Zooplankton density and diet composition of fish larvae in three bays in the upper St. Lawrence River

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Abstract.–Vegetated areas are used for spawning by many fish species including Northern Pike *Esox lucius* and Muskellunge *E. masquinongy.*This research was designed to examine the timing of the development of the aquatic community in Northern Pike and Muskellunge nursery areas. Simultaneous collections of zooplankton and fish larvae were made by pushing paired, 0.15 m^2 250 µm-mesh nets in three bays in the upper St. Lawrence River. More than 31 taxa of zooplankters and 17 fish species were collected dominated by *Polyphemus*, *Diapahanasoma*, and Yellow Perch. Northern Pike were estimated to be capable of feeding on potential forage fish just prior to the peak forage fish density and Muskellunge larvae were capable of feeding near the end of the peak forage fish density in Buck Bay. Both species were capable of feeding approximately one week prior to the peak forage fish density in Flynn Bay. This one additional week could allow the Northern Pike and Muskellunge larvae to prey on fish at nearly double the cross-sectional area from the previous week. Northern Pike could increase their potential advantage if they were spawned in the flooded meadows. The warming of the shallower water at an earlier date and the high density of zooplankton would allow Northern Pike larvae to reach the nursery bay at a much larger size than those Northern Pike and Muskellunge that were spawned in the shallow but cooler water of the bay.

Few habitats undergo as much seasonal change as do the shallow aquatic areas at northern latitudes: from an ice-covered surface and sediments that are devoid of vegetation in winter to open water and profuse bottom vegetation by mid-summer. These changes provide multiple seasonal habitat types that can support differing life history strategies that, in total, produce a complex and dynamic community. These features are characteristic of the embayments of the upper St. Lawrence River that provide important nursery areas for fish larvae, various zooplankton, and other invertebrates.

Vegetated areas are used for spawning by many fish species and provide a refuge from predation for fish larvae (Werner et al. 1983) as well as supporting an extensive assemblage of invertebrates, many of which are preyed upon by fish larvae (Keast and Eadie 1985; Engel 1990). Two fish species that are endemic to the St. Lawrence River, Northern Pike *Esox lucius* and Muskellunge *E. masquinongy*, use the vegetated areas for spawning and their larvae and juveniles use these areas as nurseries. Northern Pike have spawned historically in seasonally-flooded meadows surrounding the bays but in recent years have been found to spawn in the nearshore and deeper water areas when vegetation is present (Farrell et al. 1996). Muskellunge spawn in the nearshore areas over the first new growth of vegetation.

The populations of Northern Pike and Muskellunge have undergone dramatic declines in the St. Lawrence River over the past 30 years (McCullough and Klindt 1997; Farrell 1998) and Muskellunge populations have decreased elsewhere (Dombeck et al. 1984). Spawning habitat alteration has been proposed as a probable cause for the decline in Muskellunge and Northern Pike populations (Trautman 1981; Dombeck et al. 1986). The regulation of water flow in the St. Lawrence River has had an impact on the shallow emergent vegetation and has facilitated the formation of dense monocultures of *Typha*. The presence of vegetation has been implicated as a behavioral cue in Northern

Pike spawning (Bry 1996), but Northern Pike do not spawn in *Typha* (Franklin and Smith 1963). Elimination of the seasonally-flooded meadows would restrict spawning Northern Pike to the habitats in shallow water or in deeper, cooler water if vegetation is not present in shallow water due to ice-scouring. Restricting spawning of Northern Pike could create a mismatch in the timing of Northern Pike larvae and their zooplankton and forage fish prey. It could also affect Muskellunge larvae as there would then be competition from the displaced Northern Pike that would spawn in the shallow water.

This research was designed to examine the timing of the development of the aquatic community in Northern Pike and Muskellunge nursery areas. Three questions were posed to examine the time of appearance of esocids, zooplankton, and forage fish:

1—is the mean density of potential forage fish larvae different among bays?

2—is the appearance of forage fish matched with increasing zooplankton density?

3—is forage fish density matched with the estimated inception of the consumption of fish larvae by Northern Pike and Muskellunge?

Study sites

Buck, Lindley, and Flynn bays are oriented in a SW to NE direction (Fig. 1) and are affected by the prevailing westerly and southwesterly winds. The extreme interior of Buck Bay is sheltered from the full force of the wind by the surrounding granite hills and by Wolfe, Hickory, and Arabella islands. Lindley Bay has been formed by the accumulation of sediment between the NW tip of Club Island and Grindstone Island. This narrow strip of land has been colonized by willow *Salix* and cattail *Typha*. Two small islands, Whiskey and Papoose, to the SW of Lindley Bay provide some protection from SW winds. Lindley Bay and Flynn Bay can be connected by water during sustained SW winds or by high water level. Channels maintained intermittently by beavers *Castor canadensis* and muskrats *Ondatra zibethicus* also traverse the land and *Typha* between the bays in some years. The sediments in most of Flynn Bay can be stirred up with a SW wind and the SW part of the bay can be affected similarly by a strong NE wind. Water movement within the bays is caused primarily by wind action rather than river current: the tributaries contribute the only measurable water current (<1 cm/s) and this is primarily during spring runoff and rainfall. Lindley Bay is the smallest of the three bays at 10.4 hectares (ha), Buck Bay has a surface area of 18.3 ha, and Flynn Bay is the largest of the three bays at 69 ha.

Methods

Simultaneous collections of zooplankton and fish larvae were made by pushing paired, 0.15 m^2 250 µm-mesh nets (1:8 mouth dia to length) for 2 min. The nets were mounted in a PVC frame that was mounted on the bow of a small boat. Samples were taken in random locations in two areas in Buck and Lindley bays and in three areas in Flynn Bay. Areas were delineated by the presence or absence of vegetation. Sampling depth began just below the water surface. Boat speed (0.7 m/s) was constant during the sample collection. The collected material, including any plants, was washed into a 19-L bucket where the plants were shaken to dislodge any organisms and then the plants were discarded. The remaining sample was washed through the net into jars and preserved in 10% formalin. Three pairs of samples were taken in each bay on each collecting date at approximately weekly intervals from May through August in 1996 and 1997 (n=432). Sampling began after dusk (1800–2000 h) to reduce gear avoidance and started later as the season progressed.

Flowmeters were not used in the nets because any vegetation caught on the flowmeter bridle could impede the motion of the flowmeter rotor. The maximum sample duration was estimated by taking five samples at 1 and 2 min (without flowmeters) in the sampling site, moving the boat to open water with the collected samples remaining in the nets, and then continuing the sample for an equal time with flowmeters mounted in the nets. Flowmeter readings of the samples were compared to readings taken from samples taken in open water only. Similar flowmeter readings (counts/s) between the two types of samples would indicate that there was no measurable decrease in filtration efficiency (Conrow et al. 1990). A maximum sample duration of 2 min was possible without a decrease in efficiency. This sample time did not account for accumulated algae which was present in some samples. The algae would have decreased the filtering efficiency, with the volume filtered being overestimated and the resulting density underestimated.

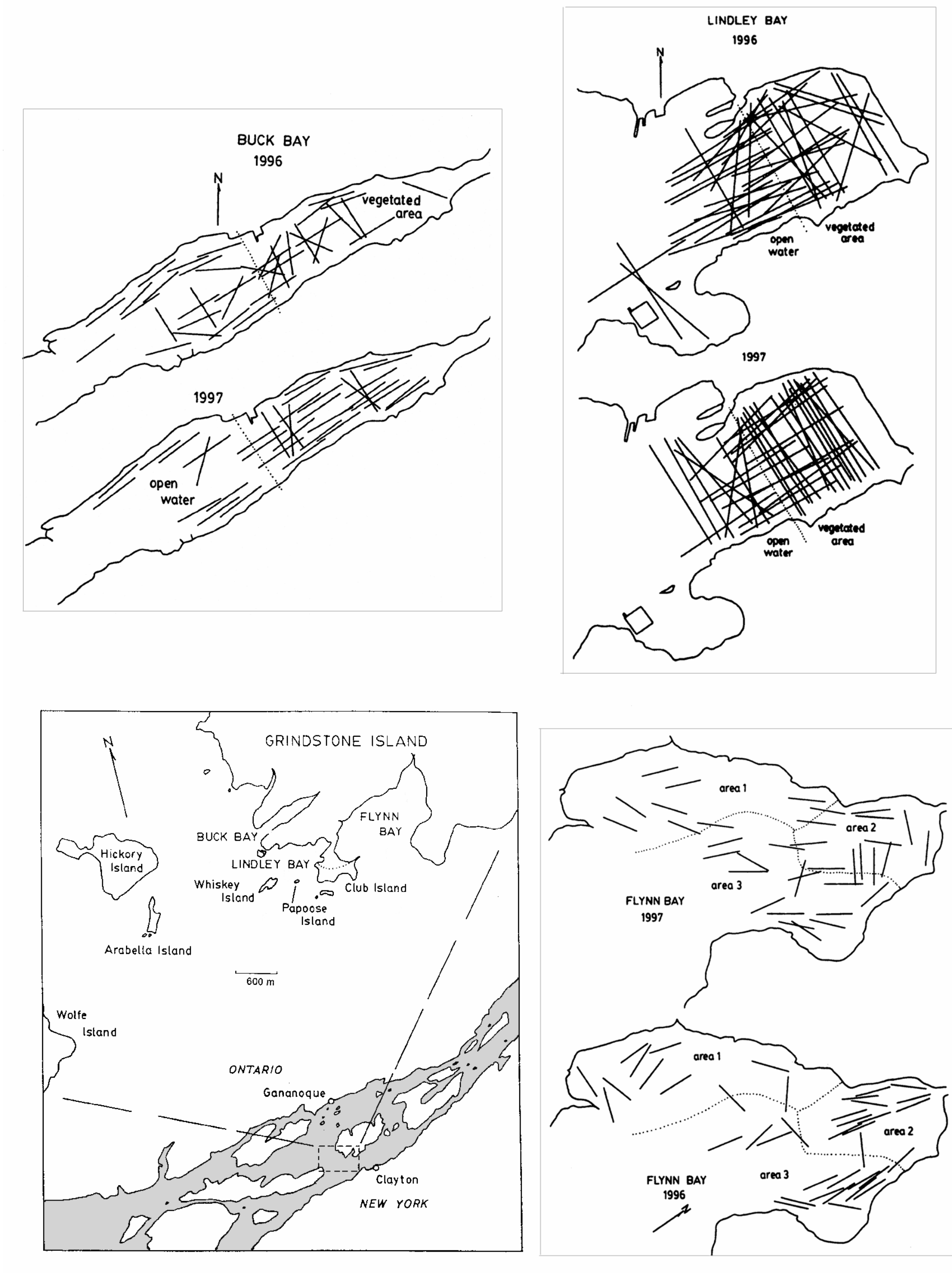


Figure 1. Location of study bays in the St. Lawrence River (lower left) and the estimated tracks of each pushnet sample in 1996 and 1997.

Dense surface patches of vegetation and algae were avoided during sampling whenever possible. Some samples were retaken when vegetation or algae reduced the forward speed of the boat. Mean sample volume in each year was estimated by averaging the distance traveled in five successive 2 min samples over a measured distance in the sampling site.

Five single-net samples of zooplankton were taken in the meadow areas of Buck and Flynn bays on 28 April, 1997, to estimate the zooplankton density that would be available to Northern Pike that were spawned in the meadows. Northern Pike larvae were seen in the meadows on 28 April. The samples were taken with a 250 µm-mesh dipnet which sampled an estimated 0.038 m^3. The plankton were identified and counted using the same methods used for the pushnet samples. No samples of this type were taken in Buck or Flynn bays in 1996 since there was no Northern Pike spawning in the meadow areas and no samples were taken in Lindley Bay since it did not have a meadow area.

Water temperature and dissolved oxygen (YSI meter) were measured at surface and bottom at one of the three sample pairs in each study site on each sampling date. Water temperature was also measured every 2 h at one site in each bay with Onset recorders. pH (Oakton electronic meter) and alkalinity (LaMotte test kit) were measured only at the water surface.

Algae (primarily *Spirogyra*) was prevalent in some samples and was removed in the laboratory prior to counting the organisms. The algae was examined separately and any remaining organisms were returned to the sample. Fish larvae and fish eggs were removed from the sample and treated separately. The zooplankton of each sample were placed in 500 ml of water, stirred, and three successive 5 ml subsamples were removed by pipette. The contents of each subsample were identified and counted into various organism taxa. The average count of the three subsamples for each organism category was multiplied by 100 to estimate the mean number in the sample (Wetzel and Likens 1991) and the mean sample number was divided by the estimated volume filtered to estimate the sample density of each category. A survey of the genera of copepods and cladocerans that were present was made as the subsamples were processed. Not all copepods and cladocerans were identified so there may have been additional genera present.

Sample locations were numbered consecutively and assigned post-hoc to either vegetated or open water areas (based on the midpoint of the sample) in Buck and Lindley bays and to three geographical locations in Flynn Bay. Area 1 of Flynn Bay was poorly vegetated during most of the spring and early summer and as vegetation developed in mid-summer, the area became thick with algae. Vegetation developed earlier in area 2 than in the other areas, and area 3 was less vegetated in summer. The vegetation that was present was dispersed and included more stands of *Scirpus* and *Carex* reeds than in the other areas. Area 3 also had some open water closer to the bay mouth. Relative seasonal density of six taxa of zooplankters (calanoid and cyclopoid copepods, *Bosmina*, *Polyphemus*, *Diaphanasoma*, and other cladocera) was compared among these areas.

Fish larvae were identified by category, counted, measured (TL), and a maximum of 50 digestive tracts from each taxa in each sample was removed for analysis. Gut contents were estimated from the entire digestive tract from those larvae in which the stomach had not developed but only from the stomach if it had developed. The remainder of the gut was not examined to avoid any bias due to variable digestive rates of prey (Gannon 1976; Sutela and Huusko 2000). Diet analysis was made only on larvae that had inflated gas bladders under the assumption that these larvae would be capable of feeding. The contents of the digestive tracts were identified into the same categories used for zooplankton and counted.

Statistical analyses (SAS Institute, Inc. 1988) were made using an overall alpha of 0.05. The mean catch of zooplankton and fish larvae among sample pairs within each bay was compared using analysis of variance to determine if there was a bias in catch due to sampling net position. The density of potential forage fish prey (Alewife *Alosa pseudoharengus*, Golden Shiner *Notemigonus crysoleucas*, Spottail Shiner *Notropis hudsonius*, and Carp *Cyprinus carpio*) among bays, and among areas within bays (both years combined), was compared using the nonparametric Kruskal-Wallis chi-square approximation on ranked densities. Multiple comparisons were made using the Tukey test.

Yellow Perch *Perca flavescens* densities among bays and among areas were examined separately using the same method. Nonparametric tests were used because the data distributions of forage fish and Yellow Perch were not normally distributed.

Results

Sampling. Sample distance was approximately 87 m and sample volume was estimated to be 13.3 m^3 in 1996 and 14.6 m^3 in 1997. This sampling distance resulted in greater coverage of Buck and Lindley bays (Fig. 1) than of Flynn Bay. There was no significant statistical difference in the mean catch of zooplankton between the sample pairs within each bay so the paired samples were pooled for analysis.

Table 1. Pairwise statistical results of sample pair comparisons for 1996 and 1997. df=1 in each test.

	1996		1997	
	F	*P*	*F*	*P*
Zooplankton	0.38	0.53	0.15	0.7
Fish larvae	0.02	0.89	0	0.99

Temperature. Surface and bottom water temperature was similar between years and among bays in both years. Water temperature rose gradually from 10°C in early May to a maximum of 27°C in mid-August in 1996 and in mid-July in 1997. Water temperature in the marsh areas was 4° –6°C higher than in the bays until the third week of May.

Dissolved oxygen. Seasonal patterns of dissolved oxygen were similar in both years and oxygen saturation was near or greater than 100% during all sampling periods other than in June.

pH. Water in each bay was generally basic. pH values ranged from 7.3–9.2 (mean=8.1, n=99). Decreases in pH were observed after periods of heavy rain but pH values did not decline to levels that would be detrimental to fish.

Alkalinity. Alkalinity (as total $CaCO_3$) ranged from 90–140 mg/l (phenophthalein alkalinity was zero) and there were no trends in values during the season or among bays.

Zooplankton density. The estimated density of all taxa combined was higher in the Flynn Bay marsh than in the Buck Bay marsh (Table 2). Cyclopoid copepods were the most abundant taxa in both marshes. The density of *Bosmina*, *Diaphanasoma*, and other cladocera were similar in the Buck Bay marsh but the density of *Bosmina* was lower than the density of *Diaphanasoma* and other cladocera in the Flynn Bay marsh. The density of 31 taxa was estimated from the samples (Table 3). Some of these taxa are not considered to be planktonic (e.g. midges, hydra, damsel- and dragonflies, leeches, caddisflies, planaria, and oligochaetes) but were captured as the nets disturbed the plants on which these organisms live. Many of the non-planktonic organisms were utilized as food by fish larvae so they were included as zooplankton.

The mean density of cladocerans (all taxa combined) was higher than the density of copepods in Buck and Flynn bays in both years but the difference was greater in 1996. The density of these two taxa were similar in Lindley Bay in 1996 but cladocerans were more abundant in Lindley Bay in 1997 due, in part, to a 72% decrease in cyclopoid copepod density. Cladoceran abundance was also lower but only by 24%.

Copepods decreased in abundance in early spring and then increased in abundance in June and August. This pattern was evident in each year and in all areas of the study bays (Figs. 2 and 3). *Bosmina* density increased in June, decreased in July, and then increased in August. The density of the other cladocera group increased in spring but was more variable during the summer, perhaps reflecting the variable contribution from the genera that were combined in the group (Table 3). *Bosmina* density in the spring was low in areas 2 and 3 in Flynn Bay in 1996, in all areas of Flynn Bay in 1997, and in both areas of Buck Bay in 1997. *Bosmina* density was similar in 1996 in Buck Bay, area 1 in Flynn Bay, and in both areas of Lindley Bay in spring of both years.

Polyphemus was the most abundant genus in Lindley Bay in each year and reached its peak abundance in August (Fig. 4). Density of *Polyphemus* in Lindley Bay was up to 80 times higher than in Buck or Flynn bays. Mean density was higher in 1996 than in 1997.

Diaphanasoma was the most abundant genus in Buck and Flynn bays in 1996 but not in 1997 (Table 3). *Diaphanasoma* density was low in the spring, increased from June to July, and was variable in August (Fig. 4).

Fish larvae density. Larvae of 17 fish species were collected in the pushnet samples (Table 4).

Table 2. Estimated mean density (number/m^3) of zooplankton in marsh areas of Buck and Flynn bays on 28 April 1997.

Taxa	Buck Bay	Flynn Bay
Calanoid copepod	6	35
Cyclopoid copepod	394	1,235
Harpacticoid copepod	6	88
Diaphanasoma	112	412
Bosmina	88	206
Other cladocera	129	412
Oligochaete	29	29
Midge larva	88	29
Dragonfly nymph	23	59
Beetle larva	59	59

Yellow Perch dominated the fish larvae accounting for 93% of the total number caught. Sunfish (all unidentifed centrarchids that were less than 9.0 mm TL) were second in abundance at 3.1%. Yellow Perch mean density was highest in Buck Bay in 1996, and second in abundance in Buck Bay in 1997. Yellow Perch mean density in Buck Bay was an order of magnitude greater than Yellow Perch mean density in all other bays. The highest single sample density of Yellow Perch was 659/m^3 on 26 May 1996 in Buck Bay and accounted for 44% of all Yellow Perch collected.

Most fish species were low in density in each study bay. Only Alewife, Yellow Perch, and sunfish occurred at densities greater than 1.0/m^3 in a single sample in 1996, the remainder were at densities less than 0.5/m^3. Alewife, Yellow Perch, sunfish, Golden Shiner and Pumpkinseed *Lepomis gibbosus* exceeded 1.0/m^3 in at least one sample in 1997. Largemouth Bass *Micropterus salmoides* were abundant in a single sample (60/m^3) but were otherwise collected at less than 0.5/m^3. Muskellunge eggs were collected in one pushnet sample in Buck Bay but larvae of Muskellunge and Northern Pike were not collected in the pushnet samples. Both were collected in dipnet samples along with Longnose Gar *Lepisosteus osseus*, White Sucker *Catastomus commersoni*, and Redhorse Sucker *Moxostoma* spp. The seasonal density of *Coregonus* and Burbot *Lota lota* was underestimated since the majority of these larvae would have hatched prior to the start of sampling (Auer 1982).

There was no significant statistical difference in the ranked densities of Yellow Perch among the study bays in 1996 (χ^2=1.09, P=0.58, df=2) but Yellow Perch ranked density was significantly higher (χ^2=7.36, P=0.02, df=2, Tukey critical value =3.38) in Buck Bay than in Lindley Bay (but not Flynn Bay) in 1997. The mean density of Yellow Perch was greater in Buck Bay in 1996 due to a few large catches, and without these, the density among bays was similar by sample and sample date. The ranked density of potential forage fish (Alewife, Golden Shiner, Carp, and Spottail Shiner) was significantly higher (χ^2=9.37, P=0.009, df=2, Tukey critical value=3.34) in Buck Bay in 1996 and 1997 (χ^2=8.94, P=0.01, df=2, Tukey critical value =3.34) than in the other bays due to a higher density of Alewife in 1996 and Golden Shiner in 1997. Density of potential forage fish was not significantly different in Lindley and Flynn bays. The first question posed in this study asked if there was a difference in forage fish density among bays? The answer is yes and that Buck Bay had a higher density of forage fish than the other bays in these two years.

Six fish categories (Yellow Perch, Alewife, Brook Silverside *Labidesthes sicculus*, sunfish, Golden Shiner, and Spottail Shiner) were caught in vegetated and open water areas of Buck and Lindley bays and in all areas of Flynn Bay. Ten species (Largemouth Bass, Smallmouth Bass *Micropterus dolomieu*, Rock Bass *Ambloplites rupestris*, Pumpkinseed, Bluegill *Lepomis macrochirus*, Carp, Bluntnose Minnow *Pimephales notatus*, Fathead Minnow *Pimephales promelas*, Banded Killifish *Fundulus diaphanus*, and Tessellated Darter *Etheostoma olmstedi*) were collected only in the vegetated areas (and areas 1 and 2 in Flynn Bay). *Coregonus* was collected only in area 3 of Flynn Bay. Burbot were caught in the vegetated area of Buck and Lindley bays but only in area 3 of Flynn Bay. There was no significant difference in potential forage fish density (both years combined) by area within bays (Buck Bay, χ^2 =0.36, P=0.54; Lindley Bay, χ^2=2.22, P=0.14; Flynn Bay, χ^2=0.71, P=0.70).

The length frequency distributions of five of six fish species exhibited an expected pattern of greater abundance of recently-hatched larvae declining progressively as the larvae increased in length. Few recently-hatched Golden Shiner larvae were captured and the largest proportion captured was between 16–20 mm in length (Fig. 5). Yellow Perch and Carp were less available to the sampling

Table 3. Mean zooplankton density (number/m^3) collected in pushnets in the three study bays in 1996 and 1997. Number of samples was 216 in each year.

	1996			1997[1]		
Taxa	Buck	Lindley	Flynn	Buck	Lindley	Flynn
Copepods[2]:						
Calanoid	265	857	531	139	744	358
Cyclopoid	424	915	835	174	252	381
Harpacticoid	0.1	0.3	1	0.2	0.2	0.3
Polyphemus	32	1,502	18	5	1,050	7
Leptodora	1	18	2	1	6.3	18
Diaphanasoma	815	84	1436	9	26	54
Daphnia	5	21	360	0.7	27	166
Holopedium		0.03	0.07		0.1	0.2
Bosmina	27	137	38	27	111	90
Other cladocera[3]	1,092	298	1,000	289	128	577
Ostracod	69	12	207	419	17	555
Oligochaete	8	6	10	100	5	25
Midge larva	10	8	12	16	5	9
Midge pupa	0.03	0.3	0.3	0.4	0.8	1
Midge adult	0.07		0.1	0.1	0.6	0.2
Mosquito pupa		0.03	0.03	0.03	0.03	0.06
Mosquito adult					0.03	
Biting midge	0.03		0.03	0.06		0.8
Mayfly nymph	0.3	0.1	0.4	0.2	0.06	0.06
Dragonfly nymph		0.03	0.03			
Caddisfly larva	1	5	3	1.4	2	4
Hydra	6	7	5	13	5	10
Water mite	14	6	29	26	7	17
Amphipod	12	3	55	5	0.8	190
Diptera larva	0.07	0.1	0.03	0.06	0.03	
Asellus		0.03	0.03			0.1
Damselfly larva	0.1	0.2	0.4	1	0.6	0.2
Beetle larva	22	5	3	0.8	0.03	0.3
Planaria	0.6		0.8	0.6	0.3	0.8
Leech			0.2	0.03		
Aquatic caterpillar	0.03		0.1	2	0.06	0.2

[1] *Mysis relicta* and *Bythotrephes cederstroemi* were observed in the samples but their density was not estimated.

[2] Genera included *Epischura*, *Eurytemora, Leptodiaptomus*, *Skistodiaptomus*, *Acanthocyclops*, *Diacyclops*, *Mesocyclops*, and *Tropocyclops*.

[3] Genera included *Acroperus*, *Alona*, *Bunops*, *Ceriodaphnia*, *Chydorus*, *Eurycercus*, *Eubosmina*, *Pleuroxus*, *Scapholeberis*, *Sida*, and *Simocephalus*.

gear than the other potential prey species at fish lengths greater than 14 mm. Gear avoidance did not appear to occur in the more abundant species. The low number of larger Yellow Perch may be the result of their transition to a more demersal life (Mills and Forney 1982).

Fish larvae diets. Eighteen zooplankton taxa were identified in the diets of fish larvae collected in the three study bays. Copepods were the primary prey (by number) for the majority of fish species (Tables 5–7). Three zooplankton taxa were consumed at less than 0.01% by a single fish species: *Leptodora* by Golden Shiner; *Daphnia* by Yellow Perch, and diptera larvae by Banded Killifish. More fish taxa utilized *Bosmina* in Flynn Bay in 1997 than in any other bay or year.

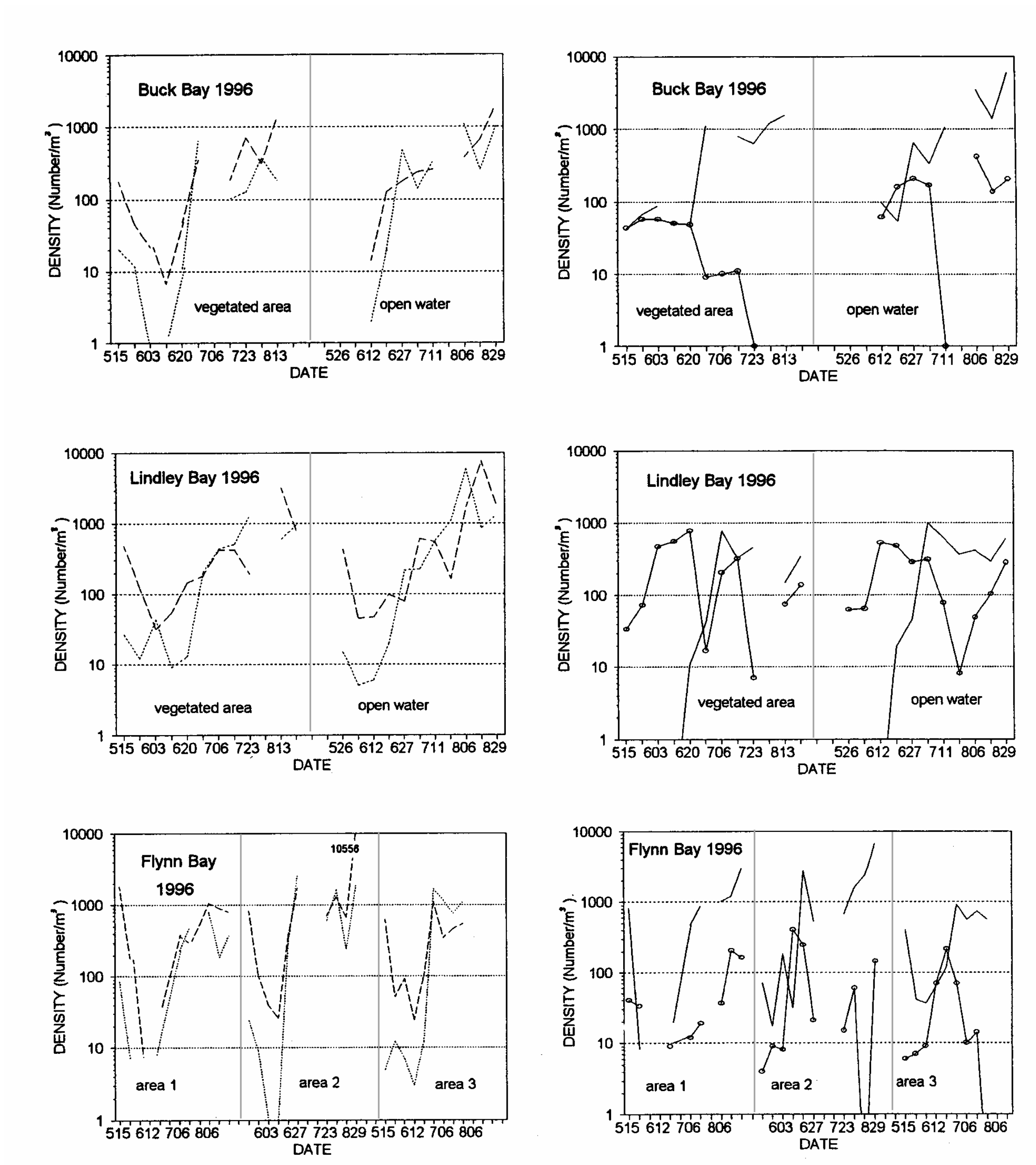
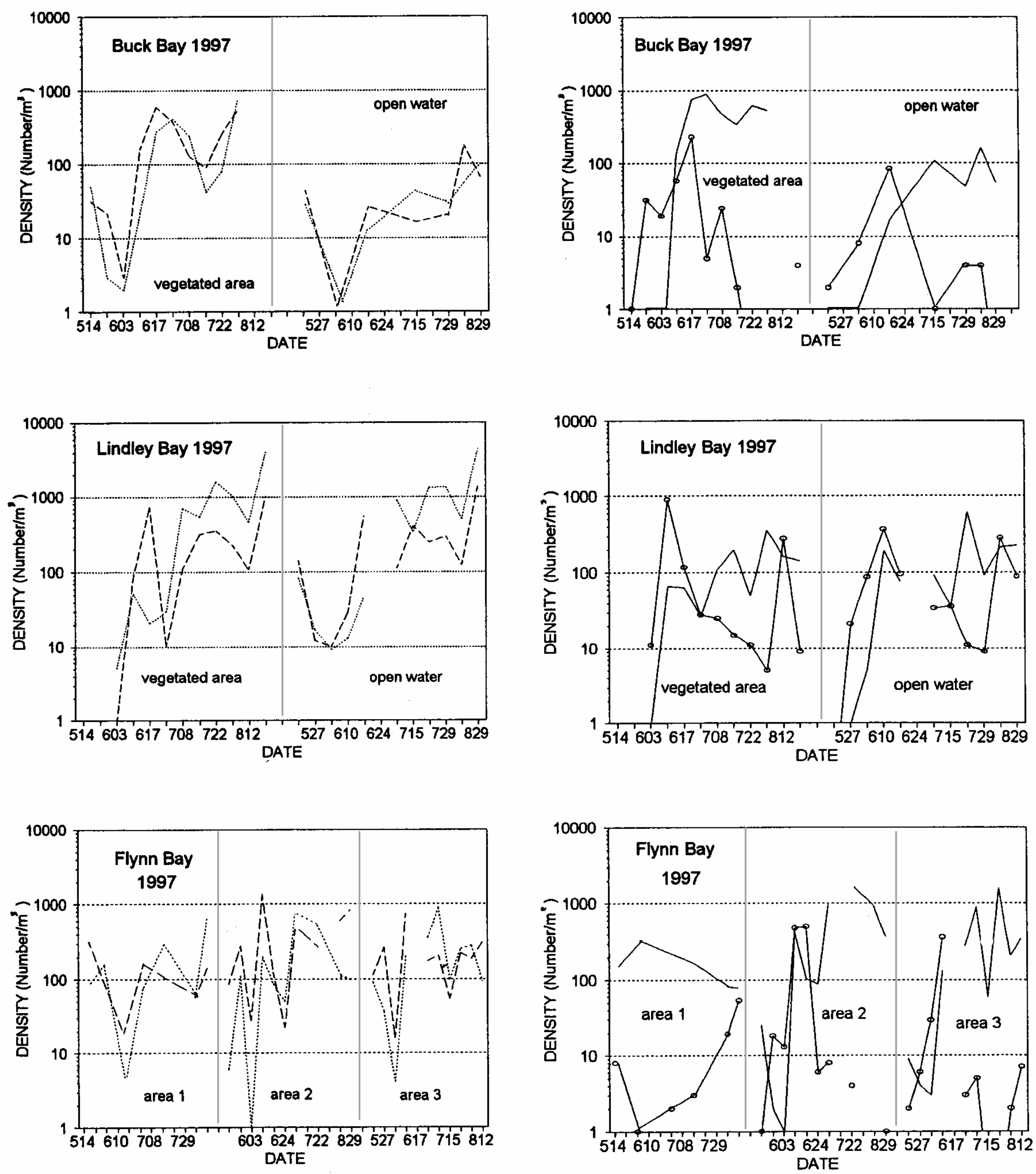


Figure 2. Seasonal mean density (log scale) of four primary zooplankton prey of fish larvae in vegetated and open water areas of Buck and Lindley bays and in three areas of Flynn Bay in 1996. The zooplankton taxa are calanoid copepods (dotted line), cyclopoid copepods (dashed line), *Bosmina* (open circle), and other cladocera (solid line).

Fish were consumed infrequently and only by Yellow Perch, Largemouth Bass, and Smallmouth Bass.

The diet of Yellow Perch was primarily of copepods except for Yellow Perch in Buck Bay in 1996 where the diet included a greater percentage of *Bosmina*, other cladocera, and rotifers (Table 5). The sunfish diet was primarily copepods and rotifers with less than 1% cladocera except in Flynn Bay (1997) where cladocera comprised 51% and copepods comprised less than 25% (Table 6). Copepod density was lower in Flynn Bay in 1997 than in 1996 and cladocera density was higher. The diet of Alewife was poorly described as more than



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70% of those examined did not have food in their alimentary tract except for those examined in Buck Bay in 1996 where 53% of the fish examined contained prey taxa. The primary prey for those Alewife was copepods.

Bosmina was a primary prey only for Golden Shiner and Spottail Shiner. The relatively high density of *Polyphemus* (Lindley Bay) and *Diaphanasoma* (Buck and Flynn bays, 1996) resulted in an increased level of consumption but not by all fish species: Brook Silverside and Spottail Shiner consumed a greater percentage of *Polyphemus* while sunfish and Golden Shiner consumed more *Diaphanasoma*. Yellow Perch was the only species in which a marked period of low feeding success (26–27% fish without food) was

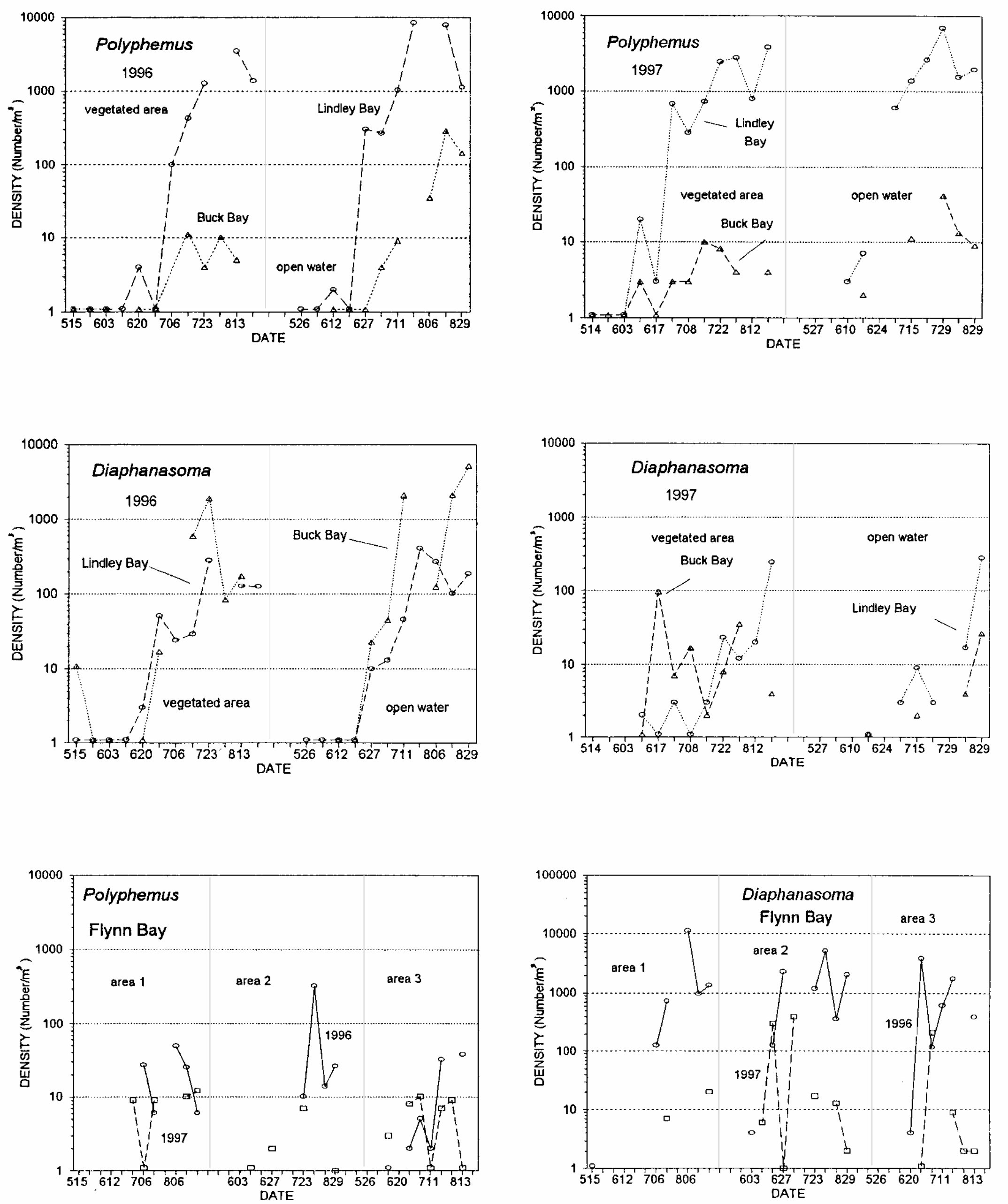

Figure 4. Seasonal mean density (log scale) of *Polyphemus* and *Diaphanasoma* in the three study bays in 1996 and 1997.

seen. Lower feeding success occurred from 26 May–3 June in both years and coincided with low copepod density (Buck Bay, 1996) or decreasing copepod density (Flynn Bay, 1997). More than 80% of all Yellow Perch examined that did not have food in their stomachs occurred during this period. The percentage of Yellow Perch that were without food in Lindley and Flynn bays (1996) and in Lindley and Buck bays (1997) ranged from 12 to 15%. The diet of Yellow Perch in Buck Bay (26 May–3 June) included fewer copepods (15.6%) and more *Bosmina* (48%) than in the other bays. The percentage of copepods consumed in Flynn Bay

Table 4. Mean fish density (number/m^3) and number of fish collected in pushnets in the three study bays in 1996 and 1997. Sample volume was 13.3 m^3 in 1996 and 14.6 m^3 in 1997. Number of samples was 216 in each year.

	1996			1997			Total
Taxa[1]	Buck	Lindley	Flynn	Buck	Lindley	Flynn	collected
Yellow Perch	25	2.1	5.2	17.4	1.23	8.4	57,333
Alewife	0.2	0.1	0.05	0.09	0.25	0.08	691
Brook Silverside	0.006	0.04	0.05	0.01	0.03	0.04	169
Sunfish (< 9 mm)	0.08	0.2	0.7	0.3	0.4	0.3	1,926
Largemouth Bass			0.002	0.9		0.007	839
Smallmouth Bass						0.001	1
Rock Bass	0.001			0.001	0.001		3
Pumpkinseed[2]				0.03	0.008	0.006	34
Bluegill	0.001						1
Burbot				0.002	0.006	0.002	9
Coregonus[3]			0.001				1
Carp			0.006	0.02	0.006	0.03	51
Golden Shiner	0.01		0.01	0.3	0.006	0.04	473
Spottail Shiner		0.002	0.009	0.005	0.05	0.04	76
Bluntnose Minnow		0.002					2
Fathead Minnow		0.001	0.003				4
Banded Killifish	0.001	0.008	0.006	0.002		0.01	24
Tessellated Darter			0.006			0.01	11

[1] Northern Pike, Muskellunge, Longnose Gar, White Sucker, and Redhorse Sucker were caught by dipnet but not pushnet.

[2] Pumpkinseed were probably present in 1996 but were less than 9 mm TL so were identified only as sunfish.

[3] Species identity could not be determined but it was either Lake Herring or Lake Whitefish.

(26 May–3 June) was 60% and the diet included 18% bivalves (glochidia possibly from *Elliptio complanata*) and fewer *Bosmina* (16%).

The degree to which forage fish are successful in moving from endogenous to exogenous feeding depends on the appropriate timing of fish and zooplankton. Yellow Perch density increased in late May as copepod density decreased. Cladocera density increased at this time but it was not a major prey of Yellow Perch in all areas. Yellow Perch that hatch earliest may be at a disadvantage in regards to copepod prey but may be able to survive in some areas by consuming cladocerans. Spottail Shiner, Carp, and Golden Shiner density increased during the first two weeks in June, which was similar to the time that copepod and cladoceran density also increased. Alewife density increased in late June, which would be during the increase in zooplankton. These forage fish species were better matched in time with zooplankton prey. The answer to the second question posed in this study, is the appearance of forage fish matched with increasing zooplankton density, would be that four of the five species were well matched in time with zooplankton but that Yellow Perch were less well matched.

Forage fish density and esocids.

The last question that was posed in this research asked if the peak in forage fish density was matched in time with the estimated start of fish consumption by Northern Pike and Muskellunge larvae. The timing was estimated by using the date of collection of Northern Pike and Muskellunge eggs, bay water temperature profiles, time required for development, and cross-sectional area estimates of prey fish.

Northern Pike eggs were collected in Buck Bay on 27 May 1997, and the resulting larvae would be capable of feeding at 13 mm by mid-June (Fig. 6). Forage fish (Alewife, Carp, Spottail Shiner, Golden Shiner) density near this date was less than 0.14/m^3 and of those species present, only Golden Shiner could be consumed by 13 mm Northern Pike. The other species would have cross-sectional areas larger than the maximum that Northern Pike could accomodate. Yellow Perch were also

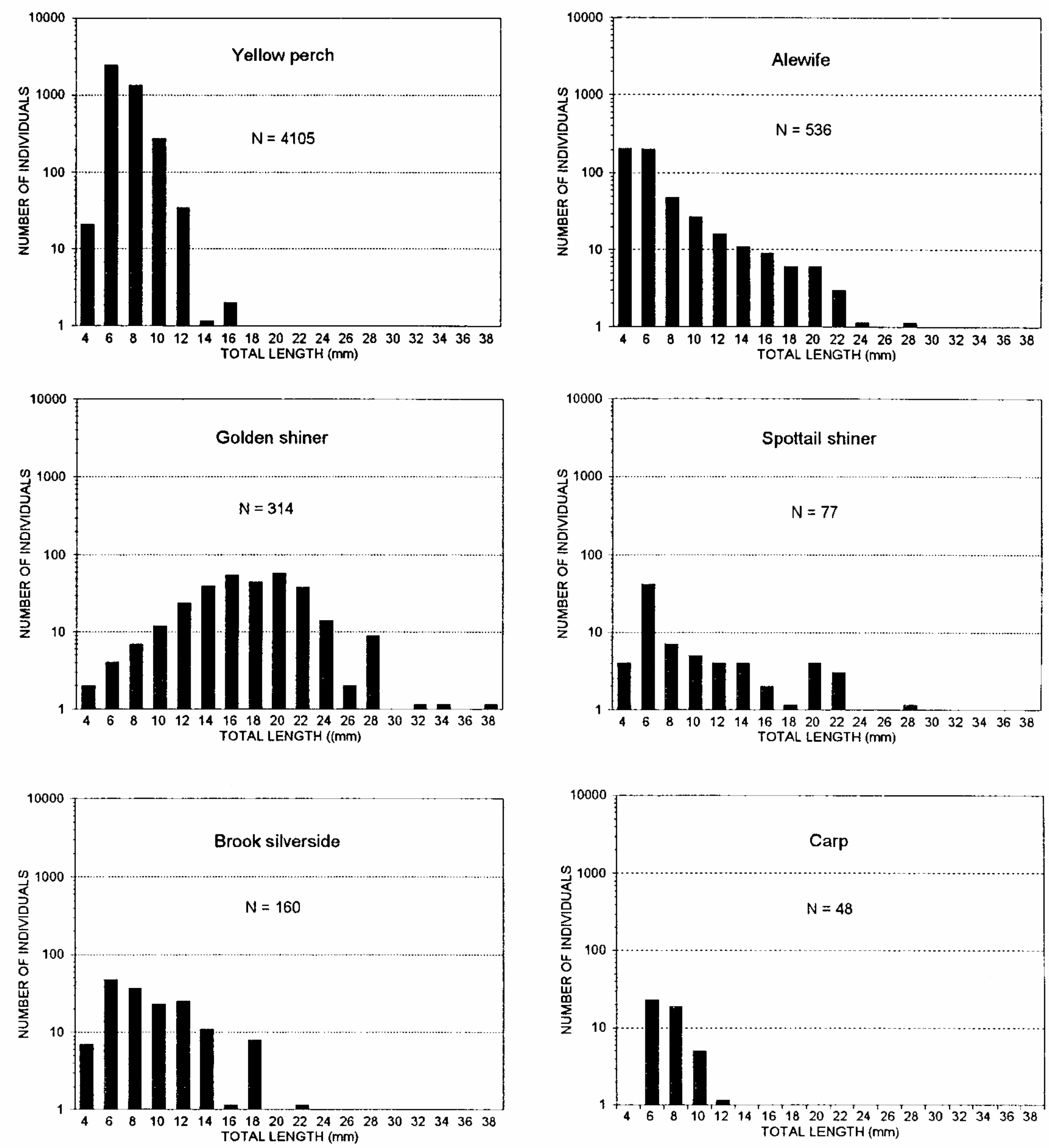

Figure 5. Length frequencies (log scale) of potential prey fishes of Northern Pike and Muskellunge. N is the number measured. Frequency values of 1 were raised to 1.15 so that they would appear on the graph.

present at 0.6/m^3 but less than 10% of those could be consumed by Northern Pike at 13 mm. The majority of Yellow Perch were greater than 8 mm TL and their cross-sectional area would be too large for these Northern Pike. These Northern Pike could grow to 19 mm after another week, which would place them near the peak of the forage fish density. The peak density of forage fish was 14/m^3 in Buck Bay (1997) and occurred from 24 June–8 July. These larger Northern Pike could consume Carp (up to 9 mm), and Spottail Shiner and Golden Shiner (up to 11 mm). Carp (5.8–6.0 mm) and Spottail Shiner (8–11 mm) collected at this time could be consumed by Northern Pike but only a small percentage of the Golden Shiner (9–13 mm). Golden Shiner accounted for 92% of the forage fish

Table 5. The percent (by number) of prey taxa in the diets of fish larvae collected by pushnet in Buck Bay. Unidentified sunfish that were less than 9 mm TL were combined as sunfish.

	Fish taxa 1996							
Prey taxa	Yellow Perch	Sunfish	Alewife	Golden Shiner	Brook Silverside	Bluegill	Banded Killifish	Rock Bass
Copepod	25	89	70	17	18	12	48	33
Polyphemus				0.8				
Diaphanasoma	0.3	9	10	3				
Bosmina	24	0.1	3	61		43		
Other cladocerans	21	0.1		16		45	52	
Water mite				0.3				64
Amphipod				0.3				3
Rotifer	30	2	17		82			
Bivalve		0.5						
Beetle larva				0.3				
Number examined	672	58	78	12	3	1	1	1
Mean TL (mm)	7.6	6.1	6.8	15.8	13.5	—	—	—
Size range (mm)	6.2-16.3	5-7.5	4.5-20.8	4.8-25	9.2-21.5	15.3	9	21.5
Empty stomachs (%)	31	3	47	0	0	—	—	—

	Fish taxa 1997[1]							
Prey taxa	Yellow Perch	Sunfish	Alewife	Golden Shiner	Large-mouth Bass	Pumpkin-seed	Brook Silverside	Spottail Shiner
Copepod	82	41	50	15	38	47	18	11
Polyphemus				3				
Diaphanasoma	0.3	0.3			2	0.4		
Daphnia	<0.1							
Bosmina	11	1	42	61	10	14	18	63
Other cladocerans	0.4	0.1		0.3	42	6		11
Ostracod				2	2	1		4
Midge larva				2	4	8		
Water mite				1	0.3			
Amphipod	<0.1				0.5			
Rotifer	2	56	8	14		22	64	
Bivalve	4	0.2		2				11
Fish					<0.1			
Oligochaete					1	1		
Number examined	201	61	29	58	39	21	7	3
Mean TL (mm)	8.3	6.1	7.8	17.2	21.1	13.8	8.9	11.2
Size range (mm)	6.7-11.7	5.3-8.5	5.2-17.8	5.3-34	12-37	9.2-21.8	6.2-14.3	6-14.3
Empty stomachs (%)	10.9	14.7	83	15.5	0	0	14.3	0

[1] Other fish taxa collected (and their primary prey taxa) were Rock Bass (copepod), and Banded Killifish (other cladocerans). Carp stomachs did not contain food.

Table 6. The percent (by number) of prey taxa in the diets of fish larvae collected by pushnet in Lindley Bay. Unidentified sunfish that were less than 9 mm TL were combined as sunfish.

	Fish taxa 1996								
Prey taxa	Yellow Perch	Sunfish	Alewife	Brook Silverside	Pumpkin-seed	Banded Killifish	Spottail Shiner	Bluntnose Minnow	Fathead Minnow
Copepod	91	68	60	50	61	39		22	100
Polyphemus		0.1	1	24					
Diaphanasoma		6	29	0.3	13				
Bosmina	0.4	0.4	10	8	25	1		22	
Other cladocerans	8			0.2		59	93	55	
Midge larva		<0.1		0.1	0.3	1			
Amphipod		<0.1							
Rotifer	0.3	25		12			7		
Bivalve	0.2								
Number examined	311	87	15	31	10	5	2	1	1
Mean TL (mm)	7.7	6.5	9.8	12.5	10.3	8.3	—	—	—
Size range (mm)	6.3-14	5.2-8.5	6-23	6.3-22.7	9-13.5	7.7-9	6.2-8.2	10	6
Empty stomachs (%)	17.4	6.9	86.7	3.2	0	20	0	—	—

	Fish taxa 1997[1]						
Prey taxa	Yellow Perch	Sunfish	Alewife	Spottail Shiner	Brook Silverside	Golden Shiner	Pumpkin-seed
Copepod	82.6	77.9	50	77.1	88.9	39	100
Polyphemus	0.5			18.7			
Diaphanasoma	0.1					11	
Bosmina	0.9	0.2		2.1	11.1	50	
Other cladocerans	14.5		50				
Midge larva				2.1			
Rotifer		21.8					
Bivalve	1.4						
Number examined	95	56	26	25	7	5	2
Mean TL (mm)	8	6.5	8.2	7.6	8.9	15.4	—
Size range (mm)	6.8-12.5	5.1-8.5	5.5-16.2	5.7-13.5	6-14.2	11.3-20.5	9.5-10
Empty stomachs (%)	10.9	14.7	83	15.5	0	40	0

[1] Carp and rock bass were collected but their stomachs did not contain food.

density. Yellow Perch at this time would be too large for Northern Pike. One Northern Pike egg and one larva were collected in deep water in Buck Bay (1996) but there was no water temperature data to allow for exogenous feeding estimates (Fig. 6).

Muskellunge eggs were collected in Buck Bay on 17 and 19 June, 1997, and these larvae would be capable of feeding by early July (Fig. 6). Muskellunge at 13 mm could consume forage fish up to 6 mm. Yellow Perch would be too large for Muskellunge at this time. Golden Shiner accounted for 75% of the forage fish (at 1.7/m^3) and ranged from 12–18 mm. Alewife (4–5 mm) and Spottail Shiner (>13 mm) were collected at densities of less than 0.6/m^3. Only Alewife could be consumed by Muskellunge at 13 mm. No Carp were collected.

Muskellunge eggs were collected on 23 May, 1996, in Flynn Bay and these larvae would be capable of feeding by the third week of June (Fig. 7). Only Spottail Shiner (5–6 mm) and Alewife

Table 7. The percent (by number) of prey taxa in the diets of fish larvae collected by pushnet in Flynn Bay. Unidentified sunfish that were less than 9 mm TL were combined as sunfish.

	Fish taxa 1996[1]								
Prey taxa	Yellow Perch	Sunfish	Alewife	Brook Silverside	Golden Shiner	Banded Killifish	Spottail Shiner	Tessellated Darter	Carp
Copepod	83	80	40	16	3	6		25	5
Polyphemus					1.4				
Diaphanasoma	0.4	16		0.8	8				
Daphnia	<0.1								
Bosmina			40	80	71				
Other cladocera	14	0.5		0.4	35	22			90
Water mite					3				
Ostracod	<0.1					59		75	5
Midge larva	<0.1				1.4	11			
Amphipod						1.4			
Rotifer	0.7	3	20	0.8			100		
Bivalve	0.4	0.4		2					
Fish	<0.1								
Number examined	354	135	42	25	10	3	3	3	2
Mean TL (mm)	8.1	6.5	8.5	10.1	13.2	15.5	6	6.6	—
Size range (mm)	6.2-12.8	5.0-8.5	5.0-14.0	5.2-17.3	10-20	7.8-20	6-6.2	5.8-7.5	6.3-7.3
Empty stomachs (%)	16.4	21.5	95.2	48	20	33	0	33	0

[1] Other fish taxa collected (and their primary prey taxa) were Pumpkinseed sunfish (*Bosmina*); Fathead Minnows were collected but did not contain food.

	Fish taxa 1997[2]								
Prey taxa	Yellow Perch	Sunfish	Alewife	Brook Silverside	Golden Shiner	Pumpkin-seed	Spottail Shiner	Carp	Banded Killifish
Copepod	72	24	5	25		4	1	7	0.7
Polyphemus				2.5					
Diaphanasoma	0.3	0.5				0.4			
Daphnia	<0.1								
Bosmina	12	25	41	42	79	70	82	3	4
Other cladocera	2	26	3	12	3	24	10	88	16
Ostracod	<0.1						3		61
Midge larva						1		1	
Water mite			0.2						17
Rotifer	2	11			15		1		
Bivalve	11	12	51	17			4		
Beetle larva					1.4				
Leech						0.3			
Number examined	242	38	31	23	31	19	18	14	8
Mean TL (mm)	7.9	7.3	14.6	10.2	14.6	11	11.3	8.7	10.8
Size range (mm)	5.5-16	5.0-8.8	7.7-27.5	6.3-13.8	6.7-19.5	9.3-15.5	5.5-22	6.7-11.7	7.8-19.7
Empty stomachs (%)	25.6	23.7	67.7	47.8	35	0	61.1	21.4	12.5

[2] Other fish taxa collected (and their primary prey taxa) were Largemouth Bass (copepods) and Smallmouth Bass (copepods).

(4.5–5 mm) were collected at this time and at densities of 0.3/m^3. Both of these species could be consumed by 13 mm Muskellunge. Muskellunge could grow to 16–17 mm by 6 July which would be at the period of peak density of forage fish (6–23 July). Muskellunge at these lengths could consume Carp and Spottail Shiner up to 7 mm, Golden Shiner up to 9 mm, and Alewife up to 11 mm. Yellow Perch would be too large for these Muskellunge. Golden Shiner (at 15 mm), Carp (6 mm), Spottail Shiner and Alewife (5–15 mm), were collected during this period at 1.5/m^3. Alewife accounted for 82% of the density. These Muskellunge could consume Carp, shorter Spottail Shiner, and most of the Alewife but not the Golden Shiner that were collected during this period.

Northern Pike eggs were collected on 8 and 14 May, 1997, in Flynn Bay and these larvae would be capable of feeding by mid-June (Fig. 7). Only Yellow Perch (at 1/m^3) and Spottail Shiner (0.15/m^3) were collected at this time. Northern Pike at 13 mm could consume Yellow Perch that were 7 mm and shorter (20% of total) and all of the Spottail Shiner. The peak of forage fish density occurred from 24 June–8 July. Carp, Alewife, and Golden Shiner were collected during this period at densities of less than 0.6/m^3 but only Alewife and Carp could be consumed by Northern Pike at 19 mm.

Northern Pike would be capable of feeding on fish larvae at nearly the same time as the peak in forage fish density in Buck Bay but many of the available fish larvae had grown larger than what could be consumed by Northern Pike. Muskellunge larvae were estimated to be capable of feeding on fish larvae at the time that the peak in forage fish density was declining. Larvae of Northern Pike and Muskellunge became capable of feeding on fish larvae nearly a week prior to the peak of forage fish density in Flynn Bay and would have a longer period in which to prey on fish larvae. Thus, these Northern Pike and Muskellunge larvae were not well matched in time with their forage fish prey in Buck Bay but they were well matched to forage fish prey in Flynn Bay.

Discussion

All of the copepod taxa and most of the cladoceran taxa collected in this study have been reported previously from the St. Lawrence River or Lake Ontario (Watson and Carpenter 1974; Mills and Forney 1982; Balcer et al. 1984). Cladocera genera that were collected in this study that have not been reported previously were *Bunops*, *Pleuroxus*, *Scapholeberis*, and *Simocephalus*. These genera, with the exception of *Bunops*, have been collected in Ontario lakes north and west of the St. Lawrence River (Brandlova et al. 1972) as well as in lakes Erie, Michigan, and Superior (Balcer et al. 1984). The presence of these genera may reflect the low amount of sampling done previously in the study sites and in the St. Lawrence River.

There is some disagreement in the literature about the distribution of the cladocerans *Holopedium*, *Polyphemus*, and *Sida*. Pennak (1978) and Thorp and Covich (1991) state that *Holopedium* is restricted to soft water (<20 mg/l of calcium) and that *Polyphemus* and *Sida* are generally found only in soft water. Balcer et al. (1984) list these three genera as occurring in all of the Great Lakes and note that lakes Huron and Michigan have relatively hard water. Mills and Forney (1982) reported that calcium concentration in the St. Lawrence River was 42 mg/l (1976–1978) and state that the level of calcium appeared to be increasing. *Holopedium* was collected in low abundance in the St. Lawrence River study bays which are considered to be hard water. *Polyphemus* was quite abundant in Lindley Bay and *Sida* was abundant for short periods in Flynn and Buck bays.

The seasonal abundance of zooplankton in Lake Ontario increases from a low point in April to peak abundance in August and September (Watson and Carpenter 1974) and a similar pattern is seen in zooplankton biomass in the St. Lawrence River (Mills and Forney 1982). Cyclopoid copepods have been generally more abundant than calanoid copepods during the 1980s in the eastern basin of Lake Ontario (Johannsson et al. 1991) and in the St. Lawrence River (Mills and Forney 1982). The dominance of cyclopoid copepods in Lake Ontario may be due to predation pressure by Alewife and *Mysis relicta* (LeBlanc et al. 1997). Seasonal copepod density in this study followed a similar pattern although there appeared to be a secondary peak in abundance in April followed by a decline in May. The mean density (all bays combined) of cyclopoid copepods was similar to that of calanoid copepods in the three study bays with some variation among bays within years.

The abundance of copepods in the meadow areas of Buck and Flynn bays in late April

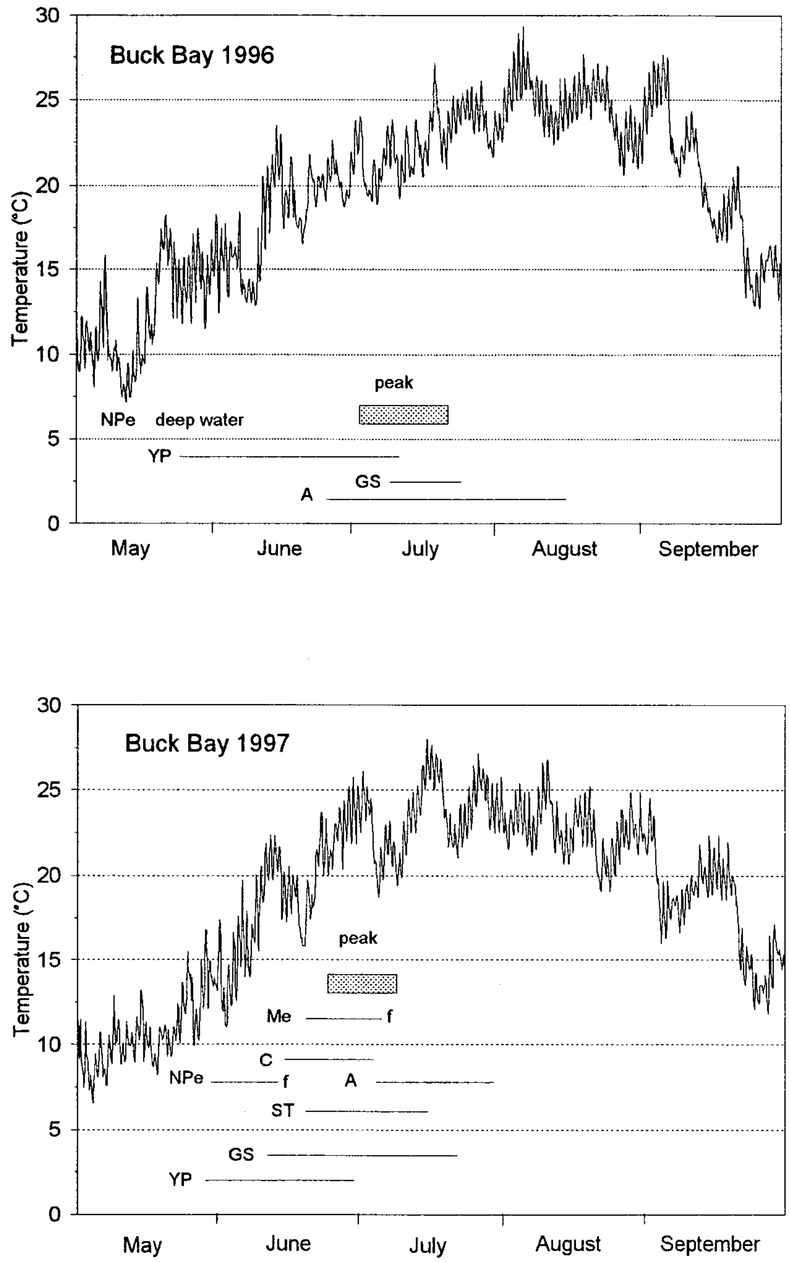

Figure 6. Water temperature in Buck Bay, seasonal and peak occurrence of potential forage fish, and estimated first feeding by esocids collected as eggs. Key to species: A–Alewife, C–Carp, GS–Golden Shiner, ST–Spottail Shiner, YP–Yellow Perch, Me–Muskellunge eggs, NPe–Northern Pike eggs, and "f", estimated time of first feeding.

was considerably lower than the maximum found under similar conditions by Franklin and Smith (1963; *Cyclops* only; 15,000/m^3) in Minnesota and by Fago (1977; up to 142,000 copepods/m^3) in Wisconsin. Cladocerans ranged from none in Franklin and Smith (1963) to 17,900/m^3 in Fago (1977). Their study areas were more than 1 ha in size, more than 100 times larger than the flooded meadows in this study. This may explain the difference in density of copepods and cladocerans between the study sites. The marshes in the St. Lawrence River study bays have undergone major

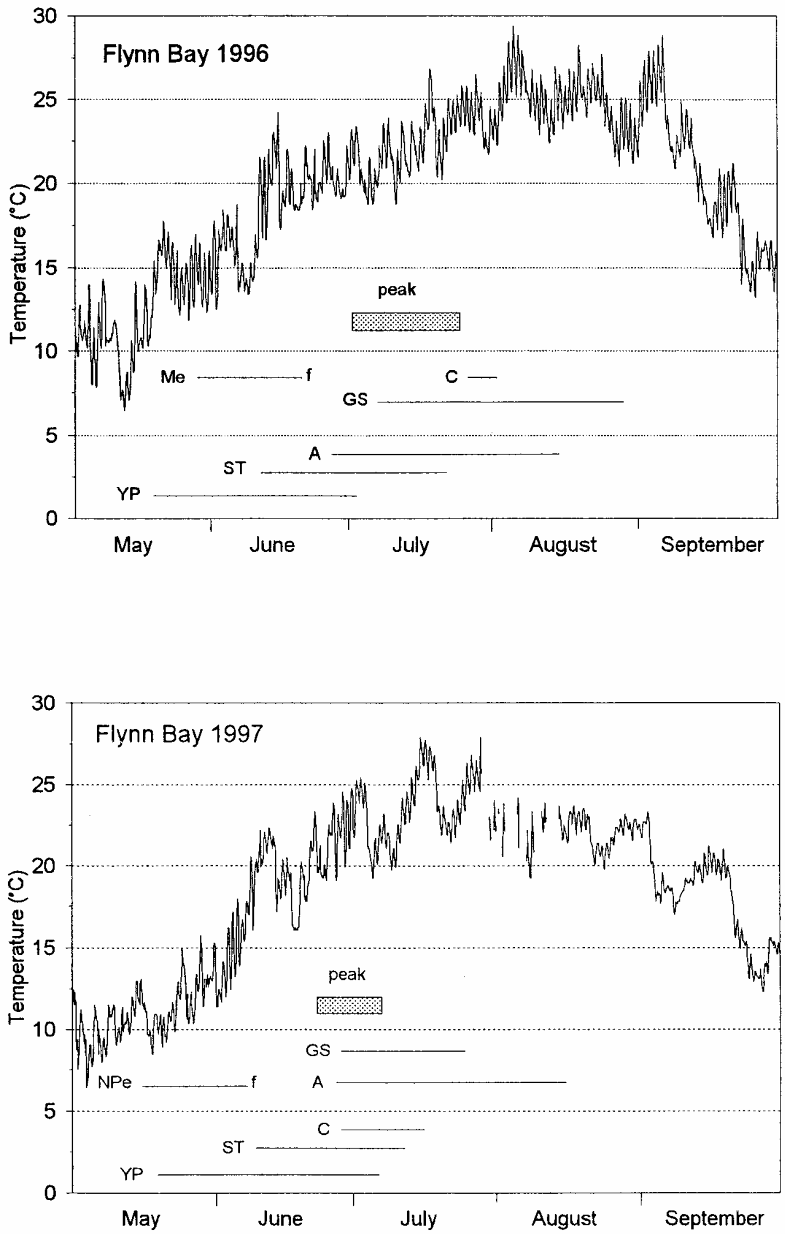

Figure 7. Water temperature in Flynn Bay, seasonal and peak occurrence of potential forage fish, and estimated first feeding by esocids collected as eggs. Key to species: A–Alewife, C–Carp, GS–Golden Shiner, ST–Spottail Shiner, YP–Yellow Perch, Me–Muskellunge eggs, NPe–Northern Pike eggs, and "f", estimated time of first feeding.

alterations due to water level control and *Typha* colonization but may still be able to produce greater densities of zooplankton with increased frequency and duration of flooding. In any case, the importance of the meadows is evident, especially for Northern Pike larvae, in that the meadows support a fairly high abundance of zooplankton prey that would likely increase in density during the Northern Pike nursery period as water temperatures increase.

Seasonal abundance of the larvae of most fish species in the present study was similar to that found by Hughes (1987) in Flynn Bay with the exception of Alewife and Spottail Shiner, which were not collected by Hughes. Seasonal abundance was also similar to that found by Leslie and Timmins (1992) in Hamilton Harbour, Ontario, and by Chubb and Liston (1986) in Pentwater Marsh on Lake Michigan. Species dominance was dissimilar among these three sites. Yellow Perch, which dominated the St. Lawrence River fish larvae community, were not abundant in the other studies. Alewife and Gizzard Shad *Dorosoma cepedianum* dominated the fish larvae community in Hamilton Harbour while Carp was the most abundant species in Pentwater Marsh. Gizzard Shad were not collected by Hughes (1987) or in the present study. A greater number of species (34) was collected in Hamilton Harbour than in Pentwater Marsh (approx. 18 species) or in the St. Lawrence River (22 species) perhaps as a result of a greater diversity of sampling methods in Hamilton Harbour. There are more than 10 additional species present in the St. Lawrence River (Smith 1985) that were not caught in pushnets or by dipnet.

Fish larvae peak density was generally lower in the St. Lawrence River study bays than that found by Chubb and Liston (1986) except for Alewife, which was similar in density to the density of herring in Pentwater Marsh. The peak density of Yellow Perch in the St. Lawrence River was more than 1000 times higher than in Pentwater Marsh. Carp peak density in Pentwater Marsh was more than 400 times higher than that in the St. Lawrence River. Both were the dominant fish species in their respective study sites. Pentwater Marsh, however, is not truly comparable to the St. Lawrence River study bays as it has a much greater vegetated area of less than 1 m depth (60% of total area) and is not fronted to the lake by an open bay mouth. Flynn Bay has the largest submergent vegetative area (<1 m depth) of the St. Lawrence River study bays at approximately 25% of total area.

Buck Bay had a significantly greater density of potential forage fish but this density was due, in part, to the abundance of Alewife (in 1996), which has not been confirmed as a prey species of Northern Pike or Muskellunge larvae. Golden Shiner, a known prey species, was significantly greater in density in Buck Bay in 1997 but the density of forage fish in the other bays was not significantly different from each other. That this involves only one species, Golden Shiner, would suggest that statistical differences in density may not translate into biological ones. Density of any species can be influenced to a great amount by a few large catches and may not represent the density of larvae available to the predator. It would seem more logical that the density of forage fish may be similar among the bays but with a wide variation in short term abundance.

Relatively few zooplankton taxa of those collected were important in the diets of the fish larvae examined in the study areas. Copepods, *Bosmina*, and other cladocera were the primary taxa consumed by fish larvae and were the most abundant taxa, with the occasional exceptions of *Polyphemus* and *Diaphanasoma*. The importance of rotifers may have been underestimated due to their potentially faster rate of digestion (Gannon 1976, Sutelo and Huusko 2000) and were not sampled with the large mesh size of the collecting net. Rotifers did contribute a substantial, if inconsistent, percentage of the diet of Yellow Perch, sunfish, and Brook Silverside. *Bosmina* was the primary prey taxa of Golden Shiner and Spottail Shiner, two important prey taxa of Northern Pike and Muskellunge larvae.

The majority of fish species appeared to be well matched with the increasing density of zooplankton with the exception of Yellow Perch. Copepods, particularly calanoids, exhibited a substantial decline in density in late May just as Yellow Perch started feeding. It is possible that this decline was a result of Yellow Perch predation. The highest density of Yellow Perch occurred at this time in each bay, as much as 63 times greater density than in the following two weeks. The increased incidence of Yellow Perch that were caught without food in their guts may be an indication of the Yellow Perch production above what could be supported by the available zooplankton. The potential forage fish species, and other fish species, generally increased in density as zooplankton density increased.

The relative timing of Northern Pike and Muskellunge feeding on potential forage fish revealed a small but perhaps critical difference between Buck and Flynn bays. Northern Pike were estimated to be capable of feeding on potential forage fish just prior to the peak forage fish density in Buck Bay and Muskellunge larvae were capable of feeding near the end of the peak forage fish density. Both species were capable of feeding approximately one week prior to the peak forage fish density in Flynn Bay. This one additional week would allow the Northern Pike and Muskellunge larvae to prey on fish at nearly double the cross-sectional area from the previous week. This could be of substantial benefit considering that only a small percentage of the forage fish were of an appropriate size in any of the estimations. The shortest Yellow Perch larvae were estimated to be of an appropriate size for Northern Pike but there is no evidence that would suggest that Northern Pike larvae feed on Yellow Perch larvae. Yellow Perch larvae were always too large for Muskellunge larvae in the estimations. Alewife were of an appropriate size for both species but there is no evidence that Northern Pike or Muskellunge larvae prey on Alewife. The schooling behavior of Alewife, reported to start in fish as small as 10 mm (Cooper 1961), may lead Alewife to more open water where they would not be accessible to Northern Pike or Muskellunge. It must be noted that the estimations apply only to the Northern Pike and Muskellunge that were collected as eggs. It is likely that there were eggs spawned earlier than those collected and those larvae would have an improved chance of feeding successfully.

If timing is important then the fish that spawn at the optimal time would have the advantage. It is unknown how much of a difference in timing can be accomodated without risking reduced growth or starvation. Northern Pike could increase their potential advantage if they were spawned in the flooded meadows. The warming of the shallower water at an earlier date and the high density of zooplankton would allow Northern Pike larvae to reach the nursery bay at a much larger size than those Northern Pike and Muskellunge that were spawned in the shallow but cooler water of the bay. This would also reduce the potential for competition between Northern Pike and Muskellunge for similarly-sized prey. The timing of hatching of esocids and the hatching of the forage fish species thus becomes an important conjunction in the feeding success of Northern Pike and Muskellunge larvae.

Acknowledgments

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