Colonization of Inland Lakes in the Great Lakes Region by Rainbow Smelt, *Osmerus mordax*: Their Freshwater Niche and Effects on Indigenous Fishes[1]

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Rainbow smelt, *Osmerus mordax*, have colonized numerous inland lakes in eastern North America, primarily as a result of introductions by humans. Smelt often establish large populations in these lakes and influence indigenous fishes both directly (predation) and indirectly (competition). Smelt have a eurythermal life history, which results in spatial segregation of their larvae, juvenile, and adults, and are omnivorous feeders, eating a range of food types from zooplankton to fish. As a result, smelt interact strongly with a wide spectrum of prey and predator species. Effects on other species are mediated via food web interactions resulting in recruitment and growth changes in some species and redirection of energy flow and storage. Species most often affected are cold-water and cool-water species whose niches are most similar to juvenile and adult smelt. Increased growth rates of Atlantic salmon (*Salmo salar*) and lake trout (*Salvelinus namaycush*) and recruitment failure of lake whitefish (*Coregonus clupeaformis*) are the best documented responses to invasion by smelt. Many other species are probably also affected, although the effects vary greatly between lakes. Variation in the smelt metabolic niche (as expressed by relative growth efficiency) is due to variations in prey size and availability and is reflected in differences in smelt body size between lakes. Smelt body size, in turn, is related to the variable effects that they have on other species.

L'éperlan arc-en-ciel, *Osmerus mordax*, a colonisé, surtout suite à son introduction par l'homme, un très grand nombre de lacs intérieurs de l'est de l'Amérique du Nord. Les populations d'éperlan ont souvent été importantes et ont influé sur les poissons indigènes de façon directe (prédation) et indirecte (compétition). L'éperlan a un cycle vital eurytherme, ce qui se traduit par une ségrégation spatiale des larves, des juvéniles et des adultes, et est omnivore, se nourrissant d'une large gamme de proies qui vont du zooplancton aux poissons. Tout ceci est à l'origine de fortes interactions avec une large gamme d'espèces proies et prédatrices. Les effects sur les autres espèces se produisent par l'intermédiaire d'interactions au sein du réseau alimentaire qui résultent en des modifications du recrutement et de la croissance de certaines espèces et en une réorientation des flux énergétiques et du stockage. Les espèces les plus souvent affectées sont les espèces d'eaux froides et fraîches dont les niches s'apparentent le plus à celles des éperlans juvéniles et adultes. On compte, parmi les effets les mieux connus de l'invasion par l'éperlan, l'accroissement des taux de croissance du saumon de l'Atlantique (*Salmo salar*) et du touladi (*Salvelinus namaycush*) et l'échec du recrutement chez le corégone de lac (*Coregonus clupeaformis*). Bon nombre d'autres espèces sont probablement affectées, mais les effets varient fortement d'un lac à l'autre. La variation de la niche métabolique de l'éperlan (exprimée par l'efficacité relative de la croissance) découle de variations de la taille et de la disponibilité des proies et se traduit par des écarts de la taille des éperlans entre les lacs. La taille des éperlans est à son tour fonction des effets variables de cette espèce sur les autres espèces.

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Rainbow smelt, *Osmerus mordax*, is an indigenous species of glaciomarine origin in many freshwater lakes of eastern North America (Kendall 1926; Dadswell 1974). In the region of the Great Lakes, however, this species has been widely introduced, beginning with an intentional and successful introduction to Crystal Lake, Michigan, in 1912 (Creaser 1925). Subsequent expansion of range in the Great Lakes is well documented (Van Oosten 1947; Dymond 1944; Christie 1974; Bergstedt 1983). Rainbow smelt have rapidly expanded their range in Ontario in recent years, having first appeared in three of the largest lakes, Simcoe, Nipissing, and Nipigon, in 1961, 1964, and 1976, respectively (Borecky et al. 1982; MacCrimmon et al. 1983a; K. Jorgenson, Ontario

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Ministry of Natural Resources (OMNR), North Bay, pers. comm.). Numerous small lakes have also been invaded during this period, raising concern about the possible effects on several important sport and commercial species, including lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), lake herring (*Coregonus artedii*), and walleye (*Stizostedion vitreum vitreum*). Speculation about the effects of rainbow smelt on fish communities in the Laurentian Great Lakes (Smith 1968; Christie 1972; Christie et al. 1972; Smith 1972; Regier 1973) and in smaller inland lakes (Loch et al. 1979; Hassinger and Close 1984) has prompted this concern.

Rainbow smelt affect other fishes directly by predation on their young (O'Gorman 1974; Foltz and Norden 1977; Selgeby et al. 1978; Stedman and Argyle 1985; Loftus and Hulsman 1986), but also indirectly by changing food web structures and routes of energy flow in aquatic systems. Smelt redirect energy flow by serving as an alternate or primary prey (Eck and Brown 1985) and as a competitor of indigenous species (Crowder et al. 1981) or both. Christie (1974) speculated that replacement of indigenous planktivores (deepwater ciscoes and lake herring) in Lake Ontario by rainbow smelt and alewife (*Alosa pseudoharengus*) has resulted in a loss of verticle vectoring of energy from the abyss of the lake. The efficiency of nutrient cycling in lakes dominated by smelt is, therefore, also in question, as is the influence of shifting patterns of energy flow on size-linked species interactions and ultimately on community structure.

The aim of this study is to identify the types of lakes and fish communities that have been successfully colonized by rainbow smelt, to document the apparent effects of rainbow smelt on other fish species, and to describe the trophic and spatial relationships between rainbow smelt and other species in freshwaters. The size spectrum of the smelt diet in relation to relative growth efficiency (Kerr and Ryder 1977) and distributional life history is compared in freshwater and marine habitats to evaluate the phenotypic plasticity of the rainbow smelt niche and the species' corresponding roles in vectoring of energy in lakes. Kerr and Ryder (1977) described the metabolic niche of percid species in Lake Erie using growth efficiency (K) as a niche separator. Different K-lines indicated different realized niches within the same habitat. We take growth efficiency patterns to be a reflection of species interactions associated with prey resource utilization and therefore of the ecological role of a species in a given habitat.

We employ a large data base for lakes in Ontario, Canada, to describe the types of lakes and fish communities invaded by rainbow smelt and compare case studies of rainbow smelt introductions throughout eastern North America for evidence of effects on other species. New information on diet and growth efficiency is reported and data on distribution, diet, and species interactions are summarized from the published literature.

Methods

Data on the distribution of rainbow smelt in Ontario have been obtained through computer searches of the Lake Inventory Data Base (LIDB), Ontario Ministry of Natural Resources (OMNR), which at the present time contains information on limnological characteristics and fish species for 8842 Ontario lakes; the Fish Species Distribution Data Base, based on records of the National Museums of Canada and Royal Ontario Museum; and through a questionnaire sent to each of 47 OMNR field offices located throughout Ontario. Two data sets were generated: one consists of a list of all lakes known to contain rainbow smelt, their latitude, longitude, OMNR administrative Region and District, watershed, date, and source of introduction, and the type of information documenting the presence of smelt; the second data set contains selected limnological characteristics of these same lakes and the fish species present. Information was also compiled on the status of the existing fish community prior to and after the introduction of rainbow smelt.

Stomach analyses were performed on 225 rainbow smelt captured by gill nets in Lake Huron during August and September 1984 to determine the relationships between smelt body size and their degree of piscivory and maximum prey size.

Results

Distribution of Rainbow Smelt in Ontario

Rainbow smelt are known to occur in 194 inland lakes in Ontario, although 7 of these are tentative designations based on unconfirmed reports (Fig. 1). This species is also found in all five Laurentian Great Lakes. Indigenous populations occurred in four inland lakes in eastern Ontario (Muskrat, Dore, Golden, and possibly Timiskaming) as a result of inundation by the Champlain Sea, ca. 11 000 yr B.P. (Radforth 1944). The origin of smelt in Lake Timiskaming (elevation 178 m) is unknown, but Dymond (1937) noted that the Champlain Sea extended to the head of Lake Timiskaming. Coleman (1941, p. 94) also noted this possibility. The Champlain Sea did reach 210 m above sea level near Ottawa (Coleman 1941; see also Prest 1976), 38 m above present-day Lake Timiskaming, and four species of invertebrates of "glaciomarine origin" occur in Lake Timiskaming (Dadswell 1974), supporting the contention that rainbow smelt is an indigenous resident. Most Ontario lakes containing smelt lie within the drainage basins of the Great Lakes and St. Lawrence River, with the exception of several lakes near Quetico Park which are within the Arctic watershed.

Introduction by humans appears to be the primary means of invasion and colonization. This is indicated by the strong association of lakes containing rainbow smelt with urban and cottage development. In all cases, introductions have been unofficial and, in many cases, probably unintentional. The majority of these introductions have probably resulted from inadvertent fertilization and release of eggs into the new environment during processing (cleaning) of sexually mature smelt captured elsewhere during spring spawning runs. Intentional introduction, through the release of adult smelt or by transporting and releasing fertilized eggs (Richardson and Belknap 1934), has also undoubtedly occurred in some instances.

The secondary mechanism of colonization is movement through interconnected waterways (Kriksunov and Shatunovsky 1979). In Ontario, for example, smelt were recorded in St. Nora Lake near the headwaters of the Gull River in the 1950s and subsequently have become established in 13 downstream lakes in the Gull River chain spanning a distance of approximately 40 km. Similar movement has occurred in the Rainy River watershed in northwestern Ontario and is suspected in others.

Lakes colonized by rainbow smelt range in size from a few hectares to tens of thousands of square kilometres (the Great Lakes). In general, they are moderately deep lakes with average mean and maximum depths of 11.6 and 35.7 m, respectively, and range from slightly acidic to alkaline, having medium transparency and low productivity (Table 1). The number of fish

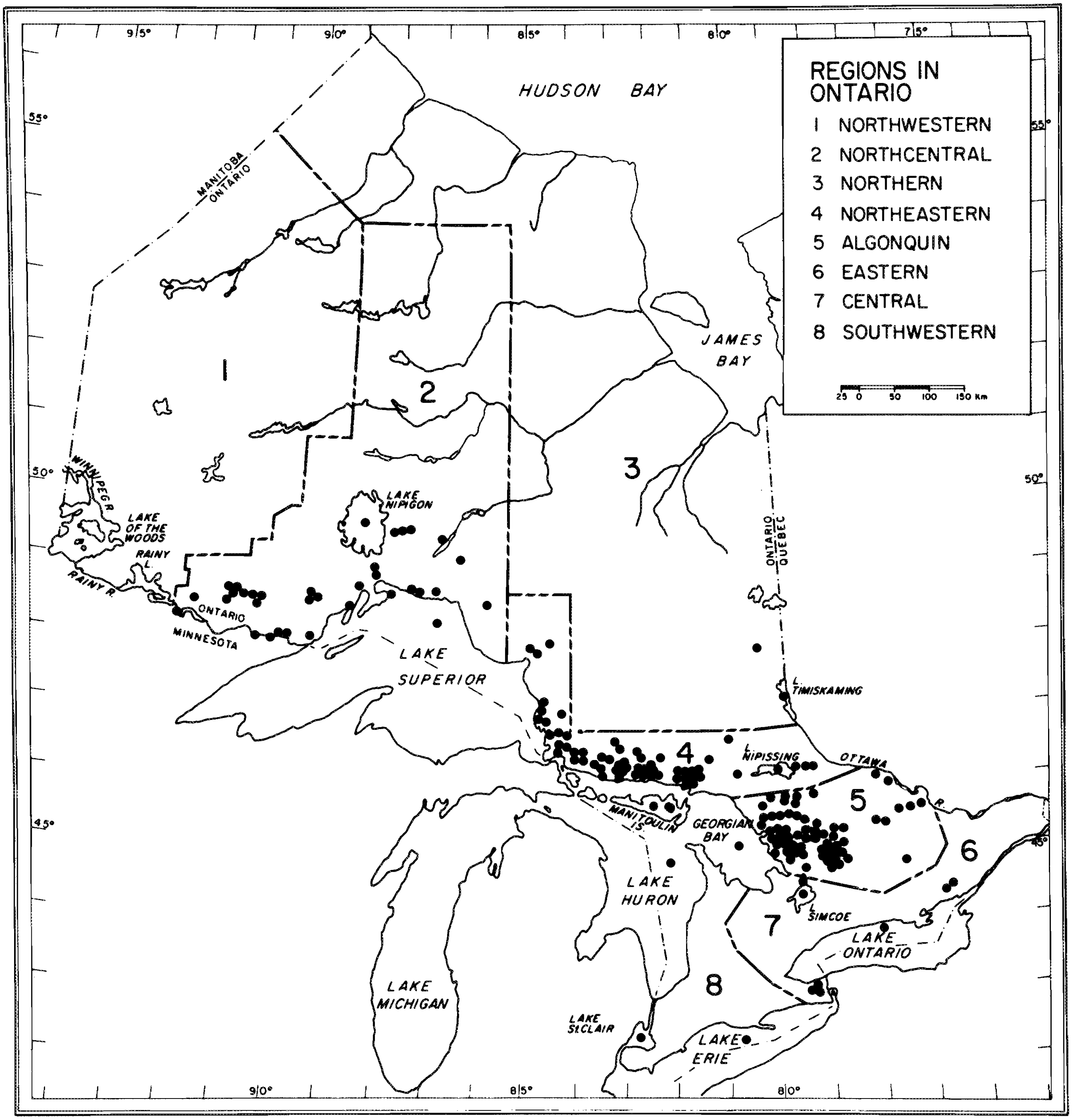

FIG. 1. Distribution of lakes in Ontario inhabited by rainbow smelt.

species present in Ontario lakes successfully invaded by rainbow smelt populations varied from 2 to 62 in inland waters and from 67 to 114 in the Great Lakes (Ryder 1972) prior to invasion by smelt. Species number in these lakes varies directly in proportion to lake size (Table 2).

Surface area explains 41.9% of the total variability in species number in inland lakes inhabited by rainbow smelt, and elevation alone explains 5.7%; when combined, these variables explain 43.5% of the variation (Table 2, equations 1–3). When the Great Lakes are included in the analysis, surface area and elevation explain 63.6 and 16.1%, respectively, of the total variation in species number, and the species–area coefficient increases from 0.164 to 0.199. Again, area alone accounts for most of the variation, elevation accounting for about 1.2% of the total variation when both variables are combined (Table 2, equations 4–6). Other variables that are correlated with species number are lake perimeter, shoreline development factor, mean and maximum depth, total dissolved solids, and alkalinity, but all have negligible effects when combined with surface area and elevation. Neither transparency nor morphoedaphic index (MEI, Ryder 1965) is significantly correlated with species number in these lakes.

Species Associations in Ontario Lakes Invaded by Rainbow Smelt

The frequency of occurrence of 36 fish species is compared for 187 lakes containing rainbow smelt and all 8842 lakes (both

TABLE 1. Summary of morphometric, limnological, and fish species information for 187 lakes reported to have populations of rainbow smelt. The data are not complete for all lakes. Alkalinity is determined as total fixed endpoint.

Parameter	Number of lakes	Mean	Minimum	Maximum	Median	Lower quartile	Upper quartile
Elevation (m)	173	278.1	123.0	457.0	270.0	221.0	328.0
Area (km^2)	177	52.3	0.1	4,480.0	3.0	1.2	9.6
Perimeter (km)	173	38.4	1.4	933.2	14.2	8.0	34.8
Volume (10^6 m^3)	168	35.2	0.4	1,230.0	3.0	0.9	10.7
Mean depth (m)	169	11.6	2.0	38.7	9.5	6.8	14.9
Maximum depth (m)	181	35.7	4.0	213.5	27.5	19.5	43.0
Total dissolved solids (mg/L)	135	49.4	5.5	231.4	36.0	27.0	57.9
Alkalinity (mg/L)	170	25.0	4.0	145.4	17.1	12.0	27.3
Surface pH (May–Aug.)	173	7.2	6.0	9.3	7.0	6.8	7.5
Hypolimnion pH	158	6.5	5.5	9.0	6.4	6.0	6.8
Secchi (m)	172	4.9	1.3	10.5	5.0	3.6	5.9
MEI (TDS/mean depth)	128	5.9	0.6	45.3	3.7	2.2	7.6
Number of fish species[a]	179	11.3	3.0	63.0	10.0	8.0	12.0

[a]Census of the Family Cyprinidae may not be complete.

TABLE 2. Linear regression values and statistical significance for number of species versus lake surface area and elevation in Ontario lakes inhabited by rainbow smelt.

No.	Variables (Dependent × independent)	n	$y = a + bx$ a	b	S_b	b/S_b	p	R^2 (%)
	Inland Ontario lakes							
1	log no. spp. × log area (km^2)	177	0.91	0.164	0.015	11.2	≤0.01	41.9
2	log no. spp. × log elevation (m)	172	2.03	−0.419	0.131	−3.2	≤0.01	5.7
3	log no. spp. × log area	170	1.39	0.159	0.015	10.6	≤0.01	42.3
	× log elevation			−0.194	0.104	−1.9	≤0.05	1.2
	Inland Ontario lakes and the Great lakes combined							
4	log no. spp. × log area	182	0.89	0.199	0.011	17.1	<0.01	63.6
5	log no. spp. × log elevation	177	3.09	−0.847	0.146	−5.8	<0.01	16.1
6	log no. spp. × log area	175	1.54	0.188	0.012	15.7	<0.01	64.0
	× log elevation			−0.262	0.102	−2.6	<0.01	1.3

with and without smelt) in the LIDB (Table 3). White sucker (*Catastomus commersoni*), smallmouth bass (*Micropterus dolomieui*), and yellow perch (*Perca flavescens*) are found in 70% or more of the lakes inhabited by rainbow smelt. These species are found more frequently in smelt lakes than in Ontario lakes in general, especially smallmouth bass which are four times more common in smelt lakes than in other Ontario lakes. A strong positive association is also found between smelt and lake trout (percent difference +33.9), lake whitefish (percent difference +35.8), and lake herring (percent difference +23.8) (Table 3), species that are usually found in deep, cold lakes. Rock bass (*Ambloplites rupestris*), pumpkinseed (*Lepomis gibbosus*), brown bullhead (*Ictalurus nebulosus*), and burbot (*Lota lota*) are also strongly associated with rainbow smelt (percent differences >19.5). Of these species, white sucker, yellow perch, lake whitefish, lake herring, burbot, and brown bullhead are probably indigenous to most of the lakes they cohabit with smelt. Many of the other species associated with rainbow smelt have been widely introduced, especially in the Algonquin and Northeastern regions of Ontario (Fig. 1) where rainbow smelt are most common. This suggests the common influence of human activity in determining the patterns of distribution for several species, especially those associated with angling, including species that have been extensively stocked (lake trout, smallmouth bass) and others that are used as bait (Cyprinidae, Percidae) or are transported inadvertently with bait by anglers.

Case Studies of Rainbow Smelt Introductions

Of the case studies that we have recorded (Table 4), 13 of 24 involve recruitment declines of lake whitefish (the Fish River lakes (Warner and Fenderson 1963) are counted as a single case, but comprise eight lakes, seven of which have had introductions of rainbow smelt; lake whitefish subsequently disappeared from these lakes; Fish Lake, which is the headwater lake in the chain, has been colonized by smelt only relatively recently and is now experiencing recruitment failure of lake whitefish (K. Warner, Maine Department of Inland Fish and Wildlife, Bangor, ME)), and 5 of 19 report declines in lake herring. In eight others (Champlain, Crystal (Michigan), Gull (Michigan), Owasco, Sebago, Golden, Timiskaming, and Skootamatta), either lake whitefish or lake herring, or both, appear to be relatively successful in the presence of rainbow smelt. Whitefish and lake herring are absent in the two Ontario lakes with large indigenous smelt populations (Dore and Muskrat), and indigenous smelt are rare or have disappeared from two lakes that continue to support

TABLE 3. Comparison of the frequency of occurrence of selected fish species in 187 inland lakes in Ontario with rainbow smelt populations and in all 8842 surveyed lakes with and without smelt.

Species name	Status (n = native, i = introduced, e = exotic, b = bait)	187 smelt lakes No. of lakes	187 smelt lakes % of total	8842 survey lakes No. of lakes	8842 survey lakes % of total	% difference
Common white sucker	n	106	88.3	5960	67.4	+20.9
Smallmouth bass	n–i	88	73.3	1605	18.2	+55.1
Yellow perch	n	84	70.0	5266	59.6	+10.4
Lake whitefish	n	68	56.6	1837	20.8	+35.8
Lake herring	n	66	55.0	1878	21.2	+23.8
Lake trout	n–i	63	52.5	1646	18.6	+33.9
Rock bass	n–i	57	47.5	1293	14.6	+32.9
Pumpkinseed	n–i	56	46.7	1848	20.9	+25.8
Brown bullhead	n	49	40.8	1153	13.0	+27.8
Northern pike	n	45	37.5	3880	43.9	−4.4
Burbot	n	41	34.2	1281	14.5	+19.7
Bluntnose minnow	n–b	34	28.3	999	11.3	+17.0
Spottail shiner	n–b	32	26.7	1472	16.6	+10.1
Walleye	n–i	27	22.5	2345	26.5	−4.0
Longnose sucker	n	24	20.0	464	5.3	+14.7
Largemouth bass	n–i	24	20.0	724	8.2	+11.8
Creek chub	n–b	22	18.3	834	9.4	+8.9
Rainbow trout	e	19	15.8	269	3.0	+12.8
Brook trout	n–i	19	15.8	1767	20.0	−4.2
Golden shiner	n–b	17	14.2	1066	12.6	+1.6
Common shiner	n–b	15	12.5	981	11.1	+1.4
Iowa darter	n	15	12.5	1484	16.8	−4.3
Blacknose shiner	n–b	12	10.0	1549	17.5	−7.5
Brook stickleback	n	12	10.0	405	4.5	+5.5
Trout perch	n	12	10.0	415	4.7	+5.3
Log perch	n	12	10.0	536	6.1	+3.9
Pearl dace	n	11	9.2	894	10.1	−0.9
Northern redbelly dace	n–b	9	7.5	1563	17.7	−10.2
Lake chub	n–b	9	7.5	506	5.7	+1.8
Johnny darter	n	8	6.7	1014	11.4	−4.7
Fathead minnow	n–b	7	5.8	1196	13.5	−7.7
Emerald shiner	n–b	6	5.0	219	2.5	+2.5
Muskellunge	n–i	5	4.1	178	2.0	+2.1
Bluegill	n	5	4.1	238	2.7	+1.4
Alewife	e	4	3.3	29	0.3	+3.0

coregonines (Golden Lake and Lake Timiskaming). Other observations associated with smelt invasions include increased growth rates or change in condition of lake trout and Atlantic salmon (*Salmo salar*) (10 cases), decreased growth or recruitment of juvenile lake trout (7 cases), recruitment failure of walleye (3 cases) and burbot (1 case), and competition with or displacement of smelt by alewife (2 cases). Because of the correlative and often qualitative nature of these observations, however, none of the species responses in these case studies can be definitively attributed exclusively to the effects of rainbow smelt. Nevertheless, the evidence is relatively convincing in the cases of lake whitefish recruitment failure and growth rate changes of lake trout and Atlantic salmon.

Spatial and Trophic Niche Characteristics

In lakes, rainbow smelt have a eurythermal life history. They partition the nearshore zone from 0 to 60 m into three strata spanning warm- (young-of-the-year), cool- (yearlings), and cold-water (adults) habitats (Table 5). Adults in large lakes occupy the hypolimnion during the summer period of thermal stratification. They display a diel behaviour pattern, however, involving dispersal from the lake bottom into the water column at night, often ascending through the thermocline into the epilimnion (Ferguson 1965; Heist and Swenson 1983). Age 0 smelt, in Lake Michigan, appear to undergo an opposite diel movement from the epilimnion to the hypolimnion (Brandt et al. 1980). Yearlings are found in an intermediate position between the young and adult fish. This behavior enables smelt to utilize the spatial, thermal, and food resources of the lake bottom and entire water column, while minimizing intraspecific interactions.

Although rainbow smelt have a reputation for being "voracious" (Schneider and Leach 1977), their diet is dominated by such invertebrates as copepods, cladocerans, mysids, and insects (Table 6; Fig. 2). In cases such as Gull Lake (Burbidge 1969), Lake Erie (Ferguson 1965), and Lake Simcoe (MacCrimmon and Pugsley 1979), the extent of piscivory in smelt is quite low. Smelt are, nonetheless, capable of feeding on items as large as 6% of their body weight (Fig. 3), and given the opportunity will do so. Also, in some lakes and during certain seasons, large smelt may be almost wholly piscivorous. In Lake

TABLE 4. Summary of case history studies of the introduction of rainbow smelt and the subsequent status of Atlantic salmon (AS), lake trout (LT), lake whitefish (LW), lake herring (LH), and other species. Status codes: A = absent, P = present (no change), G = growth enhancement, R = recruitment decline, × = no noticeable change. Observations are often qualitative and do not necessarily indicate direct causal relationships with rainbow smelt. In Canadaiqua Lake, alewife recruitment increased and smelt declined.

Lake	Location	Area (ha)	Mean depth (m)	Smelt population status	Status of cold-water fish species						Reference(s)
					AS	LT	LW	LH	Other	No change	
Big Basswood Lake	Ontario	2 707	38.7	Introduced	A	G	G	A			P. Purych, OMNR, Sault Ste. Marie, pers. comm.
Canadaiqua Lake	New York	—	—	Introduced	A	P	P	R	Alewife (R)		Eaton and Kardos 1972; Kircheis and Stanley 1981
Cayuga Lake	New York	17 200	54.5	Introduced	A	P	R	R			Youngs and Oglesby 1972
Chiblow Lake	Ontario	316	23.9	Introduced	A	P	R	P			P. Purych, OMNR, Sault Ste. Marie, pers. comm.
Crystal Lake	Michigan	3 930	20	Introduced	A	P	P	P		×	Laarman 1976
Crystal Lake	Ontario	613	15.4	Introduced	A	R, G	P	R			Maher 1983
Dore Lake	Ontario	1 468	7.6	Indigenous	A	A	A	A		×	K. Buckingham, OMNR, Pembroke, pers. comm.
Devilfish Lake	Minnesota	161	4	Introduced	A	P	A	A		×	Hassinger and Close 1984
Echo Lake	Maine	96	—	Indigenous	A	A	P	A	Alewife (G)		Kircheis and Stanley 1981; Lackey 1969
Elliot Lake	Ontario	616	15.6	Introduced	A	G, R	R	P	Burbot (R)		Gray and Maraldo 1982; Maraldo et al. 1985 Maher 1983
Eva Lake	Ontario	1 709	13.5	Introduced	A	G	P	R			
Fish River lakes	Maine	8 lakes		Introduced	G	R	R	?			Warner and Fenderson 1963; K. Warner, Maine Dep. Inland Fish Wildl., Bangor, pers. comm.
Golden Lake	Ontario	3 552	8.5	Indigenous	A	A	P	?		×	Radforth 1944
Gull Lake	Ontario	996	16.5		A	P	R	P			W. Wilson, OMNR, Minden, pers. comm.
Gull Lake	Michigan	820	—	Introduced	A	P	A	P			Burbidge 1969
Lac Heney	Quebec	1 244	18.3		?	P	R	P			Legault and Delisle 1968
Lake Champlain	New York Vermont	—	—	Indigenous	P	P	P	P		×	Kendall 1927; Van Oosten and Deason 1938
Lake Simcoe	Ontario	72 500	17.0	Introduced	A	R	R	P			Evans 1978; Evans and Waring 1987
Lake Timiskiming	Ontario Quebec	29 507	35.7	Indigenous	A	P	P	P		×	K. Koski, OMNR, Temagami, pers. comm.
Loughborough Lake	Ontario	739	7.4	Introduced	A	R	R	R			Von Rosen 1970; Kunkle and Palilionis 1982
Love Lake	Maine	672	5.2	Introduced	G	?	?	?			Havey 1974
Manitou Lake	Ontario	10 461	15.1	Introduced	A	P	R	P			J. Reckahn, OMNR, South Baymouth, Manitoulin Island, pers. comm.
Moosehead Lake	Maine	30 307	—	Introduced	P	P	R	A			AuClaire 1978; Warner, Maine Dep. Fish., pers. comm.
Muskrat Lake	Ontario	1 244	17.7	Indigenous	A	A	A	A		×	Dymond 1937
Owasco Lake	New York	—	—	Introduced	A	?	?	P			Youngs and Oglesby 1972

TABLE 4. (*Concluded*)

Lake	Location	Area (ha)	Mean depth (m)	Smelt population status	Status of cold-water fish species: AS	LT	LW	LH	Other	No change	Reference(s)
Quabbin Reservoir	Massachusetts	10 125	15.2	Introduced	G	G	A	A			Bridges and Hambly 1971
Schoodic Lake	Maine	157	6.7	Introduced	G	A	A	A			Harvey 1973
Sebago Lake	Maine	11 643	31.6	Indigenous	P	?	P	?		×	Kendall 1927; Fenderson 1964
South Bay, Lake Huron	Ontario	7 490	20.2	Introduced	A	R	R	P			Henderson and Fry 1987
Sporley Lake	Michigan	96	—	Introduced	A	A	A	A	Zooplankton (R)		Galbraith 1967
Twelve Mile Lake	Ontario	715	23.1	Introduced	A	P	R	P			Loftus and Hulsman 1986
West Bearskin Lake	Minnesota	200	21.3	Introduced	A	G	A	A		×	Hassinger and Close 1984
Skootamatta Lake	Ontario			Introduced	A	R	P	P	Walleye (R)		D. Gibbs, K. Coleman, OMNR, Tweed, pers. comm.
Lucerne Lake	Wisconsin	415	7.4	Introduced	A	A	R	?	Walleye (R)		Colby et al. 1987
Fence Lake	Wisconsin	1 352	8.7	Introduced	A	A	A	A	Walleye (R)		Colby et al. 1987

Ontario, for example, fish comprised more than 45% of the dry weight of food of smelt between 150 and 200 mm between July and December and from 55 to 100% of the food of larger smelt; fish also comprised at least 79% of the food of all smelt longer than 100 mm during the summer months in Matamek Lake, Quebec (Chen 1970). Stomach analyses of rainbow smelt from Lake Huron revealed a similar increase in piscivory with body size (Fig. 4).

Rainbow smelt feed on a wide variety of fish species, including the young of large species such as lake trout, lake whitefish, and burbot. Extensive predation on young bloater (*Coregonus hoyi*), lake whitefish, lake herring, and alewife and on adult emerald shiner (*Notropis atherinoides*), has been observed in some instances (Beckman 1942; O'Gorman 1974; Stedman and Argyle 1985; Loftus and Hulsman 1986). With few exceptions, however, a high degree of piscivory in freshwater smelt reflects a high degree of cannibalism. In Lake Heney (Delisle 1969) and Matamek Lake (Chen 1970), where alternate fish prey occur at low densities, growth of piscivorous smelt may be sustained entirely by cannibalism, although in the former it is not cannibalism but predation on pygmy smelt (*Osmerus spectrum*) (Lanteigne and McAllister 1983) by the larger rainbow smelt.

In its native, marine environment, the smelt is an anadromous fish that spawns in freshwater and remains in estuarine and coastal areas at other times (McKenzie 1964; Leim and Scott 1966; Flagg 1972; Murawski and Cole 1978). Available information on the distribution of marine smelt (Rogers 1939; Murawski et al. 1980; McKenzie 1964; Ouellet and Dodson 1985a, 1985b) indicates that tidal influences and larger geographic scale result in greater spatial separation of age groups. This appears to correspond with lower levels of cannibalism in the marine environment. The marine smelt feeds on zooplankton, amphipods, shrimp, nereid worms, and small fish such as herring, mummichogs, and silversides (Marcotte and Tremblay 1948; Belyanina 1969), indicating a preference for relatively large prey. Cannibalism among marine smelt is possibly less prevalent because of greater spatial segregation of smelt size classes or because prey in marine waters tends to be more abundant and of larger size. In small inland lakes, the habitat is much more confined and less dynamic, presenting a greater opportunity for cannibalism to occur, which it does. The preference for relatively large food particles in marine waters and the high incidence of cannibalism in freshwaters indicate the propensity of smelt to eat relatively large prey. This further suggests an opportunistic strategy in freshwater in which large prey would be eaten whenever available in good supply and that the effects of smelt on indigenous fishes might, in part, depend on the availability of alternate prey.

Growth Efficiency, Body Size, and Diet

Growth efficiencies of selected smelt populations, for which size at age data are available, revealed that the metabolic niche of smelt in freshwater is highly variable (Fig. 5). The five growth efficiency curves (*K*-lines) shown span the range of growth patterns known for smelt in fresh and marine waters (Table 7). Comparison of smelt diet items versus smelt body size (Fig. 2) indicates four major diet transition points: one at 0.5 g marks the transition between small zooplankton and larger zooplankton and small mobile invertebrates (mysids and amphipods), the second at 2 g marks the transition to larger invertebrates, the third at about 10–20 g marks the initial occurrence of piscivory and cannibalism, and the fourth at about 50 g indicates initial predation on adult smelt. Comparison with Fig. 5 suggests that Lake Heney dwarf smelt, which do not exceed a body weight of 10 g, are primarily planktivores, that Lake Simcoe and Lake Superior smelt are occasional piscivores, but primarily benthivores, and that smelt in Lake Ontario and Muskrat Lake prey primarily on large invertebrates and fish. The range of *K*-lines depicted in Fig. 5 appears to describe the full phenotypic range of the metabolic niche of rainbow smelt and to reflect the ecological potential of the species in freshwater.

TABLE 5. Information on depth and temperature distribution of rainbow smelt. The temperature mode refers to the most frequently occupied temperature or region of the thermal distribution. In some cases, temperatures were calculated by the original authors, and in others, ranges were estimated from graphs or tables.

Lake	Sampling gear (depth sampled)	Life stage	Time of sampling	Distribution of rainbow smelt: Depth (m) Range	Depth (m) Maximum abundance	Temperature (°C) Range	Temperature (°C) Mode	Reference
Lake Erie (Wheatley to Port Dover)	Midwater trawl (6–46 m)	YOY	Aug.	6–15	Epilimnion	>21	>21	Ferguson 1965
			Oct.	3–40	4–5			
		Yearling	July	3–10	4–5	>15	>15	
			Oct.	10–23	18	>15	>15	
		Adult	Aug. (day)	20–46	24–46	6–10	6–7	
		Adult	Aug. (night)	18–46	20–46	6–>15	6–15	
Long Point Bay	Midwater trawl (0–40 m)	Yearling	Early May	21–38	38	—	—	Ferguson 1966
			Late May	3–10	—	7–10	—	
			Late June	—	—	10–15	—	
			July			<15	—	
			Early Aug.	24		—	—	
			Mid-Aug.	—		7–10	—	
			Sept.	35		—	—	
			Oct.	—		7–10	—	
Central and eastern basins	Midwater trawl (0–46 m)	YOY	June	<15		—	18	MacCallum and Regier 1970
			Mid-Aug.	—	10	—	—	
		Yearling	Midsummer	<18		12–18	—	
		Adults	Late Aug.	>18		—	—	
			Early summer	>18		—	—	
			Late summer	>18		—	—	
Lake Huron, Saginaw Bay	Bottom trawl (2–30 m)	YOY	July–Sept.	6–13	—	—	—	Carr 1962
			Oct.	6–18	18	—	—	
		Adult	Aug.	6–32	32	<15	—	
Lake Huron, South Bay	Otter trawl (4–58 m)	Adult	Aug.–Sept.	—	42–50	6.2–18.9	7.0	Reckahn 1970
Lake Superior, Apostle Islands	Otter trawl (3–27 m)	YOY and yearling	Apr. – July	<18–71	<18	—	>15	Dryer 1966
			July – Sept. 15	<18–35	<18	—	>15	
			Sept. 16 – Dec. 13	<18–71	<18	—	—	
		Adults	Apr. – July	18–71	46	—	—	
			July – Sept. 15	18–71	36	—	<15	
			Sept. 16 – Dec. 13	18–71	27	—	—	
Lake Superior (western arm)	Midwater trawl echo sounder (2–50 m)	All life stages	June – Aug.					Heist and Swenson 1983
			Day	2–40	25–30	—	6	
			Night	2–40	10–15	6–18	11–16	
			All times	<100	<50	—	—	
Lake Michigan	Semiballoon trawl (2–50 m)	YOY	Oct. 14 – Nov. 4	13–46	18–22	4.3–12.2	11.7–12.2	Wells 1968
		Adult	May 26	13–37	22–31	6.0–13.3	7.8–11.5	
			July 7	9–37	9–13	4.3–10.3	8.4–10.3	
			Oct. 14 – Nov. 4	9–37	13–31	5.7–11.9	10.8–11.8	
Big Sable Point, Saugatuck Ludington	Gill net	Adult	Winter	—	40–50	—	—	Rasmussen 1973
			Spring	—	<10	—	—	
			Summer	—	10–30	—	—	
			Fall	—	30–50	—	—	
Manistique	Otter trawl	YOY	Fall	9–40	18	—	—	Jaiyen 1975
		Adult		40–92	30–60	—	—	
Grand Haven	Otter trawl	YOY	Sept.					Brandt et al. 1980
			Day	—	—	3–18	13–14	
			Night	—	—	3–18	5–6	
		Adults	Day	—	—	7–18	7–16	
			Night	—	—	7–16	11–16	
20 km south of Grand Haven	0.5-m-dia. plantkton net (1–15 m)	Larva	May–Aug.	1–15	4–12	5–23.3	10–16	Tin and Jude 1983

TABLE 5. (*Concluded*)

Lake	Sampling gear (depth sampled)	Life stage	Time of sampling	Distribution of rainbow smelt: Depth (m) Range	Depth (m) Maximum abundance	Temperature (°C) Range	Temperature (°C) Mode	Reference
Cayuga Lake, New York	Gill net (7–110 m)	Adult	July–Sept.	12–55	23–35	4–17	8–10	Galligan 1962
Gull Lake, Michigan	Gill net (0–32 m)	Adult	July	8–28	12–20	10–18	10–11	Burbidge 1969
			Aug.	8–20	10–16	10–14	10–14	
			Oct.	0–28	0–20	10–14	12–14	
			Nov.	0–24	0–20	8–10	10	
Echo Lake, Maine	Gill net (10–18.2 m)	Adult	June	1.5–16.8	9–12.2	—	—	Lackey 1970
			July	1.5–15.2	9–12.2	—	—	
			Aug.	1.5–18.2	9–15.2	—	—	
			Oct.	0–16.8	9–15.2	—	—	
Sakakawea, North Dakota	Gill net 16 locations	Adult	July–Aug.	23–38	—	—	—	Berard 1978
			Aug.	27–38	—	10.8–18.3	—	
Cayuga Lake, New York	Gill net (2–31.5 m)	Adult	June 16	—	—	8.6–12.8	10.0	Dahberg 1981
			July 16	—	—	9.0–19.6	14.0	
			Aug. 18	—	—	10.0–20.6	11.9	
			Sept. 9	—	—	10.1–20.6	10.4	
			Oct. 20	—	—	13.6–14.1	13.8	
Lake Simcoe, Ontario	Gill net (5–30 m)	Adult	Aug.–Sept.	15–30	20–30	8–15	8–10	D. Evans, OMNR, Maple, unpubl. data

Discussion

Characteristics of Lakes Colonized by Rainbow Smelt

With some notable exceptions, rainbow smelt have invaded virtually all of the lake types found in Ontario from shallow to deep, small to large, productive to nonproductive (Secchi 0.5–10.5 m), and having sparse to rich fish communities. Smelt are not reported in any lakes in the LIDB having pH < 6.0 (surface water, May–August), however. This might be significant, since the majority of smelt lakes are found in Algonquin and Northeastern regions of Ontario, areas known to have low buffering capacity in their soils and to be subject to precipitation of low pH (Dillon et al. 1978). Also, Kelso and Minns (1982), using the same data set as us, found about 20% of the surveyed lakes to have surface waters of pH < 6.0. The likelihood, therefore, of smelt having had the opportunity to invade lakes with pH < 6.0 seems high. The tendency of smelt to spawn in streams and on shallow beaches at the time of ice and snow melt might result in their eggs being subject to lethal pH depressions in poorly buffered lakes. Incipient effects of acidity on reproduction of indigenous freshwater fishes in Ontario occur from about pH 4.5 to 6.5 (Harvey 1982; Peterson et al. 1982), suggesting that fish species occurrence in lakes actually colonized by smelt has probably been little affected by acid precipitation.

Rainbow smelt are usually found in lakes considered to be typical of lake trout, that is deep, cold lakes having high transparency and relatively low productivity (Johnson et al. 1977). This corresponds with a higher than expected frequency of occurrence of lake trout (52.9%), lake whitefish (56.6%), and lake herring (55.0%) in lakes inhabited by rainbow smelt. The large mean size of these lakes (52.3 km^2) further explains the species composition in that large lakes suitable for lake trout also tend to have northern pike (*Esox lucius*), walleye, and smallmouth bass (Johnson et al. 1977), species that occur with relatively high frequency in lakes with smelt.

The very high frequency of smallmouth bass (73.3%) in lakes inhabited by smelt probably arises because both species have been widely introduced by humans. Also, smallmouth bass are successful in small, deep, softwater lakes typical of lake trout and large, shallow, hardwater lakes more typical of walleye and northern pike (Johnson et al. 1977). Similarly, higher than expected cooccurrence with pumpkinseed, rock bass, and several cyprinids is probably also due to the common influence of introduction by humans.

Because the primary means of invasion is introduction by humans, the lakes that are most likely to be invaded are those having the greatest access and highest use by cottagers and fishermen. Once an introduction has occurred, the physical–chemical conditions, habitat, and the presence of other fish species presumably determine the success of the invading species. The relative importance of each of these factors is uncertain, smelt being found in a wide variety of lake types, but their frequent occurrence in deep, cool lakes is consistent with their relatively low upper incipient lethal temperature (18°C at 11°C winter acclimation temperature, Thomasson 1963) and the hypolimnetic distribution of adults during summer stratification (Table 5). Knowledge of lake and fish community types in which smelt introductions have failed would provide a better indication of the importance of these factors to the success of smelt populations, but this type of information is rare.

A study of 43 lakes in south-central Ontario (Fig. 1) found that the number of cottages per lake was a function of lake area (log no. cottages = 0.151 + 0.767 log area), with area explaining 68.4% of the total variation (A. McCombie, OMNR, Maple, unpubl. data). Invasion by smelt might therefore simply be a function of the probability of an introduction occurring,

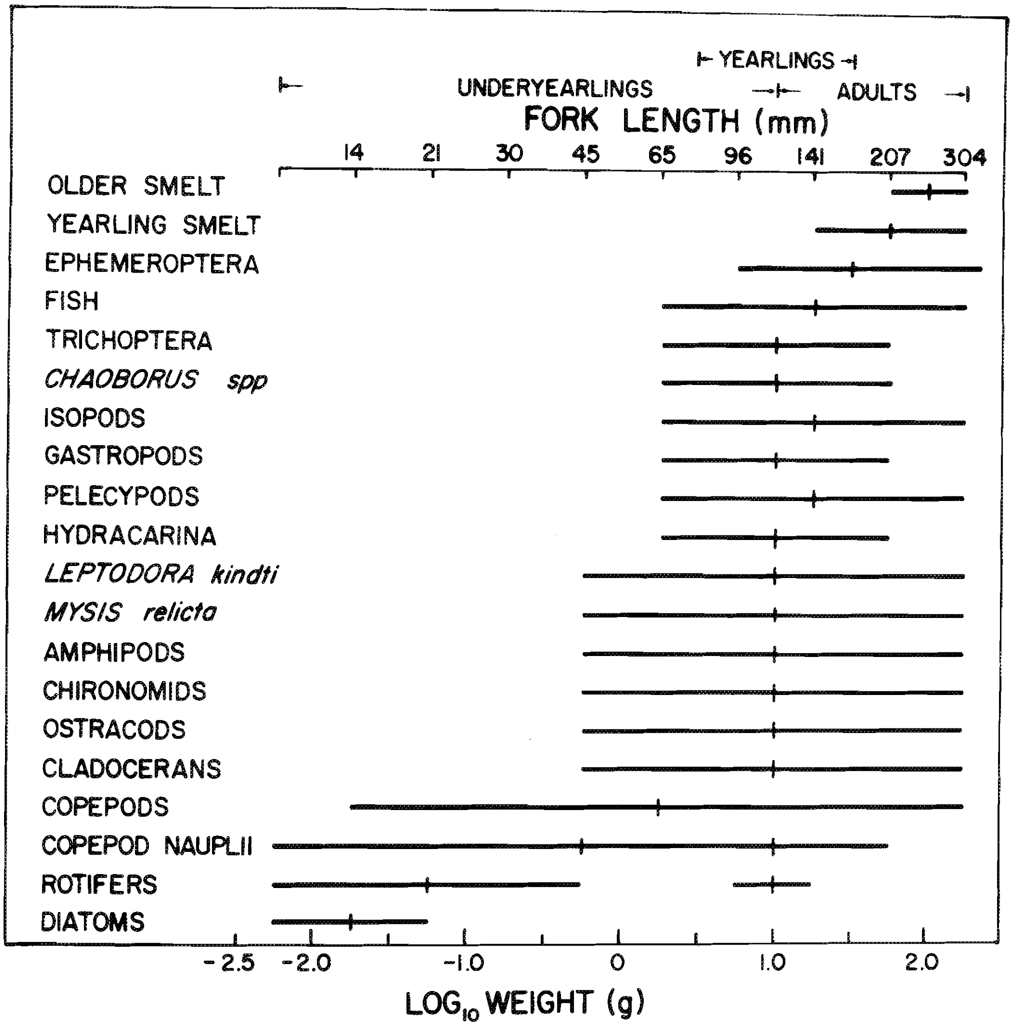

FIG. 2. Occurrence of food item types in smelt stomachs in relation to size of smelt, by size-class. Based on data from Kendall (1927), Creaser (1927), Hale (1959), Price (1963), Siefert (1972), and new data from the Bay of Quinte, Lake Ontario, Lake Simcoe, and Twelve Mile Lake, Ontario (D. O. Evans and D. H. Loftus, unpubl. data). Smelt fork lengths correspond to $\log_{10}$ body weights on the x-axis. Bars indicate the size range over which various items are eaten.

which, in turn, is a function of lake size. An intriguing possibility, however, is that large lakes might also have a greater capacity to accommodate new species, a thesis discussed by Barbour and Brown (1974). They suggested that large lakes might have fewer species than expected because of a shortage of colonists to fill the available habitats.

Lake area has limited capacity to predict the success of an introduction because area alone explains less than 50% of the total variation in species richness in our lake set (Table 1; see also Barbour and Brown 1974). Also, one species could simply be substituted for another, resulting in no change in richness. Species interactions, especially predation, may have a more important bearing on the success of smelt and other exotic invaders. Christie (1974) speculated that declines in stocks of piscivores may, in part, explain the success of exotic planktivores (including rainbow smelt) in the Laurentian Great Lakes.

Species Interactions and Effects of Smelt Introductions

Distribution and case studies of smelt invasions indicate relatively neutral coexistence between rainbow smelt and some species (smallmouth bass, white sucker, yellow perch), harmonious interaction with others, under some circumstances (lake trout, Atlantic salmon, walleye, northern pike, lake herring, emerald shiner), and possibly malevolent interaction under other circumstances (lake whitefish, burbot, walleye, lake trout, lake herring, bloater, alewife). In this section, we examine the detailed species interactions between rainbow smelt and their prey, predators, and competitors for evidence of the mechanisms by which they might affect the abundances of other species.

Smelt as prey

Smelt are utilized as food by virtually all cohabiting piscivores, including larger smelt. They are the major food item of landlocked salmon in Maine lakes (Rupp 1959, 1965; Lackey 1969; Warner 1972; Havey 1973), and following their establishment in the Great Lakes they became important in the diet of lake trout (Schneberger 1936; Hale 1959; Wright 1968). In Lake Superior, the smelt has replaced the bloater as the principal food of the lake trout (Dryer et al. 1965), and they are equally important in the lake trout diet in inland lakes (Bridges and Hambly 1971; MacCrimmon and Pugsley 1979; Hassinger and Close 1984). In the Great Lakes, coho salmon (*Oncorhynchus*

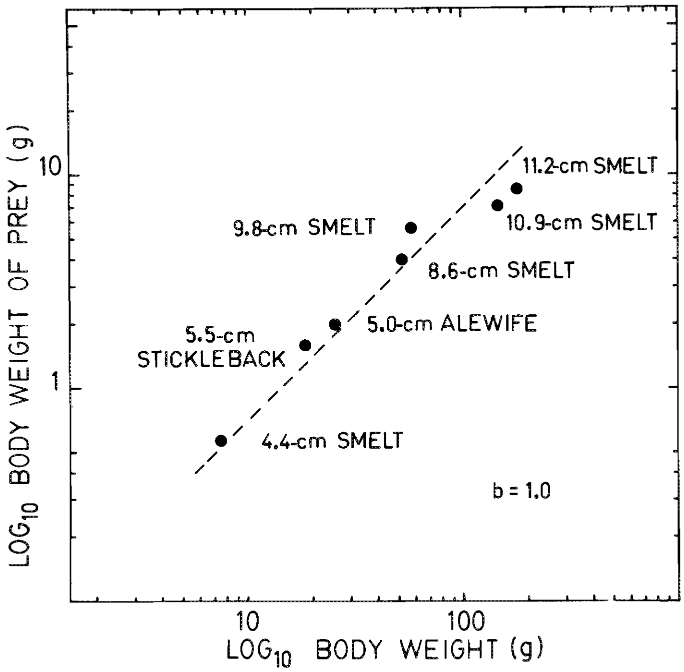

FIG. 3. Relationship between body weight of rainbow smelt and the maximum weight of ingested prey. Based on data from Kendall (1927), Creaser (1927), Hassinger and Close (1984), Stedman and Argyle (1985), and new data from Lake Huron and Twelve Mile Lake, Ontario (D. H. Loftus, unpubl. data). The broken line indicates a slope equal to 1.

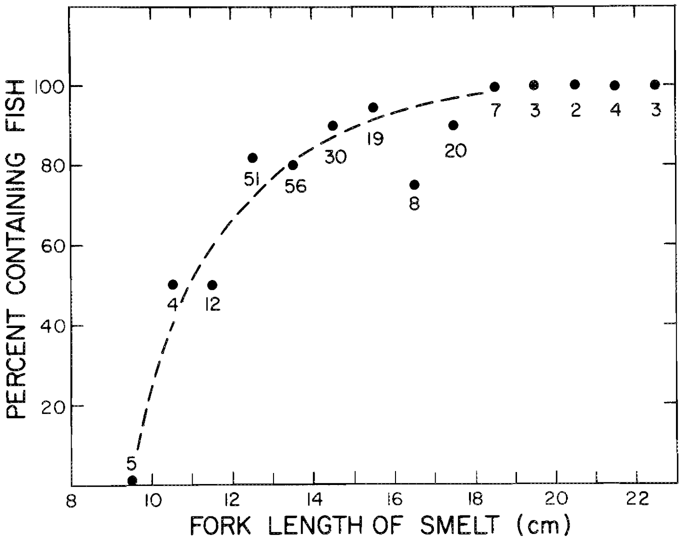

FIG. 4. Frequency of occurrence of fish in stomachs of 225 rainbow smelt containing food in their stomachs in relation to fork length. Smelt were collected in Lake Huron during August and September 1984.

kisutch) and chinook salmon (*O. tshawytcha*) are also major predators of smelt (Stewart et al. 1981; Wismer 1983; Eck and Brown 1985). Rainbow trout (*Salmo gairdneri*), brown trout (*S. trutta*), splake (*Salvelinus fontinalis* × *S. namaycush*), and, to a lesser extent, brook trout (*S. fontinalis*) utilize smelt as well (Lackey 1970; Bridges and Hambly 1971; Eck and Brown 1985). Burbot feed heavily on smelt, especially during spring (Greene 1930; Schneberger 1936; Wagner 1972), as do walleye and northern pike (Greene 1930; Johnson 1963; Wagner 1972; Berard 1978). Other predators include American eel (*Anguilla rostrata*), yellow perch, sauger (*Stizostedion canadense*), white bass (*Roccus chrysops*), white perch (*Morone americana*), and occassionally, rock bass, bowfin (*Amia calva*), lake whitefish, and longnose gar (*Lepisosteus osseus*).

Smith (1970) related that large alewives had been observed feeding on a mixed school of larval smelt and alewives and suggested that alewives could be a major predator on larval smelt in Lake Michigan. In this regard, smelt appear to have disappeared from Big Rideau Lake, Ontario, where alewives have become very abundant. Also, alewives are thought to have caused recruitment failure of smelt in Canadaiqua Lake (Eaton and Kardos 1972).

The effects of changes in smelt abundance on growth rates of predator species have been most obvious in smaller lakes where alternative prey of similar size are lacking. In Schoodic Lake, Maine, for example, Atlantic salmon increased in size following introduction of rainbow smelt, and a subsequent decline in smelt abundance resulted in decreased body condition of the salmon (Havey 1973). Similar responses were observed in Atlantic salmon, brook trout, lake trout, and possibly white perch populations in Quabbin Reservoir, Massachusetts (McCaig and Mullan 1960; Bridges and Hambly 1971). Following the establishment of smelt in West Bearskin Lake, Minnesota, the growth rate of juvenile lake trout was significantly reduced, and the size (and presumably the age) at first maturity increased (Hassinger and Close 1984). In Devilfish Lake, Minnesota, however, the growth rate of trout did not change significantly, but the condition of fish of all ages improved, and size and age at maturity increased (Hassinger and Close 1984). In contrast, Galbraith (1967) observed reduced growth and survival of planted rainbow trout in Sporley Lake, Michigan, following the introduction of smelt.

Predation on smelt by most piscivores in freshwaters indicates that smelt can have a major influence on energy transfer in these systems. In small lakes where smelt are distributed over all depths and habitats, energy sinks, as hypothesized by Christie (1974), are very unlikely to occur. In large, deep lakes, such as Lakes Ontario and Superior, loss of energy to the abyss seems very likely, given the restricted depth distribution of smelt and the absense of the former indigenous ciscoes. Our observations of the distributional and trophic niche dimensions of smelt thus concur with Christie's hypothesis of lost energetic efficiency. In all lakes, however, food web shifts caused by smelt introductions can be expected to cause major restructuring of the fish community.

Smelt as predators

Reif and Tappa (1966) found strong circumstantial evidence that the establishment of smelt in Harvey's Lake, Pennsylvania, resulted in the disappearance of its largest zooplankter (*Leptodora kindtii*) and replacement of *Daphnia pulex* by the smaller *D. dubia*. Galbraith (1967) observed a similar transformation in the zooplankton community of Sporley Lake. In this case, the establishment of smelt and fathead minnows (*Pimephales promelas*) was followed by the complete disappearance of *D. pulex* and an increase in abundance of *D. retrocurva* and *D. galeato mendotae*.

There has been little evidence of reduced abundance of organisms other than zooplankton resulting from predation by smelt, although detailed studies of such "preferred" items as *Mysis relicta*, *Pontoporeia*, and *Hexagenia* nymphs have not been undertaken. Emerald shiners, for example, apparently have remained abundant in Crystal Lake, Michigan, despite

TABLE 6. Types of food eaten and their relative importance in the smelt diet. Information is from published reports cited in the text.

Plant		
Algae	Occasional	
Animal		
Phylum Rotifera	Occasional	*Asplanchnidae* *Brachionidae* *Testudinellidae*
Phylum Annelida		
Class Oligochaeta	Rare	
Class Hirudinea	Rare	*Helobdella* sp.
Phylum Tardigrada	Rare	
Phylum Arachnida		
Class Hydracarina	Rare	
Phylum Nematoda	Rare	
Phylum Arthropoda		
Class Crustacea		
Order Amphipoda	Very common	*Gamariidae* *Talitridae* *Haustoridae*
Order Cladocera	Very common	*Bosminidae* *Chydoridae* *Daphnidae* *Leptodoridae* *Polyphemidae* *Sididae*
Order Copepoda	Very common	*Centropagidae* *Cyclopidae* *Diaptomidae* *Tremoridae* *Harpacticoida*
Order Mysidacea	Very common	*Mysis relicta*
Order Decapoda	Rare	*Astacidae*
Order Isopoda	Common	*Asellidae*
Order Ostracoda	Common	
Class Insecta		
Order Diptera	Very common	*Ceratopogonidae* *Chaoboridae* *Chironomidae* *Culicidae*
Order Coleoptera	Rare	
Order Ephemeroptera	Common	*Ephemeridae*
Order Hemiptera	Rare	
Order Odonata	Rare	*Aeschnidae*
Order Trichoptera	Rare	
Phylum Mollusca		
Class Gastropoda	Occasional	*Bulimidae* *Planorbidae* *Physidae* *Lymnaeidae*
Class Pelycypoda	Occasional	*Sphaeriidae*
Phylum Chordata		
Class Pisces		
Family Clupeidae	Common	*Alosa pseudoharengus*
Family Salmonidae		
Subfamily Coregoninae	Common	*Coregonus artedii* *C. clupeaformis* *C. hoyi*
Subfamily Salmoninae	Occasional	*Salvelinus namaycush*
Family Osmeridae	Very common	*Osmerus mordax*
Family Cyprinidae	Common	*Notropis hudsonius* *N. atherinoides*
Family Catostomidae	Occasional	*Catostomus commersoni*
Family Gadidae	Occasional	*Lota lota*
Family Gasterosteidae	Occasional	*Pungitius pungitius*
Family Centrarchidae	Rare	*Ambloplites rupestris*

TABLE 6. (*Concluded*)

Family Percidae	Common	*Perca flavescens* *Etheostoma* sp.
Family Cottidae	Occasional	*Cottus cognatus* *C. ricei* *Myoxocephalus quadricornis*
Class Amphibia Order Urodela	Rare	

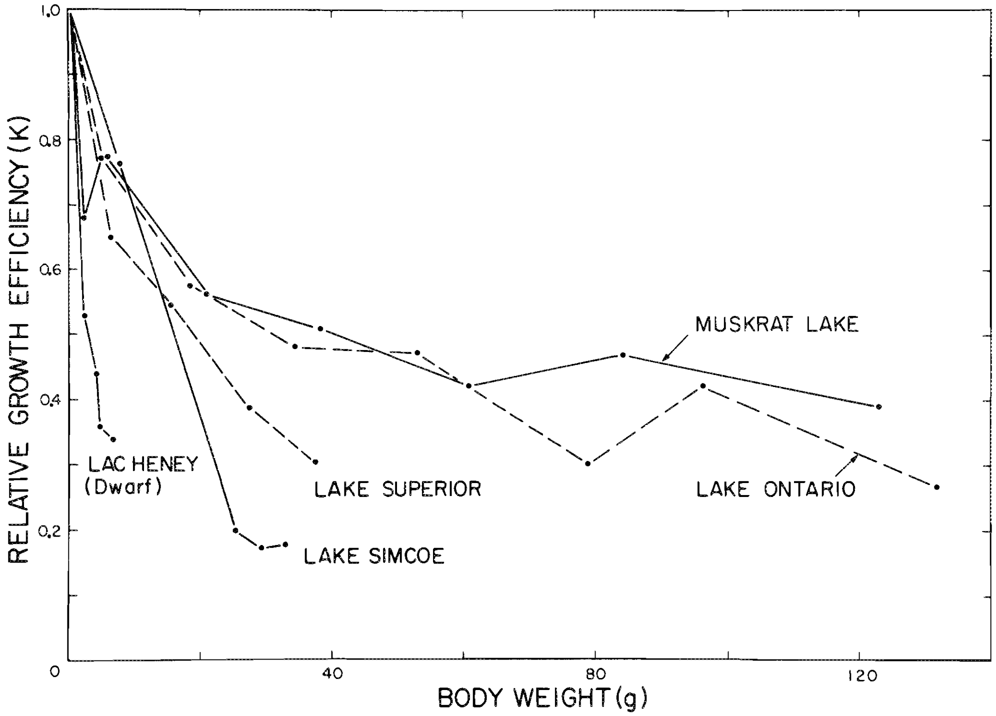

FIG. 5. Relationship between relative growth efficiency [$K_r = \Delta W/(W_i^{0.85} + \Delta W)$] and body weight where W_i is the initial body weight and ΔW is the annual growth increment (Kerr and Ryder 1977). Size at age data: Lac Heney (Delisle 1969), Lake Simcoe (Pugsley 1976), Lake Superior (Schaefer et al. 1981), Lake Ontario (Chen 1970), Muskrat Lake (O'Connor and Power 1974). Data points correspond with annual growth increments.

continuous predation by rainbow smelt since 1912 (Creaser 1925; Beckman 1942). Predation by smelt may have adversely affected recruitment of alewife (O'Gorman 1974) and bloater (Stedman and Argyle 1985) in the Great Lakes, but it has not been possible to establish a cause and effect relationship. Knowledge of the effects of smelt predation on ninespine stickleback (*Pungitius pungitius*), slimy sculpin (*Cottus cognatus*), spoonhead sculpin (*Cottus ricei*), fourhorn sculpin (*Myoxocephalus thompsoni*), darters, and burbot consists of the fact that smelt feed on them to some extent in some situations. In Lac Heney, populations of ninespine stickleback, spoonhead sculpin, fourhorn sculpin, and burbot have apparently persisted in the presence of smelt since the last glacial retreat about 10 000 years B.P. (Delisle 1969).

Lake Huron commercial fishermen reported lake trout eggs and larvae in smelt stomachs in trout spawning areas (Loftus 1980), but Hale (1959) felt that predation on Lake Superior lake trout was probably of little consequence. Loftus and Hulsman (1986) found no evidence of predation on lake trout larvae during spring in Twelve Mile Lake, although given the habitat overlap of young lake trout and adult smelt, and the ability of smelt to consume relatively large prey (Fig. 3), the potential exists for substantial predation of young lake trout (Hassinger and Close 1984). It is certain, however, that lake trout may produce strong year-classes when smelt are present (Bridges and Hambly 1971) and that successful long-standing associations between the two species exist (Kendall 1927; Delisle 1969).

Anderson and Smith (1971) estimated that smelt consumed up to 17% of the herring larvae produced in Nipigon Bay, Lake Superior, where lake herring recruitment was good, but none at all in the Apostle Islands area where recruitment was poor. Crowder (1980) stated that there is strong evidence for interaction between smelt and lake herring in Lake Michigan and felt predation on lake herring may outweigh competition in importance. In Twelve Mile Lake, smelt consumed lake herring and lake whitefish larvae over a period of 7 wk, and up to 28 and 41% of smelt stomachs with food contained these larvae, respectively (Loftus and Hulsman 1986). They concluded that predation by smelt, in combination with other sources of mortality, could explain the recent recruitment failure in lake whitefish in Twelve Mile Lake and that smelt may inflict serious damage on coregonid populations in small lakes where there is a high degree of spatial overlap between the species. In Crystal

TABLE 7. Relative growth efficiency (K_r) at age 4 yr of indigenous and introduced smelt populations in freshwater and marine environments. K_r is calculated as in Fig. 5.

Population	Weight at age 4 (g)	K_r at age 4	Reference
Marine			
Grand Riviere	88.0	0.36	Chen 1970
Miramichi	74.4	0.31	McKenzie 1957
Parker Estuary	70.0	0.14	Murawski and Cole 1978
Freshwater, indigenous			
Bill Lake	55.3	0.58	O'Connor and Power 1974
Lac Heney dwarf	6.5	0.38	Delisle 1969
Lack Heney giant	42.5	0.56	Delisle 1969
Lake Champlain	122.8	0.12	Greene 1930
Matamek Lake	65.4	0.42	Saunders and Power 1970
Mooselookneguntic	61.0	0.35	Rupp 1959
Muskrat Lake	37.9	0.51	O'Connor and Power 1974
Freshwater, introduced			
Crystal lake	56.9	0.02	Beckman 1942
Green Bay	42.5	0.40	Robinson 1973
Lake Erie	28.0	0.23	Sztramko 1984
Lake Ontario	52.6	0.47	Chen 1970
Lake Simcoe	32.6	0.18	Pugsley 1976
Lake Superior	53.9	0.28	Bailey 1964
Lake Superior	37.5	0.31	Schaefer et al. 1981

Lake, however, lake herring and lake whitefish populations coexist with rainbow smelt, and the lake continues to support fisheries for lake whitefish (Laarman 1976). Several other studies (e.g. Kendall 1927; Baldwin 1948; Delisle 1969; MacCrimmon and Pugsley 1979) have also failed to find predation on lake herring by smelt.

Smelt as competitors

Evidence of competition has been largely circumstantial and has consisted of information on habitat and diet overlaps and of changes in growth, survival, and abundance of species associated with smelt. Creaser (1927, 1929) felt that by virtue of their abundance and feeding habits, smelt might be important competitors of lake herring and yellow perch. Anderson and Smith (1971) felt that food competition between smelt and larval lake herring has caused the decline of the lake herring in Lake Superior, although competitive interaction between the two species has not been demonstrated (Lawrie 1978). Hassinger and Close (1984) interpreted a decline in growth of young lake trout in West Bearskin Lake as a response to competition with smelt. Lake Superior smelt share habitat and food with lake trout, but Hale (1959) felt that serious competition did not exist between the two species. Reckahn (1970) concluded that intraspecific competition of young lake whitefish in South Bay, Lake Huron, was probably much more significant than competition with any other fish species, including smelt.

Strong year-classes of whitefish, lake herring, and walleye in Lake Michigan (Wells and McLain 1973) and of whitefish and lake herring in Lake Huron (Berst and Spangler 1973), following the 1942–43 mass mortality of smelt, may have resulted from decreased competition, although environmental factors could possibly have been the cause (Taylor et al. 1987). Declines in walleye abundance have also been associated with increasing smelt abundance, in some cases (Schneider and Leach 1977; Colby et al. 1987; Table 4), but evidence of negative effects of smelt is circumstantial. Complete recruitment failure of lake whitefish occurred in Lake Simcoe during years of peak abundance of smelt and, subsequently, was partly restored when smelt abundance declined (Evans and Waring 1987).

The present structure of the Lake Michigan fish community indicates that considerable reorganization has taken place following the establishment of smelt and alewife (Crowder et al. 1981). Species that declined most rapidly (emerald shiners, lake herring, and deepwater ciscoes (*Coregonus johannae*)) were those with food habits similar to smelt and alewife, but those with different food habits or with the capability of shifting diets (yellow perch, trout-perch (*Percopsis omiscomaycus*), and spottail shiner (*Notropis hudsonius*)) have survived well. Crowder (1980) speculated that smelt probably interact most strongly with lake herring and that predation on young herring may outweigh competition in importance. Christie (1974) noted the collapse of herring stocks following increases in smelt abundance in the Great Lakes. The decline of lake herring in Cayuga Lake, however, has been attributed to alewife rather than smelt (Youngs and Oglesby 1972), and lake herring have produced large year-classes in Lake Simcoe in the presence of high smelt densities (Evans and Waring 1987).

Alewife and smelt appear to be serious competitors for food. Large smelt can consume larger food items than can alewife, but the staple diet of smelt appears to be small invertebrates as it is for alewife (Janssen and Brandt 1980). Rasmussen (1973) observed that in Lake Michigan, the two species utilize similar foods, but that the alewife is the more efficient feeder. In the Great Lakes, smelt have declined in abundance during periods of alewife increases (Smith 1968). Competition with alewife may have resulted in reduced growth of rainbow smelt in New England lakes, and in some cases, smelt may be completely displaced (Eaton and Kardos 1972; Kircheis and Stanley 1981). In the marine environment, alewife and smelt occur in the same areas but are spatially segregated along thermal gradients (Recksiek and McCleave 1973).

Influence of Smelt on Energy Flow in Lakes

Several lines of evidence (case studies of smelt invasions, descriptions of species interactions, growth efficiency relationships, and changes in bioaccumulation of mercury in lake trout) indicate that invasion of indigenous fish communities by rainbow smelt can have major effects on the transfer and storage of energy in these systems.

Our review of case studies revealed changes in growth rates and recruitment success of several species. Cold-water species (lake whitefish, lake trout, lake herring, and Atlantic salmon) were most often affected, as might be predicted on the basis of considerations of niche overlap (Ryder and Kerr 1982). Lake whitefish, the species which frequently declined following smelt invasions, for example, has a life history that is very similar to rainbow smelt, having a pelagic larvae, a demersal, metalimnetic juvenile, and a demersal, hypolimnetic adult (Hart 1930; Kennedy 1943; Reckahn 1970; Hoagman 1973). Smelt and lake whitefish overlap in their use of space and food at each life history stage, resulting in smelt predation on whitefish larvae and possibly competition at all life stages.

One notable feature of the species interactions of smelt in freshwater is the wide spectrum of species and trophic components involved. They feed on zooplankton, larger invertebrates, and small fish, in the water column and on the lake bottom, and they affect other fish species through resource sharing and predation. Ontogenetic shifts may occur in which smelt eat or compete with the young of species, which as adults prey on larger smelt. Smelt do not simply occupy the same trophic position as indigenous planktivores in freshwater ecosystems. Rather, they are omnivores, feeding across trophic levels, and over three levels of the particle size spectrum of lakes (Sprules et al. 1983). Effects of smelt introductions might, therefore, be expected at several trophic levels, as appears to be indicated by our case studies.

Analysis of relative growth efficiency (K_r) of smelt in freshwater revealed a broad spectrum of realized metabolic niches. The suite of K-lines described (Fig. 5) indicates the full potential from planktivory (Lac Heney) to piscivory (Lake Ontario and Muskrat Lake). Comparison of smelt diet studies in these lakes revealed that relative growth efficiency is positively correlated with the size of prey consumed. We would expect that the potential for smelt to change their pattern of growth by shifting from one K-line to another is great. This would be equivalent to changing from one prey size distribution to a larger one (Kerr and Ryder 1977). Experiments involving transplantation of small smelt to new habitats in several Maine lakes (Rupp and Redmond 1966) confirmed the major influence of environmental factors in controlling growth rates, although sympatric populations of dwarf and normal-size smelt are known (Legault and Delisle 1968; Copeman and McAllister 1978; Lanteigne and McAllister 1983). Different K-lines can reflect not only prey size, but availability of prey as well. For example, intra- and interspecific density-dependent effects on prey availability can often explain changing growth patterns of freshwater fishes (Persson 1983; Hanson and Leggett 1985) within and between lakes. Growth efficiency, therefore, is a reflection of the availability and size of prey, as well as the suitability of the physical environment, for a given species.

Variation in the metabolic niche of smelt in freshwater, as assessed by relative growth efficiency, is taken to mean that differences exist in the scope for activity (includes energy available for growth) in different lakes. We would therefore expect the magnitude of the effects on other species to vary directly with K_r. This may explain the differing effects of smelt introductions between lakes. For example, smelt have continued to coexist with lake whitefish and lake herring, two species thought to be particularly vulnerable to smelt (Smith 1972; Crowder et al. 1981), in Crystal Lake since 1912. Relative growth efficiency of smelt in Crystal Lake is among the lowest we have recorded (Table 7), although it is also relatively low in Lake Simcoe where whitefish recruitment failure coincided with increasing smelt abundance (Evans and Waring 1987).

The size spectrum of prey eaten by smelt increases with smelt body size. Therefore, the potential effects of smelt might be expected to be a function of smelt size. Lanteigne and McAllister (1983) applied this observation in recommending that pygmy smelt be managed as a forage species and that the larger rainbow smelt be managed as a gamefish for winter angling. We would caution against introducing either species in view of the potentially serious effects of rainbow smelt on indigenous species and the risks of misidentifying a small phenotype of the rainbow smelt as the pygmy smelt.

Increased growth rate and body condition of lake trout in inland lakes following smelt introductions indicates redirection of energy flow, and an opposite effect to the energy sink hypothesis proposed by Christie (1974) for large, deep lakes. Increased fat content observed in these lake trout (OMNR, unpubl. data) corresponds with our observation of elevated mercury content of lake trout flesh in lakes inhabited by smelt (OMNR and Ontario Ministry of the Environment 1984a, 1984b). MacCrimmon et al. (1983b) and Wren (1983) also found that the rate of mercury accumulation in the white muscle of lake trout accelerates, as does growth, when lake trout switch to a diet of smelt.

Conclusions

Available evidence indicates that rainbow smelt are well adapted to freshwater, having colonized most lake types available in eastern North America. They are most successful, however, in relatively large, deep lakes inhabited by cold- and cool-water fish species and have not been reported in any Ontario lakes having surface pH < 6.0 (May–August). Smelt are omnivorous in freshwater, their diet varying from small zooplankton to fish up to a maximum prey size of about 6% of their own body weight. As a result, they interact with a wide size spectrum of species and can have a major influence on energy flow and storage in lakes via food web restructuring. The metabolic niche, described here in terms of relative growth efficiency, is highly variable in freshwaters, reflecting, we conclude, differences in the metabolic scope for activity (including growth) as a consequence of food availability and prey size, as well as habitat constraints. Variation in growth efficiency might be related to the variable effects of smelt invasions on indigenous species, although this might also be confounded by intraspecific effects on both growth and recruitment (Evans and Waring 1987).

Few case studies have adequately documented the effects of invasion by rainbow smelt on indigenous freshwater fishes. Recurring observations of declines in lake whitefish populations, however, strongly suggest incompatibility with rainbow smelt, but not in every case. Other species whose growth rates and recruitment appear to be affected in some cases include Atlantic salmon, lake trout, lake herring, walleye, burbot, emerald shiner, alewife, and bloater. While further research is required to understand the apparent inconsistent effects on other species, it is clear that the risks of invasion by rainbow smelt are sufficiently high that managers should attempt to exclude this species from lakes with naturally reproducing stocks of cold- and cool-water species. Specifically, we would recommend against introducing rainbow smelt as prey for lake trout, especially in the case of naturally sustaining stocks, and in softwater areas where bioaccumulation of natural mercury could be accelerated by feeding on smelt. Exclusion of smelt is equally important for the protection of naturally sustaining lake whitefish stocks, especially in small inland lakes (Loftus and Hulsman 1986). Lack of information on the specific effects of smelt on recruitment success of most other species necessitates a cautious management approach.

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