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Aspects of the Life History of the Pond Smelt (*Hypomesus olidus*) in the Yukon and Northwest Territories

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ABSTRACT. The pond smelt (*Hypomesus olidus*) has a limited North American distribution, being restricted to the west coast of Alaska and the drainage of the lower Mackenzie River, N.W.T. This study examined an isolated population in a small tundra lake on the Yukon coastal plain. Otolith interpretation revealed that most adult fish sampled in Lake 100 were age 4+ and 5+ years, but a few individuals lived to age 8+ and 9+. Full maturity was not reached until age 5+ and repeat spawning was common. The sex ratio was skewed in favour of females. Growth was found to be slower in the Yukon population than in Alaskan and Japanese lakes. Some stunting was evident in Lake 100 pond smelt, but otherwise their meristic and morphometric characteristics corresponded with those from elsewhere. The pond smelt were primarily planktivorous in Lake 100 and there appeared to be no significant predation on them, but in the Mackenzie delta and elsewhere they are utilized as a forage species.

Key words: pond smelt, life history, food habits, *Hypomesus olidus*, Yukon

RÉSUMÉ. Dans l'amérique du nord, l'éperlan á petite bouche (*Hypomesus olidus*) est distribué le long de la côte ouest de l'Alaska et à proximité de embouchure de la riviere Mackenzie, Territoires du Nord-Ouest. C'est étude visa une population isolée, dans un petit lac situé dans la toundra de la plaine cotière du Yukon. Les lectures d'otolithes ont demontré que la plupart des adults, échantillonnés du lac 100 au Yukon, était âgée de 4+ et 5+ ans et quelques individus survivaint jusqu'à 8+ et 9+ ans. La maturité complète ne fut atteinte qu'à l'âge 5+ ans généralement, les femelles pouvaient frayer pour plusieurs années. Le rapport des sexes était penché vers les femelles. La croissance des poissons du Yukon était plus lente que celles individus de l'Alaska et du Japon. En plus l'auteur a trouvé l'évidence d'individus rabourgis dans la lac 100 au Yukon. Autrement, les caràcteres morphologiques et méristiques se resemblaient. L'éperlan à petite bouche s'aillmentait principalement de plancton et la consommation rapace sur l'éperlan dans la lac 100 était insignificante.

Mots clés: éperlan à petite bouche, biologie, alimentation, *Hypomesus olidus*, Yukon, cycle vital

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INTRODUCTION

The pond smelt (*Hypomesus olidus* Pallas) has a limited distribution in North America, being restricted to the west coast of Alaska, the watersheds of the lower Mackenzie and Peel rivers, and the rivers and lakes of the Tuktoyaktuk Peninsula, N.W.T. (Fig. 1). Despite extensive fish surveys along the north slope of Alaska and Yukon Territory during the past decade, the Yukon population described here is the only reported occurrence of this species between the Kobuk River system, Alaska, and the Mackenzie delta, N.W.T., a distance of more than 1100 km. An even larger gap (2500 km) occurs between populations in eastern Siberia and the Kara Sea drainage, U.S.S.R. McPhail and Lindsey (1970) postulate that the gap in Asia may be due to separate glacial refugia, but the reason for the gap in North American distribution is unknown.

H. olidus probably survived the most recent glaciation in the Bering refugium (McPhail and Lindsey, 1970) and may have entered the Mackenzie and Peel river systems by means of headwater capture between the Yukon or Porcupine rivers and the Upper Peel River, although the species is apparently absent from the Upper Yukon system at present. Coastal dispersion as hypothesized by McPhail and Lindsey (1970) would have almost certainly resulted in the colonization of other larger rivers or lakes on the north slope of Alaska or Yukon Territory. The Yukon population discussed in this paper probably originated from the Mackenzie delta and reached the study area some time in the past by following the band of low salinity water that seasonally extends along the Beaufort Sea coast both east and west of the Mackenzie River.

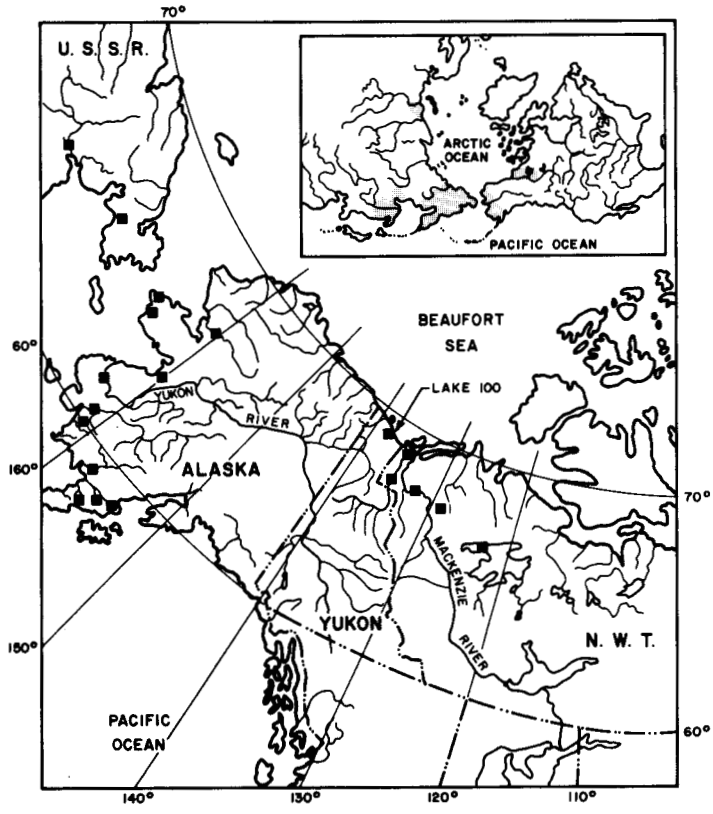

FIG. 1. Distribution of pond smelt (*Hypomesus olidus*) in North America and the world distribution of the species.

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Much of the literature dealing with the biology and distribution of members of the genus *Hypomesus* is confusing as a result of several taxonomic revisions. Prior to the work of Hamanda (1957, 1961) *Hypomesus olidus* was considered to include both anadromous and non-anadromous life-history forms; unfortunately, in separating the species, Hamanda (1961) considered the anadromous species to be *H. olidus* and described the freshwater form as a new species. McAllister (1963) noted the error and revised the genus accordingly. This latter revision was corroborated by the work of Klyukanov (1966). As a result of confusion arising from the above, Lawrence *et al.* (1984) cite Hamanda (1961) reporting anadromy among pond smelt; however, the anadromous smelt discussed in Hamanda's paper are probably *H. nipponensis*.

Bond (1982), and Lawrence *et al.* (1984) report the presence of *H. olidus* in Tuktoyaktuk harbour and coastal areas of Richards Island and the Tuktoyaktuk Peninsula. The highest salinity measured in association with any of these samples was only 5.5 (mean sea water salinity is 35; Sverdrup *et al.*, 1942), well within the salinity tolerance of many freshwater fishes. The salinity tolerance of *H. olidus* is unknown, but all populations of which I am aware are in freshwater.

There is relatively little known about the biology of *H. olidus* in North America. McPhail and Lindsey (1970) and Scott and Crossman (1973) have summarized the available information, most of which was collected incidental to other studies in Alaska.

This paper examines aspects of the life history of pond smelt isolated in a small unnamed lake (designated "Lake 100" during the Arctic Gas biological studies; deGraaf, 1974) on the Yukon coastal plain and compares this population with available data describing populations in the Mackenzie delta, Alaska and Asia.

STUDY AREA

Lake 100 is a typical monomictic tundra lake situated about 10 km southwest of Stokes Point on the coast of the Beaufort Sea (69°18′N, 138°57′W). It has a relatively small surface area (309 ha), shallow depth (3.3 m max.) and low nutrient concentrations. The water remains relatively turbid throughout the open water season (usually early July to early October) due to the combined effects of wind and degrading permafrost, which has caused extensive slumping along the northeast shore. The lake has four shoreline types: (1) rubble and coarse gravel, (2) sand beach, (3) mud and (4) peat. In some sheltered locations, mud bottoms support emergent and submergent vegetation. The lake has no permanent tributaries but receives runoff from several intermittent rivulets that drain the surrounding tundra. The outlet is a small tundra stream that eventually discharges into the Beaufort Sea at Roland Bay (<5 km due north). Streamflow and, therefore, fish movement in and out of the lake are limited to the period between June and October; the stream is frozen to the bottom for the remainder of the year, thus seasonally isolating fish in Lake 100.

METHODS

Samples of *H. olidus* were collected from Lake 100 during August 1972 and July-September 1973. Most samples were collected using a 6 m beach seine (3 mm Marquisette); young of the year were sampled using a 60 cm diameter conical net (505 μm mesh), which was pushed in front of an inflatable boat after the method of Faber (1968).

Fish required for analyses were killed in 10% formalin, then measured and weighed. Fish heavier than 1.0 g were weighed (±0.1 g) on a triple beam balance, and those lighter than 1.0 g were weighed (±0.01 g) on a torsion balance. Sex and maturity were recorded, stomachs and ovaries (from mature females) were preserved in 10% formalin, scales were collected and the sacculus otoliths were removed and stored in glycerol. In addition a subsample of fish was preserved whole for meristic and morphometric examination.

In the laboratory, otoliths were examined whole under reflected light on the dark stage of a dissecting microscope. Each pair of otoliths was examined twice independently. When these readings were not in agreement, the otoliths were examined a third time and a best estimate of age established. Ages given were considered to start during the spring of the year — i.e., a young of the year would reach age 1 during the spring of the following year. Most scales examined from Lake 100 smelt did not reveal annuli; therefore scales were considered unsuitable for aging. Hamanda (1961) reported similar problems with the use of scales for aging pond smelt, but Narver (1966) reported no such difficulties. All maturing eggs in both ovaries of mature females were counted with the aid of a dissecting microscope. Stomach contents were identified and the frequency of occurrence of foods was recorded.

RESULTS AND DISCUSSION

Meristics and Morphometrics

Meristic and morphometric characteristics of Lake 100 pond smelt conformed to the range of values described by McAllister (1963) (Table 1). The only exception was standard length/depth, where the present range was 6.3-7.1 in contrast to the described 4.2-6.3 (McAllister, 1963). This discrepancy suggests that individuals in the Lake 100 population were more slender than their counterparts elsewhere, possibly as a result of poor growth in this tundra lake.

TABLE 1. Meristic and morphometric characteristics of *Hypomesus olidus*

Character	Lake 100	McAllister (1963)
Dorsal fin rays	8-9	7-9
Caudal fin rays	19-20	19
Anal fin rays	11-14	12-16
Pectoral fin rays	10-12	10-12
Pelvic fin rays	8	8
Vertebrae	55-59	52-58
Gillrakers	26-30 (8-10 + 18-20)	26-34 (8-12 + 17-22)
Branchiostegals	6	6-7
Pyloric caecae	2	0-3
Standard length/ head length	4.2-4.8	4-5
Head length/ orbit diameter	3.1-3.7	3.3-4.9
Snout length/ interorbital	0.7-1.2	0.7-1.1
Head length/ anal ray length	1.6-2.6	1.8-2.3
Standard length/ depth	6.3-7.1	4.2-6.3
Attachment of pneumatic duct	subterminal	subterminal

Age and Growth

Growth of Lake 100 pond smelt was very slow compared to growth in the Mackenzie delta and Alaska (Table 2). Young of the year attained a mean length of 17 mm by the end of the first summer and did not reach a length of 50 mm until at least age 2+ (deGraaf, 1975). Few pond smelt sampled from Lake 100 exceeded 70 mm fork length. In Mackenzie delta, neither Stein *et al.* (1973) nor deGraaf and Machniak (1977) reported pond smelt larger than 70 mm in samples from river channels and lakes (n = >280). However, Lawrence *et al.* (1984) found these larger individuals to be relatively common, about 20% of the sample (n = 65) from coastal Richards Island and the Tuktoyaktuk Peninsula. In Black Lake, Alaska (Narver, 1966), and in Lake Ishikari-Furukawa, Japan (Hamanda, 1961), individuals 70-90 mm long were common. Both of these latter populations attained a size of 70 mm by age 2+, whereas the Lake 100 specimens did not approach this size until at least age 5+.

During the 1973 field study, significant differences ($t = 13.36$) were observed between mean fork lengths of age 1+ pond smelt sampled in July (24.3 mm) and those sampled in late August and September (33.1 m). A significant difference ($t = 4.87$, $p<0.05$) was also demonstrated between lengths of age 3+ pond smelt over the same time interval (49.0 mm vs 53.3 mm). However there was no significant difference ($t = 1.274$, $p>0.05$) between the lengths of age 5+ individuals (60.2 mm vs 61.3 mm).

Lake 100 had a unimodal distribution of fish older than young of the year due to the predominance of one year class: age 4+ (sampled in 1972) and age 5+ (sampled in 1973) accounted for about 80% of the sample (excluding young of the year). The maximum ages attained by pond smelt sampled from Lake 100 were 8+ (n = 2, sampled in 1972) and 9+ (n = 1, sampled in 1973). Most of the other studies present trimodal length-frequency distributions (Hamanda, 1961; Narver, 1966; Lawrence *et al.*, 1984). Maximum age reported in these studies was 4 years.

TABLE 2. Mean fork length (mm) by year class of pond smelt from Lake 100, Mackenzie delta and Alaska

	Lake 100			Mackenzie delta[1]			Black Lake, Alaska[2]
Age	N	x	s.d.	N	x	s.d.	x
1+	51	26.2	4.0	6	44.0	6.0	41.0-59.4
2+	10	42.4	2.8	8	53.3	4.0	75.5-80.6
3+	23	51	2.9	1	65.0		
4+	139	59.7	3.1				
5+	114	60.8	4.3				
8+	2	80.0	2.8				
9+	1	92.0					

[1] From deGraaf and Machniak (1977).
[2] From Narver (1966).

Reproduction

A few individuals (n = 6) that were extruding sex products were collected over peat bottom and near submergent macrophyte beds in Lake 100 on 17 July 1973 when the surface water temperature was 10°C, but most smelt captured at this time had already spawned. Narver (1966) reported pond smelt spawning in Black Lake, Alaska, on 26 June 1963 over an organic substrate. Pond smelt eggs in Lake Ishikari-Furukawa were adhesive and were commonly found attached to exposed willow roots in shallow water (Hamanda, 1961).

In Lake 100, the first *H. olidus* larvae were taken 25 July 1973 when the water temperature was 16°C; at that time the mean length of the larvae was 5.5 mm and 90% still had visible yolk sacs. In Black Lake the first young of the year were collected in plankton nets about 30 July (Narver, 1966). Hamanda (1961) reported that *H. olidus* eggs hatched in about 18 days at water temperatures ranging from 9.7 to 11.3°C; colder temperatures resulted in slower hatching.

Pond smelt in Lake 100 reached first maturity at age 3+. In the Mackenzie delta first maturity was recorded at age 2+ (deGraaf and Machniak, 1977). The latter corresponds with the age at maturity of pond smelt from Black Lake (Narver, 1966). By age 4+, over 90% of Lake 100 pond smelt were considered to be sexually mature, and at age 5+ 100% had matured.

Lake 100 pond smelt are apparently capable of repeated spawning. The dominant cohort in Lake 100, aged 4+ in 1972, spawned during the spring of 1973 at age 5+. Gonadal development monitored in this cohort throughout the summer of 1973 revealed that these fish had almost fully developed gonads again by mid-September in preparation for the spring of 1974. The incidence of repeat spawning in the Mackenzie delta is unknown. Neither the Alaskan population (Narver, 1966) nor the Japanese population (Hamanda, 1961) was believed to spawn more than once.

The sex ratio of the Lake 100 population was skewed, with females being most abundant (90 males vs 123 females; $x^2 = 5.1126$; $p<0.05$). In mid-September 1973, gonad weight of pond smelt in Lake 100 accounted for an average of 4.3% of the weight of mature females and 4.7% of males. At this time it was assumed that the gonads were almost completely developed, since egg size among females had reached 0.4 mm, the same size as had been encountered in ripe females taken during early July.

The gonads of both male and female pond smelt from Lake 100 and the Mackenzie delta were highly asymmetrical, with the left gonad being as much as nine times the mass of the right gonad. The right gonad appeared functional but was displaced to the posterior part of the abdominal cavity adjacent to the vent. The left ovary produced an average of 91.8% of maturing eggs in female pond smelt (n = 24 females). The fork length of female smelt from Lake 100 was related to total fecundity by the following equation: $\text{Log } F = 2.100 \log L - 0.5700$, where F = fecundity; L = fork length; N = 24; and r = 0.657. The maximum fecundity recorded was 2523 ova from a 60 mm female.

Food Habits

Pond smelt in Lake 100 were primarily planktivorous; all stomach samples included zooplankton. The type of zooplankton and diet diversity changed with increasing size of pond smelt (Table 3). Rotifers and juvenile copepods were the dominant foods of smaller pond smelt, whereas larger zooplankton were the dominant foods of larger fish. Surface food, most commonly adult dipterans (chironomids and mosquitoes), was taken by both larger and smaller pond smelt. Benthic foods occurred rarely and only in the largest individuals. Stein *et al.* (1973) recorded the presence of chironomid larvae, copepods and cladocerans in a small sample of pond smelt (fork length 30-61 mm) from the upper Mackenzie delta, and Narver (1966) found

them to be largely planktivorous. Taranetz (1937) stated that *H. olidus* resident in a small lake on Sakhalin Island ate mostly dipterans.

In Lake 100, *H. olidus* was the only pelagic planktivore present, but it is likely that ninespine stickleback (*Pungitius pungitius*) provided some degree of competition for the limited zooplankton resource. There was no evidence of significant predation upon *H. olidus* in Lake 100, although a cohabiting population of Arctic grayling (*Thymallus arcticus*) was highly piscivorous (deGraaf, 1975). In addition, a number of potential avian predators were observed in the area, including Arctic Terns (*Sterna paradisaea*) and Oldsquaw Ducks (*Clangula hyemalis*), but none was sampled.

In the Mackenzie delta, pond smelt cohabit with some 30 species of fish (Stein *et al.*, 1973). Although pond smelt constituted a relatively minor proportion of available forage species in the Mackenzie delta, they were reported in the diets of both of the principal predatory species, namely inconnu (*Stenodus leucithys*) and northern pike (*Esox lucius*) (deGraaf and Machniak, 1977). Pond smelt have been identified as a valuable forage species for salmonid fishes (Klyuchareva and Svetovidova, 1969), but in some Alaskan lakes the smelt may be a serious competitor for planktonic food with sockeye salmon (*Onchorynchus nerka*) parr (Narver, 1966; Burgner and Marshall, 1974).

TABLE 3. Percent occurrence of food organisms in the stomachs of pond smelt collected in Lake 100

	Fork Lengths (mm)			
Food Item	11-20 (N=25)	21-30 (N=11)	31-40 (N=6)	>40 (N=110)
Zooplankton				
Cladocerans		9.1%	16.7%	36.2%
Copepods				
Nauplii or copepodid	20.0%	63.6%	16.7%	5.0%
Adult		27.3%	50.0%	69.0%
Conchostracans				12.9%
Rotifers	60.0%	45.5%	100%	41.4%
Benthos				
Chironomid larvae				19.0%
Surface Food				
Adult insects		9.1%		30.0%
Fish				
Pond smelt				0.9%

CONCLUSIONS

Pond smelt in Lake 100 are a very slow-growing and long-lived population, probably as a result of the short growing season and low biological productivity of tundra lakes. However, part of the apparent difference in longevity may be due to the greater precision of the otolith method for aging slow-growing fishes, since the data presented in this paper suggest very slow growth among pond smelt after the onset of sexual maturity. This would preclude identification of year-classes of mature fish by length-frequency and could reduce the accuracy of scale ages, since few circuli would be produced when growth was slow and annuli would be indistinct. Although few pond smelt have been aged from the Mackenzie delta population, available data suggest that the growth rate may be intermediate between that of the Lake 100 population and the rates reported in southern Alaska (Narver, 1966) and Hokkaido, Japan (Hamanda, 1961). The large size and apparent migratory behaviour of the pond smelt in the Richards Island and Tuktoyaktuk Peninsula reported in recent studies (Bond, 1982; Lawrence *et al.*, 1984) are in contrast to the results presented here as a result of earlier work and, as such, are worthy of further study.

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