.11	0.28	0.01	0.05	-	0.98	–	–	–	–
P		0.4400				0.0002				–		
Brackish water species												
Stichaeus punctatus												
Occurrence	4	10	25	14	9	63	72	44	0	20	45	5
Mean Density	0.03	0.05	0.18	0.06	0.03	1.16	1.45	0.32	0	0.16	0.34	0.03
SD	0.13	0.15	0.43	0.20	0.10	1.65	3.32	0.58	–	0.35	0.50	0.12
P		0.0235				<0.0001				0.0020		
Myoxocephalus spp.												
Occurrence	1	4	3	6	4	47	50	23	0	0	5	9
Mean Density	<0.01	0.02	<0.01	0.02	<0.01	0.37	0.26	0.13	0	0	0.02	0.03
SD	0.03	0.13	0.05	0.07	0.03	0.69	0.54	0.28	–	–	0.10	0.09
P		0.5742				<0.0001				0.6300		
Gymnocanthus tricuspis												
Occurrence	6	8	8	3	4	47	22	18	0	0	5	19
Mean Density	0.02	0.03	0.06	0.01	0.02	0.23	0.08	0.06	0	0	0.01	0.04
SD	0.07	0.12	0.24	0.10	0.13	0.39	0.18	0.16	–	–	0.06	0.09
P		0.6082				0.0001				0.1830		
Mallotus villosus												
Occurrence	0	0	0	0	0	0	0	0	8	100	20	5
Mean Density	0	0	0	0	0	0	0	0	0.01	1.88	0.08	<0.01
SD	–	–	–	–	–	–	–	–	0.04	2.00	0.17	0.04
P		–				–				<0.0001		
Freshwater species												
Lota lota												
Occurrence	51	10	25	7	37	5	0	9	0	0	0	0
Mean Density	0.60	0.13	0.07	0.05	0.23	0.01	0	0.04	0	0	0	0
SD	1.12	0.51	0.13	0.22	0.45	0.06	–	0.13	–	–	–	–
P		<0.0001				<0.0001				–		
Coregonus spp.												
Occurrence	15	2	0	0	14	0	0	0	0	0	0	0
Mean Density	0.04	<0.01	0	0	0.03	0	0	0	0	0	0	0
SD	0.11	0.02	–	–	0.09	–	–	–	–	–	–	–
P		<0.0001				–				–		

Table 4. Mean length of Arctic cod larvae caught in Kuujjuarapik (K), Richmond Gulf (RG), and Belcher Islands (BI) areas in 1990. Z: Mann-Whitney statistic and P: associated probability

Area	Date	Nb of stations	Nb of larvae	% yolk-sac larvae	Mean standard length (mm) ± SD	Z	P
K	2 Jun	3	127	2.4	6.23 ± 0.72		
						4.63	< 0.0001
RG	3 Jun	3	405	2.7	5.91 ± 0.72		
K	5 Jun	3	296	0.3	7.47 ± 0.64		
						7.21	< 0.0001
BI	6 Jun	3	22	0	5.71 ± 0.71		
K	11 Jun	3	556	1.9	7.99 ± 0.75		
						17.39	< 0.0001
BI	12 Jun	3	144	0	6.06 ± 0.64		

from 1 to 25 p.s.u. and from −1.3 to 9.0°C (Table 3). This trend was already present in April–May for Arctic shanny but developed only later for sculpins. Most burbot (*Lota lota*) and all coregonid (*Coregonus clupeaformis* and *C. artedii*) larvae were clearly restricted to the warm (> 0 °C) and fresh or low salinity waters of the River or its plume (Table 3).

Spatial variations in size distributions

Differences in the size distribution of Arctic cod were detected at the larger geographic scale surveyed in June 1990 (Table 4). At a given date, the larvae caught near Kuujjuarapik were significantly larger than those captured in the Richmond Gulf and Belcher Islands areas. Most larvae had lost their yolk-sac at that time (June).

Discussion

Hudson Bay marine waters originate mostly from the adjacent Arctic ocean but are marginally influenced by inflows from the North Atlantic (Dunbar 1958). Freshwater inputs from large rivers around the Bay contribute to lower the surface salinity in coastal areas (Barber 1967, Prinsenberg 1986). As a result, three main groups of fishes are found in Hudson Bay: 19 Arctic marine species (15 genera), 15 non-Arctic marine species (13 genera), and 31 brackish and freshwater species (24 genera) (Morin and Dodson 1986). Three of the 14 families of marine fish inhabiting Hudson Bay were not represented in our samples: Zoarcidae (three Arctic species) whose reproduction is poorly documented (Scott and Scott 1988), Cyclopteridae (three non-Arctic species) whose larvae are never truly planktonic (Russel 1976), and Clupeidae (*Clupea harengus*). Adult Atlantic herring (*C. harengus*) migrate into the Kuujjuarapik coastal area in summer (C. Michel, GIROQ, Université Laval, Québec, Canada, pers. comm.). The absence of herring larvae in our samples may indicate that this species does not spawn in the spring in the area studied. The freshwater fish larvae belonged to only five of the 11 species reported to colonize either the estuary or the lower part of the Great Whale River (Auger and Power 1978, Morin et al. 1980). Larvae distributed along the river and estuary banks may have been underrepresented as we sampled only the main channel.

The ichthyoplankton was dominated by Arctic cod *Boreogadus saida*. Although densities of Arctic cod larvae in southeastern Hudson Bay were similar to those observed in high Arctic areas (Sekerak 1982, Chiperzak et al. 1990), their relative abundance was much lower. On average, they contributed only about 50% of the ichthyoplankton community off Kuujjuarapik as opposed to 85–95% in the high Arctic. This difference resulted from the high abundance of *Ammodytes* spp. larvae which accounted for more than 33% of the total (Table 2) and occurred at densities comparable to those observed in temperate seas (Potter and Lough 1987). While *B. saida* is the key species in the high Arctic marine food web (see Bain and Sekerak 1978 for a review), it may have to share this role in southeastern Hudson Bay where its distribution area overlaps that of *Ammodytes* spp., a non-Arctic species. This hypothesis is consistent with the observation that sand lance adults represent a large proportion of the diet of ringed seals (*Phoca hispida*) at least in late summer and fall in the Kuujjuarapik area (Breton-Provencher 1979).

Anadromous coregonids generally represent the most abundant component of estuarine fish communities in Hudson Bay (Morin et al. 1980). However, lake whitefish (*Coregonus clupeaformis*) and cisco (*C. artedii*) accounted only for 0.25% of the total number of larvae and 8.6% of the freshwater larvae caught in the Great Whale River – Kuujjuarapik area. Their densities remained one to two orders of magnitude lower than in the estuary of the Eastmain River in nearby James Bay (Ochman and Dodson 1982). Kemp et al. (1989) observed that adult lake whitefish and cisco represented 42 to 98% of the Salmonids and 34 to 90% of all fish species by number in five rivers entering James and Hudson Bays between 52°15′ and 60°01′N. However, the authors found that these two species accounted for only 23% of the Salmonids and 7% of all fish species in the Great Whale River. This lower abundance of adults coregonids may explain the low densities of coregonid larvae observed in the river and its estuary.

Knowledge of the early life history of the major fish species found in southeastern Hudson Bay is scarce and generally incomplete (Table 5a, b and c). Our observations complement the available information. For example, Arctic cod larvae first occurred in our samples in late April. This species therefore spawned in early winter in Hudson Bay as in most other Arctic areas (Table 5a). Data from various locations indicate that sand lance reproduces between December and April (Table 5b). In our sampling area, sand lance larvae emerged later than Arctic cod perhaps as a result of protracted embryonic development at low temperatures (Table 5b).

To our knowledge, development time of Arctic shanny (*Stichaeus punctatus*) eggs has never been documented. If spawning occurs in February–March in Hudson Bay as it does along Newfoundland shores (Table 5a) and since we first caught these larvae in mid-May (Fig. 3), egg incubation could last 2 to 3 months at temperatures below 0°C. No yolk-sac larvae of sculpin (*Myoxocephalus* spp.) and slender eelblenny (*Lumpenus fabricii*) were caught in early summer (Fig. 3). These species therefore most likely reproduce in winter as they do in the Baltic and the White Seas rather than in spring as in Alaska and off west Greenland (Table 5a and b). Winter spawning also appears to be the strategy adopted in subarctic areas by Arctic staghorn sculpin (*Gymnocanthus tricuspis*) and gelatinous snailfish (*Liparis fabricii*). Their larvae appeared in our samples during the first weeks of May (Fig. 3). Our results confirm that capelin (*Mallotus villosus*) spawn in early July in Hudson Bay as observed by Vladykov (1933).

Arctic cod larvae sampled near the Belcher Islands and the Gulf of Richmond in June 1990 were smaller, and presumably younger, than those caught near Kuujjuarapik (Table 4). This raises the question of spawning site location for this species in Hudson Bay. Spawning sites of Arctic cod in Arctic and subarctic regions are generally unknown (Bain and Sekerak 1978; Craig et al. 1982) but are presumed to be associated with ice edges (Benko et al. 1970). An ice-free area persisting annually until mid-December northwest of the Belcher Islands (Markham 1988) may provide an ice edge suitable for Arctic cod spawning. As Arctic cod eggs and larvae can be transported by surface currents over long distances (Baranenkova et al. 1966, Althukhov 1979a), the general circulation (Prinsenberg 1986) may play an important role in achieving their transport towards the coastal areas of Hudson Bay. Testing this hypothesis would require a better knowledge of the local surface current patterns (see Larouche 1989) and of the age of the larvae caught in each area.

The early life of freshwater, anadromous and marine fish in the coastal areas of southeastern Hudson Bay is strongly influenced by the outflow of the Great Whale River. At the time of river run-off, some coregonid and burbot larvae were observed in the Bay. However, their survival after the plume begins to contract remains unknown. Larvae from over 50% of the marine fish species were first caught before ice breakup in the Bay (Fig. 3) when the brackish plume was near full expansion. Ice cover and the underlying plume influence the spatial distribution of marine fish larvae, both horizontally (Gilbert et al. 1992) and vertically (Ponton and Fortier 1992).

Table 5a–c. Summary of data on spawning period, egg development duration, and size of larvae at hatching

a) most abundant Arctic marine species

Location	Spawning period	Egg development duration	Size of larvae at hatching (mm)	Reference
Boreogadus saida				
White Sea	Jan to Feb rarely Apr	77 to 79 d (−1.5 °C)	5.5 to 6.1 ave = 5.81	Altukhov 1979a
White Sea	Dec to Feb	26 to 35 d (−0.3 to 2.5 °C)	5.5±0.1	Aronovich et al. 1975
Barents Sea	Oct to Mar	–	3.5	Baranenkova et al. 1966
Barents Sea	Early spring	–	–	Benko et al. 1970
Beaufort Sea	Late Nov to early Feb	–	–	Craig et al. 1982
Barents Sea	End Dec to end Mar	1.5 to 3 months	5.5	Rass 1968
Stichaeus punctatus				
Logy Bay, Newfoundland	Feb to March	–	–	Farwell et al. 1976
Myoxocephalus quadricornis				
White Sea	Dec to Jan	–	7.0 to 11.5 ave = 8.0	Altukhov 1979b
Tuktoyaktuk, Beaufort Sea	January	–	–	Bond 1982
Alaska	Summer	–	–	Goldberg et al. 1987
White Sea	Dec to late Jan	–	–	Mukhomedianov 1967 in Khan 1971
Baltic Sea	Dec to Jan	–	–	Westin 1969
Gymnocanthus tricuspis				
Trinity Bay, Newfoundland	Fall	–	–	Ennis 1970
Liparis fabricii				
White Sea	Feb to Mar	–	–	Altukhov 1979c
USSR coast	Sep to Oct	–	–	Andriashev 1954 in Scott and Scott 1988

Table 5 (continued)

b) most abundant non-Arctic marine species

Location	Spawning period	Egg development duration	Size of larvae at hatching (mm)	Reference
Ammodytes americanus				
Fortune Bay, Newfoundland	Dec to Apr	–	–	Dalley and Winters 1987
Laboratory		135 d (2 °C)	6.2	Smigielski et al. 1984
Eastern Newfoundland	Late autumn to early winter	–	–	Winters 1989
Ammodytes dubius				
Long Island	Dec to Feb	–	3.6	Richards 1982
Scotian Shelf	–	–	4.0	Scott 1972
Eastern Newfoundland	Later than *A. americanus*	–	–	Winters 1989
Myoxocephalus scorpius				
White Sea	Nov to mid-Jan	ca. 4 months (<0°C)	7.4 to 8.6	Altukhov 1979b
US coast, North Atlantic	Nov to Feb	–	–	Bigelow and Schroeder 1953 in Khan 1971
Bay Bulls, Newfoundland	late Nov to early Dec	3 months (±0 °C)	–	Ennis 1970
Kiel Fjord, Baltic Sea	Dec to Feb	–	6.0	Lamp 1966
Gdansk Bay, Baltic Sea	Dec to end Mar	–	–	Raciborski 1984
Lumpenus fabricii				
White Sea	Oct to Nov	–	–	Altukhov 1979c
off west Greenland	July	–	–	Jensen 1964 in Scott and Scott 1988
Mallotus villosus				
Barents Sea	Feb to June	–	–	Benko et al. 1970
North Atlantic		–	6.0 to 7.0	Fahay 1983
Hudson Bay	end Jul to Aug	–	–	Vladykov 1933

c) most abundant freshwater species

Location	Spawning period	Egg development duration	Size of larvae at hatching (mm)	Reference
Lota lota				
Lake Opeongo, Canada	–	–	3.0 to 4.0	Cucin and Faber 1985
L. Angersjo, Sweden	Late Feb	–	–	Hedin 1983
Laboratory	–	52 d (2 °C)	3.7±0.1	Jaeger et al. 1981
Coregonus clupeaformis				
Mackenzie Basin	Fall	–	–	Bodaly et al. 1989
Laboratory	–	236 d (0.5 °C)	–	Colby and Brooke 1973
L. Opeongo & laboratory	Mid-Nov to Dec	155 to 175d (1.0 to 8 °C)	7.5 to 8.5	Cucin and Faber 1985
James and Hudson Bays	Late autumn	–	–	Dymond 1933
Eastmain and La Grande Riv., Canada	Autumn	–	–	Morin et al. 1981
Coregonus artedii				
Laboratory	–	182 d (0.5 °C)	13.3±0.54	Brooke 1975
Mackenzie Basin	Oct to Nov	–	–	Bodaly et al. 1989
L. Opeongo & laboratory	End Oct to mid-Nov	4 to 6 months (1.0 to 8 °C)	9.5 to 10.5	Cucin and Faber 1985
James and Hudson Bays	Early autumn	–	–	Dymond 1933
Eastmain and La Grande Riv., Canada	Fall	–	–	Morin et al. 1981

Accordingly, our highest densities of Arctic cod larvae were obtained at intermediate (15–25 p.s.u.) salinities under ice cover and in salinities in excess of 25 p.s.u. when light limitation was alleviated after ice breakup.

Although limited to the spring and summer periods, our observations provide new insights into the poorly known early life history of fish species in subarctic coastal areas. At those intermediate latitudes, the distributions of Arctic and temperate marine fish species overlap and, contrary to the situation further north, more than one species may dominate the ichthyoplankton community. Processes associated with river outflow clearly influence the spatial distribution of marine fish larvae in the coastal zone. They also affect the flushing in the Bay of freshwater and anadromous species. It can thus be hypothesized that interannual variations in the timing of the spring freshet, in the extent of the plume underneath the ice, and the timing of ice breakup significantly impact on the environmental conditions encountered by the young stages of several fish species in subarctic coastal areas such as southeastern Hudson Bay.

Acknowledgements. This study is part of a collaborative project between GIROQ and the Canadian Department of Fisheries and Oceans (Institut Maurice Lamontagne). Field and laboratory work was funded in part by grants to L. Fortier from NSERC and DFO, and by grants to GIROQ from NSERC and the Fond FCAR of Québec. Helicopter time was provided by DFO. The Centre d'études nordiques (Université Laval) provided accommodation at its field station in Kuujjuarapik where we benefited from the assistance of the superintendent C. Coté. Special thanks to R. Drolet, C. Dutil, and M. Gilbert for their contribution to this study. G. Bergeron, M. Bolduc, M. Frenette, L. Girard, N. Hamel, L. Michaud, D. Morissette, M. Parent, J. Ponton, M.-A. Rémillard, J.-G. Rondeau, M. Salathé and S. Tourangeau helped in the field or the laboratory.

References

Alexander V (1980) Interrelationships between the seasonal sea ice and biological regimes. Cold Regions Sci Technol 2:157–178

Altukhov KA (1979a) The reproduction and development of the Arctic cod, *Boreogadus saida*, in the White Sea. J Ichthyol 19:93–101

Altukhov KA (1979b) On the biology of the early stages of development of some White Sea fishes. Vopr Ikhtiol 19:117–127

Altukhov KA (1979c) A contribution to the biology of noncommercial and rare fish species from the White Sea in the early stages of development. Vopr Ikhtiol 19:1079–1090

Apollonio S (1961) The chlorophyll content of Arctic sea ice. Arctic 14:197–200

Aronovich TM, Doroshev SI, Spectorova LV, Makhotin VM (1975) Egg incubation and larval rearing of Nagava (*Eleginus navaga* Pall.), Polar cod (*Boreogadus saida* Lepechin) and Arctic flounder (*Liopsetta glacialis* Pall.) in the laboratory. Aquaculture 6:233–242

Auer NA (1982) Identification of larval fishes of the Great Lakes basin with emphasis on the Lake Michigan drainage. Great Lakes Fishery Commission, Ann Arbor, MI 48105. Special Pub. 82–3, pp 744

Auger F, Power G (1978) Compléments des études ichtyologiques de l'embouchure de la Grande rivière de la Baleine, du détroit de Manitounuk et de l'estuaire de la Petite rivière de la Baleine. GIROQ, rapport à l'Hydro-Québec. (Projet Grande Baleine, Etudes océanographiques dans la baie d'Hudson; Mandat d'avant-projet préliminaire Hydro-Québec/OGB 76-1), pp 59

Bain H, Sekerak AD (1978). Aspects of the biology of Arctic cod, *Boreogadus saida*, in the central Canadian Arctic. Report for Polar Gas Project by LGL Limited, Toronto, Ontario, pp 104

Baranenkova AS, Ponomarenko VP, Khokhlina NS (1966) The distribution, size and growth of the larvae and fry of *Boreogadus saida* (Lepechin) in the Barents Sea. Vopr Ikhtiol 6:498–518

Barber FG (1967) A contribution to the oceanography of Hudson Bay. Marine Sciences Branch, Dept of Energy, Mines and Resources, Ottawa. Manuscript Report Series No 4: pp 69

Benko YK, Dragesund O, Hognestad PT, Jones BW, Monstad T, Nizovtsez GP, Olsen S, Seliverstov AS (1970) Distribution and abundance of 0-group fish in the Barents Sea in August-September 1965–1968. Int. Coun. Explor. Sea Coop Res Rep Ser A:35–47

Bodaly RA, Reist JD, Rosenberg DM, McCart PJ, Hecky RE (1989) Fish and fisheries of the Mackenzie and Churchill River basins, northern Canada. In: Dodge DP (ed) Proc Int Large Rivers Symp Can Spec Publ Fish Aquat Sci No 106:128–144

Bond WA (1982) A study of the fishery resources of Tuktoyaktuk Harbour, southern Beaufort sea coast, with special reference to life histories of anadromous coregonids. Can Tech Rep Fish Aquat Sci No 1119, pp 90

Breton-Provencher M (1979) Etude de la population de phoques annelés (*Phoca hispida*) et des autres Pinnipèdes de la région de Poste-de-la-Baleine (Nouveau-Québec). GIROQ, rapport à l'Hydro-Québec, projet Grande-Baleine (Mandat d'avant-projet préliminaire OGB/76-1), pp 148

Brooke LT (1975) Effect of different constant incubation temperatures on egg survival and embryonic development in lake whitefish (*Coregonus clupeaformis*). Trans Am Fish Soc 104:555-559

Chiperzak DB, Hopky GE, Lawrence MJ, Lacho G (1990) Marine ichthyoplankton data from the Canadian Beaufort Sea shelf, July and September 1984. Can Data Rep Fish Aquat Sci 779, pp 45

Colby PJ, Brooke LT (1973) Effects of temperature on embryonic development of lake herring (*Coregonus artedii*). J Fish Res Bd Canada 30:799–810

Craig PC, Griffiths W, Haldorson L, McElderry H (1982) Ecological studies of Arctic cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska. Can J Fish Aquat Sci 39:395–406

Cucin D, Faber DJ (1985). Early life studies of lake whitefish (*Coregonus clupeaformis*), cisco (*Coregonus artedii*) and yellow perch (*Perca flavescens*) in Lake Opeongo, Ontario. Ontario Fish Tech Rep Ser No 16, pp 28

Cushing DH (1975) Marine ecology and fisheries. Cambridge University Press, New York, pp 278

Dalley EL, Winters GH (1987) Early life history of sand lance (*Ammodytes*), with evidence for spawning of *A. dubius* in Fortune Bay, Newfoundland. Fish Bull 85:631–641

Drolet R, Fortier L, Ponton D, Gilbert M (1991) The production of fish larvae and their prey in subarctic southeastern Hudson Bay. Mar Ecol Prog Ser 77:105–118

Dunbar MJ (1958) Physical oceanographic results of the "Calanus" expeditions in Ungava Bay, Frobisher Bay, Cumberland Sound, Hudson Strait, and northern Hudson Bay, 1949–1955. J Fish Res Bd Canada 15:155–201

Dunn JR, Vinter BM (1984) Development of larvae of the saffron cod, *Eleginus gracilis*, with comments on the identification of Gadid larvae in Pacific and Arctic waters contiguous to Canada and Alaska. Can J Fish Aquat Sci 41:304–318

Dymond JR (1933) Biological and oceanographic conditions in Hudson Bay. 8. The coregonine fishes of Hudson and James Bay. Contrib Can Biol Fish 8:1–12

Ennis GP (1970) Reproduction and associated behaviour in the shorthorn sculpin, *Myoxocephalus scorpius* in Newfoundland. J Fish Res Bd Canada 27:2037–2045

Faber DJ (1976) Identification of four northern blenioid fish larvae in the Canadian Atlantic Ocean (Stichaeidae, Lumpenidae). J Fish Res Bd Canada 33:1798–1802

Fahay MP (1983) Guide to early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. J Northw Atl Fish Sci 4, pp 423

Farwell MK, Green JM, Pepper VA (1976) Distribution and known life history of *Stichaeus punctatus* in the northwest Atlantic. Copeia 3:598–602

Gilbert M, Fortier L, Ponton D, Drolet R (1992) Feeding ecology of fish larvae across the Great Whale River plume in seasonally ice-covered southeastern Hudson Bay. Mar Ecol Prog Ser 84:19–30

Goldberg SR, Yasutake WT, West RL (1987) Summer spawning in the fourhorn sculpin, *Myoxocephalus quadricornis*, from Alaska. Can Field-Nat 101:457

Gosselin M, Legendre L, Demers S, Ingram RG (1985) Responses 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 microalgae. Mar Ecol Prog Ser 29:289–298

Gosselin M, Legendre L, Therriault J-C, Demers S (1990) Light and nutrient limitation of sea-ice microalgae (Hudson Bay, Canadian Arctic). J Phycol 26:220–232

Hedin J (1983) Seasonal spawning migrations of the burbot (*Lota lota* L.) in a coastal stream of the northern Bothnian sea. Fauna Norrlandica 6:1–20

Horner RA (1976) Sea ice organisms. Oceanogr Mar Biol Ann Rev 14:167–182

Houde ED (1989) Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish Bull US 87:471–485

Hunter JG (1968) Fishes and fisheries. In: Beals CS (ed) Science History and Hudson Bay. Canada Dept Energy, Mines and Resources, Ottawa, pp 360–378

Iles TD, Sinclair M (1982) Atlantic herring: stock discreteness and abundance. Science 215:627–633

Ingram RG (1981) Characteristics of the Great Whale River plume. J Geophys Res 86 C3:2017–2023

Ingram RG, Larouche P (1987) Variability of an under-ice river plume in Hudson Bay. J Geophys Res 92(C):9541–9547

Jaeger T, Nellen W, Schaefer W, Shodjai F (1981) Influence of salinity and temperature on early life stages of *Coregonus albula*, *C. lavaretus*, *Rutilus rutilus* and *Lota lota*. Rapp. P.-v. Réun. Cons Int Explor Mer 178:345–348

Kemp A, Bernatchez L, Dodson JJ (1989) A revision of coregonine fish distribution and abundance in eastern James-Hudson Bay. Env Biol Fish 26:247–255

Khan N (1971) Comparative morphology and ecology of the pelagic larvae of nine Cottidae (Pisces) of the northwest Atlantic and St. Lawrence drainage. Thesis, Univ. of Ottawa, Ottawa, pp 234

Lamp F (1966) Contribution to the biology of the sea scorpions *Myoxocephalus scorpius* (L.) and *Taurulus bubalis* (Euphr.) in the Kiel Fjord. Kieler Meeresforschungen 22:98–120 (Fish Res Board Can Transl Ser No 902, pp 48)

Larouche P (1989) Spring surface circulation patterns detected using remote sensing of drifting ice floes in Hudson Bay, Canada. Proc. Int. Geoscience and Remote Sensing Symposium (IGARSS), Vancouver, Canada, pp 780–782

Larouche P, Galbraith PS (1989) Factors affecting fast-ice consolidation in southeastern Hudson Bay, Canada. Atmosphere-Ocean. 27:367–375

Legendre L, Ingram RG, Poulin M (1981) Physical control of phytoplankton production under sea ice (Manitounuk Sound, Hudson Bay). Can J Fish Aquat Sci 38:1385–1392

Legendre L, Demers S, Therriault J-C (1989) Responses of Arctic sea-ice micro-algae to light and temperature: physiological adaptations and ecological implications. Rapp. P.-v. Réun. Cons Int Explor Mer 188:115–120

Lepage S, Ingram RG (1991) Variation of upper layer dynamics during breakup of the seasonal ice cover in Hudson Bay. J Geophys Res 96(C7):12711–12724

Markham WE (1986) The ice cover. In: Martini IP (ed) Canadian Inland Seas. Elsevier Oceanography, Series 44. Elsevier., Amsterdam, pp 101–117

Markham WE (1988) Ice atlas: Hudson Bay and approaches. Environment Canada, Atmospheric Environment Service, pp 123

Morin R, Dodson JJ (1986) The ecology of fishes in James Bay, Hudson Bay and Hudson Strait. In: Martini IP (ed) Canadian Inland Seas. Elsevier Oceanography, Series 44, Elsevier, Amsterdam, pp 293–325

Morin R, Dodson JJ, Power G (1980) Estuarine fish communities of the eastern James-Hudson Bay coast. Env Biol Fish 5:135–141

Morin R, Dodson JJ, Power G (1981) The migrations of anadromous cisco (*Coregonus artedii*) and lake whitefish (*C. clupeaformis*) in estuaries of eastern James Bay. Can J Zool 59:1600–1607

Ochman S, Dodson JJ (1982) Composition and structure of the larval and juvenile fish community of the Eastmain River and estuary, James Bay. Nat Can 109:803–813

Ponton D, Fortier L (1992). Vertical distribution and foraging of marine fish larvae under the ice cover of southeastern Hudson Bay. Mar Ecol Prog Ser 81:215–227

Potter DC, Lough RG (1987) Vertical distribution and sampling variability of larval and juvenile sand lance (*Ammodytes* sp.) on Nantucket shoals and Georges Bank. J Northw Atl Fish Sci 7:107–116

Prinsenberg SJ (1986) The circulation pattern and current structure of Hudson Bay. In: Martini IP (ed) Canadian Inland Seas. Elsevier Oceanography, Series 44, Elsevier, Amsterdam, pp 187–204

Raciborski K (1984) Migration, reproduction, growth and feeding of *Myoxocephalus scorpius* (L.) in Gdansk Bay (South Baltic). Pol Arch Hydrobiol 31:109–118

Rass TS (1968) Spawning and development of polar cod. Rapp. P.-v. Réun. Cons Perm Int Explor Mer 10:135–137

Richards SW (1982) Aspects of the biology of *Ammodytes americanus* from St. Lawrence River to Chesapeake Bay, 1972–75, including a comparison of the Long Island Sound postlarvae with *Ammodytes dubius*. J Northw Atl Fish Sci 3:93–104

Runge JA, Ingram RG (1988) Underice grazing by planktonic calanoid copepods in relation to a bloom of ice microalgae in southeastern Hudson Bay. Limnol Oceanogr 33:280–286

Runge JA, Therriault J-C, Legendre L, Ingram RG, Demers S (1991) Coupling between ice microalgal productivity and the pelagic, metazoan food web in southeastern Hudson Bay: a synthesis of results. In: Sakshaug E, Hopkins CCE, Oritsland NA (eds) Proc. Pro Mare Symp. on Polar Marine Ecology, Trondheim, 12–16 May 1990. Polar Res 10:325–338

Russel FS (1976) The eggs and planktonic stages of British marine fishes. Academic Press, London pp 524

Scott JS (1972) Eggs and larvae of northern sand lance (*Ammodytes dubius*) from the Scotian Shelf. J Fish Res Bd Canada 29:1667–1671

Scott WB, Scott MG (1988) Atlantic Fishes of Canada. Can Bull Fish Aquat Sci 219, pp 731

Sekerak AD (1982) Young-of-the-year cod (*Boreogadus*) in Lancaster Sound and Western Baffin Bay. Arctic 35:75–87

Smigielski AS, Halavik TA, Buckley LJ, Drew SM, Lawrence GC (1984) Spawning, embryo development and growth of the American sand lance *Ammodytes americanus* in the laboratory. Mar Ecol Prog Ser 14:287–292

Tourangeau S, Runge JA (1991) Reproduction of *Calanus glacialis* under ice in spring in southeastern Hudson Bay, Canada. Mar Biol 108:227–233

Vladykov VD (1933) Biological and oceanographic conditions in Hudson Bay. 9. Fishes from Hudson Bay region (except the Coregonidae). Contrib Can Biol 8:15–49

Westin L (1969) The mode of fertilization, parental behaviour, and time of egg development in fourhorn sculpin, *Myoxocephalus quadricornis* (L.). Inst Freshwat Res Drottningholm Rept 49:175–182

Wilson CV (1973) The climate of Québec. Part 1. Climatic atlas of the province of Québec. Canadian Meteorological Service, Climatological Studies 11, pp 350

Winters GH (1989) Life history parameters of sand lance (*Ammodytes* spp.) from the coastal waters of eastern Newfoundland. J Northw Atl Fish Sci 9:5–11