Ecosystem effects of Rainbow Smelt (*Osmerus mordax*) invasions in inland lakes: A literature review

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ECOSYSTEM EFFECTS OF RAINBOW SMELT (*Osmerus mordax*) INVASIONS IN INLAND LAKES: A LITERATURE REVIEW

by

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ABSTRACT

Rooney, R.C., and Paterson, M.J. 2006. Ecosystem effects of rainbow smelt (*Osmerus mordax*) invasions in inland lakes: a literature review. Can. `Tech. Rep. Fish. Aquat. Sci. 2845: iv + 33 p.

Rainbow smelt (*Osmerus mordax*) have invaded many North American inland lakes, and their distribution continues to expand. Their broad dietary and habitat tolerances permit smelt to interact with numerous trophic levels, including zooplankton, planktivores, benthivores, and piscivores. Major concerns include the potential for rainbow smelt to extirpate native planktivores through a combination of competition and predation, their potential to weaken sport and commercial fisheries through competition and predation on juvenile game fish, and their potential to produce a trophic cascade that accelerates eutrophication. Enhancing adult piscivore populations has proven effective at reducing smelt populations; however, preventing smelt invasion is the preferred management strategy. Accidental and deliberate introduction by humans has been the primary mode of smelt range expansion, thus programs should be aimed at increasing public awareness of the risks of smelt invasion. Future research should examine multiple scales and should include both pelagic and benthic components because smelt have the potential to impact ecosystems at all levels. Recently developed models that forecast smelt distribution should be combined with current distributional data to help managers prioritize lakes at a greater risk of invasion. Investigation into the interaction between smelt invasion, climate change, and expanding human settlements is also necessary.

RÉSUMÉ

Rooney, R.C., Paterson, M. 2009. Les effets sur l’écosystème des lacs intérieurs lors de l'envahissement de l’éperlan arc-en-ciel (*Osmerus mordax*) : une recherche documentaire. Rapp. Tech. Can. Sci. Hallieut. Aquat. 2845 : v + 30 p.

Plusieurs lacs en Amérique du Nord ont connu l’envahissement ainsi qu’une distribution répandue de l’éperlan arc-en-ciel (*Osmerus mordax*). L’éperlan a une diète et un habitat divers ce qui lui permet interagir avec plusieurs niveaux trophiques qui inclus le zooplancton, les planctonivores, les organismes benthiques et les piscivores. L’éperlan cause des inquiétudes pour les écosystèmes aquatiques qu’il envahi telles que causer la disparition d’espèces de planctonivores indigènes par moyen de la prédation et la compétition, causer l’affaiblissement des populations des poissons commerciaux et sportives par moyen de la prédation et la compétition avec les juvéniles de ces espèces, et l’accélération de l’eutrophication due à la possibilité de provoquer des changements en cascade à travers les niveaux trophiques. Les populations d’éperlans peuvent être contrôlées par l’accroissement de la population de poissons piscivores. Désormais, la meilleure stratégie est la prévention de l’envahissement de cette espèce. Le mode principal d’établissement de l’éperlan dans un nouveau territoire est l’introduction par l’homme, soit accidentelle ou intentionnelle. Pour cette raison, les programmes d’éducation doivent renseigner le public des risques de l’envahissement de l’éperlan. Les conséquences de l’éperlan arc-en-ciel peuvent être subissent à tous les niveaux trophiques et alors, les recherches futures devraient inclure l’étude des habitats pélagiques et benthiques ainsi que, les multiples échelles temporales et spatiales. Les modèles récents qui prédisent la distribution de l’éperlan devraient inclurent les plus nouveaux renseignement au sujet de leur distribution afin d’aider au gestionnaire de prioriser les lacs avec le plus grand risque d’envahissement. Il est aussi nécessaire d’examiner les interactions entre l’envahissement de l’éperlan, le changement climatique et l’expansion des habitations humaines.

RAINBOW SMELT: AN INVASIVE SPECIES

Many freshwater lakes in North America are being affected by the invasion of exotic fish species. Invasive fishes are replacing indigenous fish resulting in a homogenization of fish communities (Rahel 2002). The economic cost of invasive fish on commercial fisheries is enormous; an estimated $4.5 billion USD for the Great Lakes Basin alone and another $1 billion USD for the remaining USA (Pimentel 2005). The ecological costs of these invasions have been equally serious, although not so easily assigned a dollar value. Invasive species may induce changes in invaded ecosystems at all levels of organization, including individuals, populations, communities, and whole ecosystems (Simon and Townsend 2003). It is therefore necessary to use a multilevel approach to examine the impact of an invasive species (Vitousek 1990).

Rainbow smelt (*Osmerus mordax*) is an exotic species with an expanding range in North American lakes. Typically, rainbow smelt are small (8 to 36 cm total length) pelagic schooling fish that are predominantly found in the mid-water column and feed mainly on invertebrates (Scott and Crossman 1998). Rainbow smelt have broad habitat tolerances (Evans and Loftus 1987) and integrate pelagic and benthic food webs as generalist feeders (O'Connell et al. 2005, Vander Zanden and Vadeboncoeur 2002). Invasion by rainbow smelt may alter the habitat use and diet of individuals of indigenous species through competition or predation (Evans and Loftus 1987), affect the abundance and distribution of native populations (e.g. Hrabik et al. 1998, Loftus and Hulsman 1986), affect community composition and structure (e.g. Beisner et al. 2003, Reif and Tappa 1966), and change the flow and storage of energy and nutrients within a lake (e.g. Lammens et al. 1985, Siegfried 1987). Rainbow smelt can affect all trophic levels through both direct and indirect interactions, such as trophic cascades.

The objective of this review is to explore the potential effects of rainbow smelt invasion on small lake ecosystems. There are three components that influence the impact of rainbow smelt. First, its current distribution and mechanisms of dispersal will determine the likelihood that a given lake will be exposed to smelt propagules. Second, the specific habitat and diet tolerances of the exotic species will determine whether lakes exposed to propagules can support a self-sustaining population. Third, the interactions between rainbow and resident taxa will dictate the magnitude of impact an invasion will have on a given lake (Vander Zanden and Olden 2008). Data from the Laurentian Great Lakes are considered only to elucidate processes potentially occurring in smaller lake systems where data are lacking. This is because the Great Lakes have been affected by many forces acting simultaneously with smelt invasion, such as invasion by exotic sea lamprey (*Petromyzon marinus*), alewife, and *Dreissena* mussels, over-fishing, and nutrient fluctuations (Bronte et al. 2003, Cox and Kitchell 2004, Dermott et al. 1999, Myers and Worm 2003, O'Gorman et al. 2000, Rand and Stewart 1998, Ricciardi 2005). Smaller lakes offer less habitat complexity, meaning that native species may be more affected than in large lakes where greater resource partitioning is possible. Thus, the effects of smelt invasion may be more severe in small lakes. Hundreds of thousands of small isolated lakes are potentially at risk from smelt invasion. These small lakes may be refuges for specialist indigenous species that could be displaced by smelt. Given the large number of lakes at risk, we require an understanding of which lakes are most vulnerable to smelt invasion to most effectively allocate limited mitigation resources (Drake and Lodge 2006, Mercado-Silva et al. 2006, Vander Zanden and Olden 2008).

RAINBOW SMELT DISTRIBUTION IN NORTH AMERICA

CURRENT GEOGRAPHIC DISTRIBUTION

In North America, rainbow smelt are a glacial relict native to some inland waters of Maine, New Hampshire, eastern Ontario, Quebec, New Brunswick, Nova Scotia, Newfoundland and Labrador (Scott and Crossman 1998). The range of rainbow smelt, however, has been greatly extended by a combination of human introductions and natural dispersal. Rainbow smelt are now present in many lakes throughout the St. Lawrence River drainage system, including all of the Laurentian Great Lakes, many large lakes such as Lakes Simcoe, Nipissing, Timiskaming, and Nipigon, and numerous small lakes (Evans and Loftus 1987). Smelt are also present in the Hudson Bay drainage basin and are found in lakes in Minnesota, north-western Ontario, and Manitoba, including Lake Winnipeg (Franzin et al. 1994) and the Nelson River system (Remnant et al. 1997). In the USA, rainbow smelt have been reported as far west as the Missouri River in Montana, along the Mississippi River from Minnesota to Louisiana (Mayden et al. 1987, Suttkus and Connor 1979), and from numerous inland lakes in New York, Vermont, and Massachusetts (Halliwell et al. 2001).

HISTORY OF RANGE EXPANSION

Rainbow smelt are known to disperse rapidly. For example, the expansion of rainbow smelt into the Laurentian Great Lakes is well documented. Rainbow smelt invaded the Great Lakes watershed through an intentional introduction to Crystal Lake, Michigan in 1912 (Creaser 1925). They were first reported from Lake Michigan, Lake Huron, Lake Superior, and Lake Erie in 1923, 1925, 1930, and 1935, respectively (Nellbring 1989). Rainbow smelt were first reported from Lake Ontario in 1929, and probably reached it by dispersal along natural waterways from the Finger Lakes, New York, where they were intentionally introduced in 1917 (Nellbring 1989). Mayden *et al.* (1987) inferred that rainbow smelt reached the Illinois River from Lake Michigan, but that most occurrences in the Mississippi-Missouri drainage basin resulted from introductions into two reservoirs. In 1971, rainbow smelt were intentionally introduced into Lake

Sakakawea, North Dakota, and, in 1974, smelt were accidentally introduced to Lake Oahe, South Dakota (Mayden et al. 1987, Nellbring 1989). From these two reservoirs they have spread down the Mississippi River to St. Francisville, Louisiana (Suttkus and Connor 1979) and upstream as far as the North Peck Dam and the Yellowstone River, Montana (Franzin et al. 1994). More recently, rainbow smelt have invaded the Hudson Bay drainage basin, likely also assisted by intentional or accidental human transfer. Rainbow smelt were first reported in the Hudson Bay basin in 1962 in Little Eagle Lake, Ontario. In 1972, they were reported in the Rainy River system in Burntside Lake, Minnesota and Eva Lake, Ontario (Franzin et al. 1994). Rainbow smelt have since been captured in numerous lakes in the Hudson Bay drainage basin (Remnant et al. 1997), and are now reported in Hudson Bay (Franzin pers. com. 2007).

MECHANISMS OF DISPERSAL

The ability of rainbow smelt to disperse is mediated by the connectivity of lakes, the ability of smelt to move through connecting streams, and the suitability of connected lakes as rainbow smelt habitat (Hrabik and Magnuson 1999). Adult smelt may migrate upstream during spring spawning (Nellbring 1989), while fry and older fish may be washed downstream (Naesje et al. 1987). Passive downstream migration by larva may be more important than adult migration, as larvae are better able to bypass rapids, falls, and dams (Franzin et al. 1994). Natural dispersal between watersheds is not possible: rainbow smelt require a vector to assist in dispersal from one drainage basin to another (Hrabik and Magnuson 1999).

Human transfer has been the major force accelerating the range expansion of rainbow smelt (Daniels 2001, Evans and Loftus 1987, Halliwell et al. 2001, Kircheis and Stanley 1981). While this is mainly through intentional and accidental introductions, construction of canals to link previously isolated basins has also facilitated the dispersal of exotics. Hrabik and Magnuson (1999) modeled rainbow smelt dispersal in northern Wisconsin and estimated that it would take 1000 years for rainbow smelt to colonize 25% of habitable lakes if dispersal was limited to natural means. If human transport was incorporated in the model, rainbow smelt could colonize 50% of habitable lakes within 200 years. This latter estimate more closely corresponds with recent invasion rates.

Rainbow smelt have been intentionally introduced to many lakes as forage fish to support recreational and commercial fisheries of salmon (*Salmo salar*), trout (*Oncorhynchus* spp. and *Salmo* spp.), and walleye (*Sander vitreum*) (Jones et al. 1994, Kirn and Labar 1996, Rand and Stewart 1998, Stewart et al. 1981). Introductions are usually achieved by the transfer of fertilized eggs naturally deposited on burlap or the transfer of sexually mature adults in aerated containers (Kircheis and Stanley 1981). As early as 1937, concerns were raised regarding the intentional introductions of rainbow smelt (Van Oosten 1937) and intentional introductions are now illegal in many jurisdictions.

Rainbow smelt can also be transferred accidentally by humans. In New England, New York, and New Jersey, rainbow smelt introductions have been attributed to the escape of smelt used as live bait in recreational fishing (Halliwell et al. 2001). This is despite legislation and regulations prohibiting the transfer of live bait across jurisdictional boundaries (Litvak and Mandrak 1993). Other methods of accidental transfer include the release of fertilized eggs while cleaning sexually mature smelt (Evans and Loftus 1987) and the transfer of fertilized eggs attached to aquatic vegetation or rocks (Kircheis and Stanley 1981).

Lakes with elevated human traffic are at greater risk of smelt invasion. These include lakes with greater accessibility by road or trail, higher cottage density, or heavier sport fishing (Evans and Loftus 1987). Measures of recreational fishing intensity, such as the number of boat launches, may improve smelt invasion models by incorporating the role of humans as vectors for smelt transfer (Vander Zanden and Olden 2008). Public education regarding the risks posed by rainbow smelt introductions is critical to minimize accidental and intentional introductions (Hrabik and Magnuson 1999).

FUTURE DISTRIBUTION

Accurate prediction of successful invasions is a critical step in developing effective conservation strategies for vulnerable lakes (Hrabik and Magnuson 1999). Our understanding of the habitat requirements of smelt is largely correlative (e.g. Evans and Loftus 1987). Research into conditions where smelt introductions were unsuccessful would yield a more definitive understanding of habitat thresholds for smelt. Assuming that rainbow smelt were present in all suitable lakes within their native range in southern and southeastern Maine (354 lakes total), Mercado-Silva et al. (2006) used classification-tree modelling of smelt presence or absence to quantify rainbow smelt’s niche based on lake morphometry and physicochemical variables. They produced a model that correctly predicted smelt presence 82.5% of the time, and correctly predicted smelt absence 90.3% of the time.

Smelt presence may be highly predictable as a function of limnological, physical, and chemical variables (Mercado-Silva et al. 2006); however, in light of the immense number of lakes potentially at risk of invasion (>250 000 lakes in Ontario alone), such lake specific data are often not available. In addition, the primary variables constraining smelt distribution may not be the same throughout its potential range. An alternative method to ecological niche modelling has been developed using a genetic algorithm based on widely available spatial data layers (Drake and Lodge 2006). Data layers can be used even if they are not themselves determinants of habitat quality for smelt, providing it can be assumed that they are related to environmental variables that limit smelt occurrence. For example, precipitation may not directly influence smelt occurrence but precipitation data is correlated with the density of lakes and stream corridors that may affect smelt dispersal rates (Drake and Lodge 2006). Although this technique cannot predict risks to a particular lake, it can make broad-scale, spatially explicit predictions to help resource managers identify regions of greater invasion risk (Vander Zanden and Olden 2008). This would enable them to focus resources for the assessment of lake-specific risk where regional risks are greatest.

RAINBOW SMELT BIOLOGY

Once a lake has been invaded by rainbow smelt, the resulting effects will depend on their life history and resource use along diet and habitat gradients. These will determine which lakes provide the most suitable habitat and the degree to which exotic smelt directly or indirectly impact native taxa. Below, we review rainbow smelt life history, diet, and habitat usage before considering further potential impacts of smelt invasion on small lakes.

SYSTEMATICS

Rainbow smelt belong to the genus *Osmerus*, whose taxonomy has been contested. Based on meristic and morphological features and electrophoretic examinations, there appear to be two primary forms: *O. mordax*, commonly called rainbow smelt; and *O. eperlanus*, commonly called European smelt. A third form, *O. dentex*, has a North Pacific and Arctic distribution and in some areas lives sympatrically with *O. eperlanus*, however, some authors consider it a subspecies of *O. mordax* (Nellbring 1989). The three forms of smelt are sufficiently similar that some authors consider them all subspecies of to the European smelt (*O. eperlanus*) (Nellbring 1989). *O. eperlanus* and *O. mordax* make use of similar habitat and food resources, and can be considered interchangable for the purposes of this paper, but the name “rainbow smelt” is used specifically in reference to *O. mordax*.

LIFE HISTORY

Rainbow smelt can be anadromous, ascending from saltwater to freshwater to spawn, but they are also capable of completing their life history exclusively in freshwater (Scott and Crossman 1998). Landlocked adult rainbow smelt begin spawning shortly after ice-off at night in the lower reaches of streams (Kircheis and Stanley 1981). Rainbow smelt may also spawn at a lake’s shoreline but deepwater spawning is uncommon (Nellbring 1989).

The number of eggs extruded by a female is positively related to its size (McKenzie 1964). Eggs are adhesive (McKenzie 1964) and after extrusion attach to substrates such as gravel, sand, mud, or submerged vegetation (Nellbring 1989). Eggs are left unattended and hatch in 1-4 weeks, depending on water temperature (Kircheis and Stanley 1981). Estimated rates of egg survival to hatching are low, ranging from <1% to 7.2% (Nellbring 1989). Hatching success is density dependent, with lower success rates in more crowded egg masses (McKenzie 1964). After hatching, larva typically drift downstream into a lake (Nellbring 1989).

Time to sexual maturity is dependent on food supply and water temperature, as abundant food and warmer temperatures encourage faster growth (Nellbring 1989). Sexual maturity is usually reached at age II-III, with fork lengths as little as 15 cm (Kircheis and Stanley 1981). Under optimum conditions in large lakes, rainbow smelt may grow as large as 35.6 cm (Scott and Crossman 1998) and may live as long as 7+ years. In smaller lakes, maximum sizes may be substantially less (Scott and Crossman 1998).

Landlocked smelt populations periodically experience extensive die-offs. For example, post spawning die-offs are common in May or June in Lake Erie (Scott and Crossman 1998). Mass mortalities not associated with spawning have also been reported from the Laurentian Great Lakes, the Miramichi River, and lakes in the north-western USSR (Nellbring 1989). These die-offs are most often attributed to high summer temperatures or fungal/disease/parasite epidemics.

DIET

At densities that can exceed 40 000 individuals ha^{-2} (Horppila et al. 2003), rainbow smelt may constitute a significant predation pressure within a lake. The average food consumption rate of a single age II+ smelt can be as high as 0.12 g d^{-1} wet-weight, and an age IV+ smelt can consume 0.14 g d^{-1} wet-weight (Horppila et al. 2003).

Rainbow smelt food consumption rates vary seasonally. MacCrimmon and Pugsley (1979) found that all smelt captured in large Lake Simcoe, Ontario in June had food in their stomachs; 84% of those captured from July to December contained food but food intake was minimal before spawning in March and April. A similar pattern in food consumption was observed in *O. mordax* from smaller Twelve Mile Lake, Ontario (Loftus and Hulsman 1986), suggesting similar consumption rates could be expected in small lake systems.

The size of prey consumed by smelt is positively correlated with body size (MacCrimmon and Pugsley 1979, Trzebiatowski and Gaj 1978) and they are capable of consuming individual prey weighing as much as 6% of their body weight (Evans and Loftus 1987). Feeding is visual and selective (Gliwicz et al. 2004, Johnson et al. 2004).

Young-of-the-year smelt feed preferentially on small-sized zooplankton such as *Cyclops* spp., *Diaptomus* spp., copepod nauplii, rotifers, and diatoms (Evans and Loftus 1987). By August and September, at approximately 45 mm (fork length), rainbow smelt move to deeper water where temperatures range from 8 to 12°C (Nellbring 1989). They then begin selecting larger and more compact-bodied zooplankton prey such as smaller *Daphnia* spp. and calanoid copepods (Gordon 1961, Urban and Brandt 1993). As their fork length exceeds roughly 60 mm, they begin actively selecting even larger prey such as *Mysis relicta*, *Leptodora kindtii* or large *Daphnia* spp. (Johnson et al. 2004, Urban and Brandt 1993).

Although the majority of the diet consists of zooplankton, rainbow smelt are opportunistic feeders and will feed on insects including Chironomidae and *Chaoborus* spp. larva, as well as algae and amphipods, if abundant (Gliwicz et al. 2004, Lalancette 1986, MacCrimmon and Pugsley 1979, Siefert 1972). In Saginaw Bay, Lake Huron, Gordon (1961) found age I+ rainbow smelt fed heavily on Ephemeroptera in autumn, particularly *Hexagenia*. MacCrimmon and Pugsley (1979) also noted that *Hexagenia* was commonly in the guts of rainbow smelt in Lake Simcoe, Ontario. In Lake Tyrifjorden, Norway, *O. eperlanus* fed mainly on zooplankton from July to February and on benthic insects from March to June (Garnås 1982). Chironomid larva, ostracods, gastropods, and trichopterans are often recovered from rainbow smelt stomachs in both small (Evans and Loftus 1987) and large lakes (Gordon 1961). Hence, rainbow smelt can provide a link between benthic and pelagic food webs (Vander Zanden and Vadeboncoeur 2002).

Larger rainbow smelt may consume young-of-the-year fish, particularly in late winter (MacCrimmon and Pugsley 1979). Gordon (1961) found that fish were not a common source of food but could contribute a large percentage of total food volume. In July, August, and September, fish were present in 8% (n = 50), 7% (n = 124), and 23% (n = 28) of smelt stomachs but constituted 25%, 27%, and 49% of total food volume, respectively. Fish inclusion in rainbow smelt diet is strongly correlated with rainbow smelt size. For example, in Lake Huron 100% of smelt with fork lengths >170 mm contained fish in their stomach contents (Dermott et al. 1999). Therefore, fish consumption by smelt may be less common in small lakes where maximum sizes are lower. Fish species reported to be consumed by smelt include emerald shiners (*Notropis atherinoides*) (MacCrimmon and Pugsley 1979), cisco (*Coregonus artedii*) (Hrabik et al. 1998), alewife (*Alosa pseudoharengus*) (O'Gorman 1974, Stedman and Argyle 1985), young bloater (*Coregonus hoyi*) (Stedman and Argyle 1985), slimy sculpin (*Cottus cognatus*) (Brandt and Madon 1986), and young-of-the-year rainbow smelt (Gordon 1961, MacCrimmon and Pugsley 1979). Large rainbow smelt may also feed on the eggs and larva of piscivores such as lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*) (Evans and Loftus 1987).

Cannibalism among rainbow smelt may result in alternating cohort dominance, high recruitment variability, and long term population instability. Henderson and Nepszy (1989) found that recruitment per spawner was inversely correlated with the abundance of age I rainbow smelt but was not correlated with parental stock size, suggesting that cannibalism by age I smelt was critical in determining recruitment success. In Lake Miedwie, Poland, cannibalism on juvenile *O. eperlanus* constituted 93% by-weight of the diet of *O. eperlanus* 140-200 mm in length. In Lake Champlain, which straddles the boarder between New York, Vermont, and Quebec, Stetter et al. (2007) estimated that 38-93% of the mortality of age 0 smelt was the result of cannibalism by age I+ smelt.

HABITAT

Physical and chemical characteristics constrain the habitat suitability of lakes for rainbow smelt (Evans and Loftus 1987) and will also determine the distribution of smelt within a lake (Appenzeller and Leggett 1995, Gliwicz et al. 2004, Horppila et al. 2000, Urban and Brandt 1993). Rainbow smelt prefer deep, cold, oligotrophic lakes, although they are also occasionally present in shallow, small, and productive lakes (Table 1). Acidity may constrain smelt distribution as they were not observed in small lakes with pH <6.0 in surveys by Evans and Loftus (1987) or by Halliwell et al. (2001). Following snow-melt, rainbow smelt eggs may be subjected to lethal pH reductions in poorly buffered lakes typical of the Precambrian Shield. Lake area may also limit smelt habitat suitability. Evans and Loftus (1987) suggested that correlations between smelt occurrence in Ontario lakes and lake area might be due to a positive relationship between cottage density and lake area. In contrast, Hrabik and Magnuson (1999) found that human introductions occurred randomly with respect to lake size in northern Wisconsin. Mercado-Silva (2006) suggest that a combination of lake area and depth controls habitat suitability for smelt. Lakes less than 21 ha in area were often inhabited by smelt, providing they had maximum depths >20 m (Mercado-Silva et al. 2006).

Table 1. Summary of limnological and chemical habitat thresholds derived from rainbow smelt presence in 187 Ontario Lakes, adapted from Evans and Loftus (1987).

Variable	Number of Lakes Reported (n)	Mean	Minimum	Maximum
Area (km^2)	177	52.3	0.1	4480.0
Mean Depth (m)	169	11.6	2.0	38.7
Maximum Depth (m)	181	35.7	4.0	213.5
Total dissolved solids (mg/L)	135	49.4	5.5	231.4
Alkalinity (mg/L)	170	25.0	4.0	145.4
Surface pH (May-August)	173	7.2	6.0	9.3
Hypolimnion pH (May-August)	158	6.5	5.5	9.0
Number of Fish Species	179	11.3	3.0	63.0

Although often considered cold water fish, rainbow smelt are eurythermal (Evans and Loftus 1987, Nellbring 1989). Young-of-the-year are usually found near shore in warm water from 2-6 m in depth, while yearlings are found in cool water at middle depths in the pelagic zone (<35 m) (Emery 1973, Nellbring 1989). Sexually mature rainbow smelt may be found in the littoral zone during spring spawning but age II+ smelt are usually distributed throughout the profundal zone at temperatures from 6-14^{o}C and depths >15 m (Nellbring 1989). In Lake Ontario, young-of-the-year rainbow smelt are concentrated in water approximately 15 m deep but following fall turn over, migrate to water >25 m deep (Urban and Brandt 1993).

Diel vertical migrations by smelt are common during stratification (July to October). Age I+ smelt typically spend the daylight hours at depth and move upwards at night to where plankton are more abundant (Emery 1973, Nellbring 1989, O'Gorman et al. 2000). In Lake Memphremagog, Quebec/Vermont, day-time peak densities of age I+ smelt were at 30-40 m, while night-time peak density was much shallower (10-15 m), unless the epilimnion temperature exceeded 18°C, in which case they congregated just beneath the thermocline (Appenzeller and Leggett 1995). In Georgian Bay, Lake Huron, SCUBA divers observed that juvenile rainbow smelt were most common at 10 m during daylight but ascended to feed at night (Emery 1973). In Lake Memphremagog, light avoidance appears to be an anti-predation strategy as smelt predators such as lake trout and Atlantic salmon (*Salmo salar*) are visual predators whose reactive distances increase with light intensity (Appenzeller and Leggett 1995, Gliwicz and Jachner 1992). While light avoidance may limit the upper daytime distribution of rainbow smelt, the lower distribution appears to be limited by factors such as dissolved oxygen concentration (Gliwicz et al. 2004). The depth distribution of smelt may also be affected by diel migrations of important prey items such as cladocerans, copepods, and *Chaoborus* larvae.

Larval smelt may display a reverse migratory pattern. During daylight in Lake Michigan, the maximum density of adult smelt was observed from 7-8°C, while the maximum density of larval smelt was at 13-14°C. At night they switched positions in the water column (Brandt et al. 1980). This reverse diel migration pattern was also observed for larvae in Georgian Bay, which displayed peak abundance at 2 to 4 m during daylight, but at night were most concentrated 2-3 m above the sediment (Emery 1973). This could be an adaptation to cannibalism, although this pattern was not observed in Lake Memphremagog (Appenzeller and Leggett 1995).

INTERACTIONS OF RAINBOW SMELT WITH NATIVE ORGANISMS

PISCIVORE – SMELT INTERACTIONS

Rainbow smelt are consumed by many piscivorous fish (Crawford 2001, Pientka and Parrish 2002). One of the primary justifications for deliberate rainbow smelt introductions has been their suitability as forage fish for important sport and commercial fisheries (e.g. Halliwell et al. 2001, Johnson and Goettl 1999, Jones et al. 1994, Kircheis and Stanley 1981). In Lake Champlain, rainbow smelt are the major prey of lake trout, Atlantic salmon, and walleye, contributing 63.6%, 79.8%, and 41.3% of their respective diets by weight (Kirn and Labar 1996). Following their introduction to Schoodic Lake, Maine in 1965-1967, rainbow smelt became a critical component of the diet of Atlantic salmon, appearing in 100% of angled salmon stomachs by 1970 (Havey 1973). In the Horsetooth Reservoir, Colorado, rainbow smelt were introduced in 1983 and by 1989 they constituted 100% of stomach contents of walleye sampled annually in late August, replacing decapods, salmonids, and other game fish (Jones et al. 1994). Rainbow smelt may also be an important component of the diets of northern pike (*Esox lucius*) and burbot (*Lota lota*). For example, in Lake Michigan they constitute >75% of spring-time food for these two species (Wagner 1972). American eel (*Anguilla rostrata*), yellow perch (*Perca flavescens*), sauger (*Sander canadense*), white bass (*Roccus chrysops*), white perch (*Morone americana*), lake whitefish (*Coregonus clupeaformis*), bowfin (*Amia calva*), rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), splake (*Salvelinus fontinalis* x *S. namaycush*), and brook trout (*S. fontinalis*) have been reported to feed on rainbow smelt in small lakes (Evans and Loftus 1987).

The growth rates and condition factors of predatory fish often increase following rainbow smelt introductions (e.g. Havey 1973, Johnson and Goettl 1999, Jones et al. 1994). These increases may not be sustainable, however, and introducing rainbow smelt as forage fish for sport or commercial fisheries is now widely cautioned against (Evans and Loftus 1987, Johnson and Goettl 1999, Kircheis and Stanley 1981, Nellbring 1989, Ricciardi 2005). In some cases, the introduction of rainbow smelt has resulted in declines of predatory fish populations (e.g. Mercado-Silva et al. 2007).

Rainbow smelt populations can be highly variable and prone to mass mortalities, making them an unstable source of food for piscivores (Havey 1973, Kircheis and Stanley 1981, Nellbring 1989). Variability in rainbow smelt abundance may be due to cannibalism (He and Labar 1994, Lantry and Stewart 2000), predation by stocked piscivores (Hoff 2004, Johnson and Goettl 1999), disease (Chen and Power 1972, Nellbring 1989), variability in food availability (Kircheis and Stanley 1981), or competition with other planktivores (Jones et al. 1993, Kitchell and Crowder 1986). Fluctuations in rainbow smelt populations can negatively affect commercial and recreational fisheries where smelt have become the dominant forage species (e.g. Havey 1973, Johnson and Goettl 1999, Kitchell and Crowder 1986). In large lakes with high species diversity, piscivores may switch to feeding on native fish species but if exotic rainbow smelt have displaced native planktivores, a shift in diet may not be feasible.

The diet of many adult piscivorous fish often changes in proportion to their size, changing from plankton to crustaceans and insects to fish as they grow (Scott and Crossman 1998). Juvenile predatory fish may therefore be in competition with smelt for zooplankton, insects, and crustaceans. For example, in Lake Oahe, South Dakota, zooplankton were the most important component in the diet of rainbow trout <200 mm total length from May to September (Lynott et al. 1995). Rainbow smelt were only consumed by rainbow trout >201 mm (total length) and did not become the dominant food resource until trout >460 mm (Lynott et al. 1995). Similarly, Havey (1973) observed that few Atlantic salmon <300 mm in length fed on rainbow smelt in Shoodic Lake, Maine. In regions with intense fisheries, few individuals may reach the size necessary to benefit from rainbow smelt as forage fish (Kircheis and Stanley 1981). In Lake Ontario, rainbow smelt are known to eat *Mysis relicta* and slimy sculpin, both important sources of food for juvenile lake trout (Brandt and Madon 1986, Gal et al. 2006). In West Bearskin Lake, the growth rate of juvenile lake trout was reduced following the introduction of smelt, possibly because of competition with smelt for food (Hassinger and Close 1984). In Sporley Lake, Michigan, rainbow trout were introduced in 1959 and rainbow smelt in 1962 (Galbraith 1967). Initially, resource partitioning limited competition between the two: rainbow trout selected mostly *Daphnia* spp. >1.3 mm, while rainbow smelt consumed *Daphnia* spp. ranging from 0.3-0.7 mm (Galbraith 1967). By 1964, however, large-bodied *Daphnia* spp. had been eliminated and mean *Daphnia* spp. size had decreased from 1.4 mm-0.8 mm (Galbraith 1967). This led to reduced rainbow trout growth and survival (Galbraith 1967).

Rainbow smelt may also affect piscivorous fish populations through consumption of juvenile fish, larva and eggs of species that feed on rainbow smelt later in their development (Evans and Loftus 1987). This may lead to recruitment failure in fish species that rainbow smelt were introduced to feed (Kircheis and Stanley

1981). For example, Mercado-Silva et al. (2007) attributed declines in walleye recruitment in 12 small Wisconsin lakes to predation and/or competition with rainbow smelt.

In summary, competition between young piscivores and adult smelt for food resources and the predation of rainbow smelt on their eggs and larvae may offset any improvements to recruitment, adult growth rates, and condition factors achieved by introducing rainbow smelt as forage fish. Further indirect or subsidiary effects remain poorly studied. For example, rainbow smelt may relieve predation pressure on native planktivores. Future intentional introductions of rainbow smelt as forage fish for piscivores should be avoided in small lakes until we have a better understanding of these interactions.

PLANKTIVORE – SMELT INTERACTIONS

Rainbow smelt have broad dietary and thermal requirements and, thus, have substantial opportunity to interact with native planktivores. Rainbow smelt population expansions are often associated with declines in numbers of yellow perch, cisco, lake whitefish, and alewife, all of which share food and habitat with rainbow smelt (Scott and Crossman 1998). Rainbow smelt invasion has been linked with declines in condition factor (e.g. Lammens et al. 1985), abundance (e.g. Willis and Magnuson 2006), recruitment success (e.g. Cox and Kitchell 2004, Hrabik et al. 2001, Loftus and Hulsman 1986), and even extirpation of native planktivores (e.g. Hrabik et al. 1998). The generalist feeding strategy of rainbow smelt may offer them a competitive advantage if they are able to supplement their diet with food resources not available to other planktivores (Wain 1993). They may also out-compete native species because they are less dependent on tributary and wetland habitat than many native taxa and thus, are less affected by lakeside development or disturbance (Koonce et al. 1996).

The Laurentian Great Lakes and other large lakes provide sufficient heterogeneity that rainbow smelt and native planktivores may relieve competitive pressure through segregation of resource use. For example, in Lake Michigan, under summer post-spawning conditions, rainbow smelt feed on the same *Daphnia* spp. and copepods that are consumed by alewife but have different diets than spottail shiner (*Notropis hudsonius*), trout-perch (*Percopsis omiscomaycus*), and yellow perch (Crowder et al. 1981). Dietary overlap between rainbow smelt and alewife is compensated by thermal partitioning, with smelt occupying cooler water than alewife during the day and warmer water at night (Crowder et al. 1981). Aside from daytime thermal overlap with trout-perch, rainbow smelt were also thermally segregated from adults of native planktivores (Crowder et al. 1981). During stratification in Lake Ontario, alewife and rainbow smelt both exhibited size-selective predation on copepods, with dietary similarities of 80.0% and 94.3% in August and October, respectively (Urban and

Brandt 1993). As in Lake Michigan, however, this dietary overlap was compensated for by spatial segregation (Urban and Brandt 1993). Gordon (1961) noted that rainbow smelt in Saginaw Bay, Lake Huron share many prey items with yellow perch but found no evidence of food scarcity for either species. In three Finnish lakes, Lake Hoytiainen, Lake Pyhaselka, and Lake Pyhäjärvi, *O. eperlanus* were observed to occupy the same pelagic habitat as vendace (*Coregonus albula*) but were segregated by diet, with smelt acting as an ambush or intermediate predator on copepods while vendace acted as a cruising predator on cladocerans (Karjalainen et al. 1997). Hence, exotic smelt will not likely extirpate native planktivores in large lakes because of segregation along at least one resource gradient.

In small lakes, there is less opportunity for niche segregation. Consequently, competition between rainbow smelt and native planktivores is often more intense. Although rainbow smelt abundance is inversely related to whitefish, cisco, and yellow perch abundance in some smaller lakes, direct evidence of competition is often lacking. In Crystal Lake, Wisconsin, Hrabik et al. (1998) found that rainbow smelt abundance was inversely correlated with yellow perch abundance. Competition rather than predation was most likely the cause. Yellow perch and rainbow smelt hatch dates overlapped and both species inhabited the same shallow water regions and consumed the same food in spring (primarily *Diaptomus oregonensis* and *Diaptomus minutus*), producing a dietary overlap of 45-60% (Hrabik et al. 2001).

Wain (1993) compared the fish communities in two small Ontario lakes. Sandybeach Lake was dominated by rainbow smelt, whereas Little Vermillion Lake did not contain rainbow smelt and was instead dominated by yellow perch. The lakes were otherwise similar with fish communities consisting of cisco, lake whitefish, emerald shiner, and spottail shiner. The emerald and spottail shiners had low habitat and diet overlap with rainbow smelt and their population densities were similar in the two lakes (Wain 1993). In contrast, juvenile cisco were abundant below the thermocline of Little Vermillion Lake but absent in Sandybeach Lake where rainbow smelt occupied this habitat (Wain 1993). The condition factor of cisco in Sandybeach Lake was significantly lower than in Little Vermillion Lake (Wain 1993). Yellow perch, conversely, were able to avoid recruitment failure due to competition with rainbow smelt by shifting from the lower epilimnion to more littoral habitat (Wain 1993). While this permitted yellow perch to avoid competition with rainbow smelt, it likely intensified intraspecific competition by concentrating all size-classes of yellow perch in the littoral zone (Wain 1993).

In some cases, competition with smelt may force indigenous planktivores to change their diet. In Lake Tjeukemeer, the Netherlands, *O. eperlanus* size-selective feeding following their introduction depressed *Daphnia hyalina* mean body size such that they were no longer retained by the gill rakers of mature bream (*Abramis brama*). Bream exhibited poor growth and gonad development as a result and were forced to switch to feeding primarily on chironomid larvae (Lammens et al. 1985). The increased reliance of bream on chironomid larvae reduced the availability of chironomid pupae for European eel (*Anguilla anguilla*), which in turn increased their reliance on fish, particularly young-of-the-year rainbow smelt (Lammens et al. 1985).

Adult rainbow smelt may also reduce populations of native planktivores through predation, particularly on eggs and juveniles (e.g. Brandt and Madon 1986, Loftus and Hulsman 1986, Stedman and Argyle 1985). Pelagic and semipelagic eggs and larvae are more susceptible to predation by rainbow smelt than demersal eggs, and many of the species that typically decline following rainbow smelt invasion have pelagic eggs (e.g. emerald shiner, burbot, and many ciscoes) (Crowder et al. 1980, Stewart et al. 1981). Predation by rainbow smelt may be particularly important in determining recruitment success for coregonids whose spawning and nursery habitats overlap with adult rainbow smelt (Scott and Crossman 1998). In Sparkling Lake, Wisconsin, young cisco were heavily preyed upon by exotic rainbow smelt where their habitats overlapped below the thermocline. Eventually, predation by smelt resulted in recruitment failure and the extirpation of cisco in this small lake (Hrabik et al. 1998). Loftus and Hulsman (1986) also found that rainbow smelt consumed larval lake whitefish and cisco in Twelve Mile Lake, Ontario and suggested this was responsible for recruitment failure in lake whitefish and reductions in cisco abundance that occurred following rainbow smelt introduction.

In summary, interactions between exotic rainbow smelt and native planktivores may be complex, involving predation at various life stages and competition where diet and habitat use overlap. Even where spatial overlap does not occur, competition between smelt and native planktivores is possible if diel migration of zooplankton prey occurs (Hrabik et al. 1998). Where segregation and resource partitioning is possible, such as in large or heterogeneous lakes, species may be capable of coexistence. Resource partitioning may, however, force native planktivores to rely on sub-optimal habitat or food resources to alleviate competitive pressure. Where partitioning is not possible, competitive pressure may lead to the extirpation of native species, although extirpation is more commonly the result of predation than competition. To better predict the effect of exotic rainbow smelt on native planktivores, a thorough examination of diet and habitat use of all species involved is required.

ZOOPLANKTON – SMELT INTERACTIONS

Several studies have demonstrated that rainbow smelt are visual feeders that actively select for larger-bodied zooplankton. Selective feeding may lead to changes in the prey community. In Harvey’s Lake, Pennsylvania, the introduction of rainbow smelt was followed by the extirpation of *L. kindtii* (Reif and Tappa

1966) and the replacement of larger-bodied *Daphnia pulex* by smaller-bodied *D. dubia* and *Bosmina longirostris*. In Sporley Lake, Michigan, the introduction of rainbow trout, fathead minnows (*Pimephales promelas*), and rainbow smelt occurred in 1958, 1960, and 1962, respectively (Galbraith 1967). By 1964, the >1.3 mm size fraction of *Daphnia* spp. had been eliminated (Galbraith 1967). Larger bodied *D. pulex* were eliminated and replaced by smaller-bodied *Daphnia* species, including *D. retrocurva* and *D. mendota* (Galbraith 1967). In the mid 1970s, rainbow smelt were introduced to Lake George, a double-basin lake in the Adirondack Mountains, New York (Siegfried 1987). In the south basin, rainbow smelt were more abundant and smaller-bodied cladocerans and calanoids such as *B. longirostris*, *D. galeata*, *D. dubia*, and *Diaptomus sicilis* had higher abundances and standing crops. Conversely, in the north basin, large-bodied zooplankton such as *Daphnia pulicaria* and *Epischura lacustris* were more abundant. *Mysis relicta* density and standing crop were also typically lower in the south basin where rainbow smelt were more abundant. Stomach content analysis indicated that the inter-basin difference in zooplankton community structure was because rainbow smelt fed preferentially on large-bodied zooplankton (Siegfried 1987). Predation by smelt has also been implicated in the failure of *Limnocalanus macrurus* recovery in Lake Erie (Kane et al. 2004), and reductions in smelt abundance were associated with increased mean zooplankton size in a pond near Lillehammer, Norway (Hessen 1983) and in the Horsetooth Reservoir, Colorado (Johnson and Goettl 1999).

The elimination of large-bodied zooplankton after smelt introductions may lead to compensatory increases in the abundance of small-bodied zooplankton as they are freed from competition with larger-bodied invertebrate species (Brooks and Dodson 1965, Reif and Tappa 1966). Alternatively, decreases in mean zooplankton size may result from the release of smaller-bodied zooplankton from predation by invertebrates such as *Chaoborus* spp., *Mysis relicta*, and *L. kindtii* (Fedorenko 1975, Liljendahl-Nurminen et al. 2003, Lynch 1979). For example, in Lake Ontario, rainbow smelt have been shown to feed selectively on zooplanktivorous *M. relicta* (Brandt and Madon 1986), reducing predation pressure on small-bodied zooplankton (Gal et al. 2006). However, declines in mean zooplankton size following smelt invasion are not certain. In two small northern Wisconsin lakes, Crystal Lake and Sparkling Lake, the mean individual biomass of most zooplankton taxa increased following smelt introduction because previously dominant yellow perch and cisco populations were stronger zooplankton predators than the rainbow smelt that replaced them (Beisner et al. 2003). The cyclopoid *Diacyclops bicuspidatus thomasi* was the taxa most strongly released from predation and only the biomass of calanoid copepods in Crystal Lake was negatively correlated with increasing numbers of smelt (Beisner et al. 2003). Smelt are well known to favour calanoid copepods as prey (Hrabik et al. 1998, Wain 1993).

The net effect of rainbow smelt invasion on mean zooplankton body size may be a function of pre-existing planktivore community composition. In Crystal Lake, the native planktivore community was dominated by yellow perch that had large dietary overlap with introduced rainbow smelt (e.g. 61-88% perch and 72-76% smelt consumed zooplankton) (Hrabik et al. 1998). In contrast, the native planktivore community in Sparkling Lake was dominated by cisco, which are macro-zooplankton feeders, and have lower diet overlap with generalist-feeding rainbow smelt (72% cisco and 15-21% smelt consuming zooplankton). Prior to smelt introduction, the two lakes had dissimilar zooplankton communities but five years later cyclopoid copepods, particularly *Diacyclops bicuspidatus thomasi*, dominated in both lakes (Beisner et al. 2003).

INDIRECT EFFECTS

TROPHIC CASCADES AND INCREASED RISK OF EUTROPHICATION

In freshwater pelagic ecosystems, trophic cascade theory predicts that increases in planktivores may reduce herbivorous zooplankton and thereby lead to greater algal biomass, water column total phosphorus concentration, turbidity and other changes associated with eutrophication (Carpenter et al. 1985, Lynch 1979, Lynch and Shapiro 1981). Smaller-bodied grazers also release more phosphorus per unit biomass than larger-bodied grazers (Peters 1975) favouring phytoplankton growth. As a result, invasion by rainbow smelt and subsequent reductions in mean zooplankton size might be predicted to lead to greater phytoplankton biomass.

Unfortunately, few studies have examined multiple trophic levels to confirm whether smelt invasion results in trophic cascades. In the south basin of Lake George, smelt introduction increased grazing pressure on zooplankton and increased potential phosphorus recycling by zooplankton, relative to the north basin where smelt were less abundant (Siegfried 1987). Following smelt introduction, the phytoplankton community changed from dominance by diatoms and Chrysophytes to greater dominance by coccoid cyanobacteria (Siegfried 1987). Approximately 10 years after smelt were introduced, the biomass of cyanobacteria in the south basin was 300% higher than in the north basin where smelt were less abundant (Siegfried 1987). The south basin also had higher total phytoplankton biomass, chorophyll *a*, total phosphorus concentrations, and lower transparency (Siegfried 1987). Similarly, from 1984 to 1996 in Lake Pyhäjärvi, Finland, planktivorous fish biomass (mainly vendace and *O. eperlanus*) was significantly negatively correlated with total zooplankton biomass, total cladoceran biomass, large-bodied herbivorous cladoceran biomass, calanoid biomass, and positively correlated with chlorophyll *a* concentrations ($p < 0.05$) (Sarvala et al. 1997).

Hessen (1983) found that the introduction of northern pike into a pond near Lillehammer, Norway reduced *O. eperlanus* abundance, increased the abundance of cladocerans, and reduced phytoplankton biomass. In the summer preceding pike introduction, the pond experienced a bloom of the filamentous cyanobacteria *Aphanizomenon flos-aquae* and a decrease in transparency to 30 cm. Although climate was similar in the summer following pike introduction, there were no cyanobacteria blooms and transparency increased to >3 m (Hessen 1983). Changes in smelt abundance due to piscivory thereby led to water quality improvements.

BIOMAGNIFICATION OF CONTAMINANTS

Rainbow smelt invasion may affect the accumulation of persistent lipophilic contaminants (Kiriluk et al. 1995) and heavy metals such as mercury (MacCrimmon et al. 1983, Swanson et al. 2003) in top predators. This is because smelt frequently feed higher in the food chain than the native planktivores they displace (Crowder et al. 1981, Hrabik et al. 1998). This potentially increases biomagnification of contaminants from the base of the food chain to top predators.

$\delta^{15}N$ is an indicator of trophic position in food chains, with a fractionation of approximately 3-5‰ per trophic level (Peterson and Fry 1987). In a study of 10 small northwestern Ontario lakes, rainbow smelt had significantly higher $\delta^{15}N$ than all native forage species except trout-perch and juvenile walleye (Swanson et al. 2003). This increase in $\delta^{15}N$ affected piscivores: 500 mm walleye in the six lakes with smelt had mean $\delta^{15}N$ values 0.57‰ higher than those in the four lakes without smelt (Swanson et al. 2003). In Lake Ontario, however, $\delta^{15}N$ of rainbow smelt, alewife, and slimy sculpin did not differ significantly (14.12 ± 0.19 ‰, 12.93 ± 0.30 ‰, and 12.89 ± 0.25 ‰, respectively) (Kiriluk et al. 1995).

Rainbow smelt in Lake Ontario were found to have significantly higher concentrations of DDE and PCBs than *Mysis relicta*, which is the main source of food for many top predators in lakes without abundant planktivores (Kiriluk et al. 1995). As a result, smelt invasion may increase contaminant transfer to terminal predators. Evidence from 21 Ontario lakes supports this contention. The concentration of PCBs in lake trout tissue was 163% higher in lakes containing smelt than in smelt-free lakes when lakes without *M. relicta* were considered and 345% higher in lakes with smelt than in smelt-free lakes when lakes with *M. relicta* were compared (Vander Zanden and Rasmussen 1996).

Reports of the effect of rainbow smelt on top piscivore mercury concentrations are conflicting. In a study of 61 Ontario lakes, Vander Zanden and Rasmussen (1996) observed that lake trout mean mercury levels were significantly higher in lakes containing smelt than in smelt free lakes (148% greater in lake trout tissue in lakes without *M. relicta* and 186% greater in lakes containing *M. relicta*). Similarly, increases in lake trout mercury accumulation in Lake Tadenac, Ontario were attributed to smelt consumption by MacCrimmon et al. (1983) and higher concentrations and greater rates of accumulation of mercury in Lake Simcoe walleye than in pike were attributed to a greater proportion of rainbow smelt in their diet by Mathers and Johansen (1985). In contrast, rainbow smelt had significantly lower mean muscle mercury concentrations in 10 northwestern Ontario lakes than all indigenous planktivores except cisco, despite significantly higher $\delta^{15}N$ concentrations (Swanson et al. 2003). Hence, increases in rainbow smelt consumption by predatory fish does not necessarily lead to increased mercury accumulation in all cases.

ENERGY AND NUTRIENT STORAGE AND FLOW

Lakes invaded by rainbow smelt often undergo food web restructuring that can affect energy and nutrient storage and flow within the ecosystem. Observed increases in growth rate (Havey 1973, Jones et al. 1994), condition factor (Hassinger and Close 1984), and fat content (Evans and Loftus 1987) of adult piscivores in lakes to which smelt are introduced suggests a retention of energy in higher trophic positions, at least temporarily (Johnson and Goettl 1999). Where rainbow smelt invasions have been correlated with elevated phytoplankton biomass, energy and nutrient storage is shifted towards lower trophic levels. In some cases, this shift has occurred primarily towards phytoplankton species that have lower food value for zooplankton, such as cyanobacteria (Siegfried 1987).

Rainbow smelt may also link otherwise segregated ecosystem components or may exploit a novel combination of resources, producing changes in energy flow within a lake. For example, smelt invasion may result in niche shifts in native species, creating new channels of energy flow. In Lake Tjeukemeer, the Netherlands, invasion by *O. eperlanus* forced adult bream to switch from a pelagic diet of *Daphnia hyalina* to a benthic diet of chironomid larvae, which in turn forced eel to switch from a diet of chironomid pupae to a piscivorous diet of *O. eperlanus* (Lammens et al. 1985). Swanson et al. (2003) found that the trophic position (based on $\delta^{15}N$ values) that yellow perch and cisco occupied in six northwestern Ontario lakes with rainbow smelt did not differ from their trophic position in four nearby lakes without rainbow smelt. Swanson et al. (2003) conclude that rather than provoking a shift in trophic position in native planktivores, rainbow smelt made use of a previously unexploited combination of resources, creating a new energy pathway.

Changes in community composition may also affect nutrient and energy flow rates. For example, a shift towards smaller-bodied zooplankton may lead to an acceleration of nutrient recycling within a lake (Henrikson et al. 1980) as zooplankton body size is inversely related to nutrient turnover rates (Carrillo et al. 1996, Peters 1975). Changes in phytoplankton community composition may also affect nutrient flow, as algal cell volume is negatively correlated with photosynthetic rate and nutrient cycling (Desortova 1976).

In summary, smelt feed on multiple trophic levels and have broad habitat requirements; therefore, they have a large capacity to affect energy and nutrient storage and flow within an invaded lake. A summary of some of the impacts attributed to smelt invasion in small lakes are listed in Table 2.

Table 2. Evidence for potential effects of rainbow smelt introductions to small lake ecosystems.

Effect	References
Piscivore-smelt	
Increases in growth rates and condition of native adult piscivores	Havey (1973); Hassinger and Close (1984); Evans and Lofthus (1987); Jones et al. (1994); Johnson and Goettl (1999)
Decreased growth, recruitment, and survival of native juvenile piscivores	Galbraith (1967); Kircheis and Stanley (1981); Hassinger and Close (1984); Evans and Lofthus (1987); Johnson and Goettl (1999)
Declines in piscivore population sizes	Mercado-Silva et al. 2007
Planktivore-Smelt	
Declines in growth rates and condition of native planktivorous	Lammens et al. (1985); Wain (1993)
Declines in recruitment and population sizes of planktivorous fish	Lofthus and Hulsman (1986); Evans and Lofthus (1987); Hrabik et al. (1998); Hrabik et al (2001); Krueger and Hrabik (2005); Willis and Magnuson (2006)
Changes in spatial distribution of native planktivorous fish	Lammens et al. (1985); Wain (1993)
Plankton-smelt	
Decreases in large-bodied zooplankton	Reif and Tappa (1966); Galbraith (1967); Hessen (1983); Siegfried (1987); Johnson and Goettl (1999); but see Beisner et al. (2003)
Increased phytoplankton biomass and productivity	Hessen (1983); Siegfried (1987); Sarvala et al. (1997)
Contaminants	
Increases in contaminant concentrations in native fish	Vander Zanden and Rasmussen (1996, PCBs, Hg); MacCrimmon et al. (1983; Hg); but see Swanson et al. (2003; Hg)

MITIGATION AND REMEDIATION

PREVENTION OF ECOSYSTEM IMPACTS OF SMELT

Efforts to prevent further dispersal of rainbow smelt are best directed at reducing human transfers because this is the most important mechanism behind continued rainbow smelt range expansion (Hrabik and Magnuson 1999). To prevent dispersal of rainbow smelt into unaffected lakes, greater public education is required (Hrabik and Magnuson 1999). The risks of releasing live bait should be a major focus of education campaigns (Litvak and Mandrak 1993). The implementation of risk reduction techniques in the bait industry could also help prevent unintentional smelt introductions by reducing the incidence of misidentified bait. Inspection of live bait at bait shops and boat landings is likely to be an effective, albeit expensive, prevention strategy (Drake and Lodge 2006). Upstream dispersal of rainbow smelt may be prevented by use of temporary physical barriers during spring smelt spawning. For example, a 1 m head dam will prevent upstream migrations by spawning rainbow smelt. A potential problem is that dams may interfere with the migration of indigenous species that move upstream during smelt spawning (Hrabik and Magnuson 1999). Downstream migration by larvae is more difficult to limit.

REMEDIATION

Massive fish removal by intentional over-fishing or rotenone has successfully reduced rainbow smelt populations in some lakes (Henrikson et al. 1980, Horppila et al. 1996). Rotenone is toxic and is an increasingly unpopular method of fish removal. In some instances, increased abundance of large piscivores also effectively reduced rainbow smelt populations. For example, in Lake Fence and Lake Crawling Stone, Wisconsin, the implementation of a 37.5 cm minimum length in the walleye fishery led to increases in the walleye population from 3.2 kg ha^{-1} to 9.7 kg ha^{-1} and from 7.2 kg ha^{-1} to 25.4 kg ha^{-1}, respectively (Krueger and Hrabik 2005). Subsequent reductions in rainbow smelt biomass and condition factor in Fence Lake and the extirpation of rainbow smelt from Crawling Stone Lake were attributed to increased walleye predation (Krueger and Hrabik 2005). Rainbow smelt reductions were associated with the recovery of the native cisco population, with cisco biomass increasing from 1.6 kg ha^{-1} to 23.0 kg ha^{-1} in Fence Lake and from 1.2 kg ha^{-1} to 82.5 kg ha^{-1} in Crawling Stone Lake (Krueger and Hrabik 2005). Declines in smelt numbers following natural recovery or stocking of grown-out piscivores have been reported from lakes ranging in size from Lake Superior (Cox and Kitchell 2004) to a small pond near Lillehammer, Norway (Hessen 1983). This suggests that, regardless of lake size, the recovery of native piscivores may re-establish indigenous planktivore community structure without the need for rotenone application.

KNOWLEDGE GAPS

Range expansion of rainbow smelt is occurring rapidly and the primary literature on the distribution of rainbow smelt is out of date. The most recent peer-reviewed article on the North American distribution of rainbow smelt was published in 2001, describing the range of rainbow smelt in New England, New York, and New Jersey using data from 203 lakes and reservoirs sampled between 1991 and 1996 by the US Environmental Protection Agency's Environmental Monitoring and Assessment Program (Halliwell et al. 2001). Distributional data from northwestern Ontario, southeastern Manitoba, and northeastern Minnesota were collected during the same period and published in 1994 (Franzin et al. 1994) and 1997 (Remnant et al. 1997). Since that time, updates on the distribution of rainbow smelt have been recorded in the grey literature. Information regarding the current range of rainbow smelt should be gathered from this literature and assembled to give a coherent picture of its current range. This information should then be combined with forecasts of the potential range changes (e.g. Drake and Lodge 2006, Mercado-Silva et al. 2006) to identify areas where prevention and remediation actions would be most effective.

The use of rotenone, intentional over-fishing, minimum size restrictions for game fish, and stocking of grown-out piscivores are potentially effective methods to eliminate exotic rainbow smelt populations, but preventing smelt from invading new water bodies is best. Further research into methods for limiting the dispersal of rainbow smelt through lake districts is required. While the prevention of human transfer is the most effective way to limit the range expansion of rainbow smelt, the efficacy of temporary low head dams in preventing upstream dispersal by adults should be examined and strategies for limiting downstream dispersal by larvae should be investigated.

Much of the evidence correlating increases in smelt density with decreases in the density of other forage fish is circumstantial and it is often unclear whether competition or predation from exotic smelt is responsible for observed community changes. The rapidity with which effects develop may hinder research into causal mechanisms as the collection of pre-invasion data and detailed sampling during initial community shifts requires advance knowledge of an impending invasion. Research confirming competitive interactions and identifying potentially limiting resources would assist managers of lakes with naturalized exotic smelt populations.

While the effects of rainbow smelt on zooplankton prey populations have been relatively well studied, the dominant pathways of effect require further research. It is unclear whether changes in zooplankton body size associated with rainbow smelt invasions result from release from competition with larger-bodied zooplankton (because of size-selective feeding by rainbow smelt) or to release from predation by invertebrate predators (which smelt feed upon preferentially).

Previous research has increased our understanding of the habitat and dietary requirements of smelt and their ability to impact lake ecosystems through direct and indirect interactions with indigenous taxa at multiple organisational scales. Relatively little research has been conducted on how these factors may be affected by climate change and changing land use. Some research suggests that smelt invasion may mask the effects of climate change on lakes in Wisconsin (Willis and Magnuson 2006). It has also been suggested that climate change and increased human settlement may facilitate the spread of exotic species, but whether this is true for rainbow smelt has yet to be examined. Exploration of the effects of climate and land-use change on the dispersal of rainbow smelt will improve our ability to forecast its future distribution and accurately focus resources in areas at high risk of invasion (Bierwagen et al. 2008).

It is unrealistic to focus exclusively on pelagic food webs, as rainbow smelt are generalist feeders that also utilize the benthos in profundal and littoral habitats (Vander Zanden and Vadeboncoeur 2002). More research is required on the effects of rainbow smelt invasion on benthic invertebrates given their importance in rainbow smelt diets. Reliance of exotic smelt on benthic food sources could integrate benthic and pelagic food webs, affecting energy and nutrient flow and storage within a lake. The effects of rainbow smelt invasion on benthos may also be indirect, through compensatory niche shifts by forage fish in competition with smelt for pelagic food sources (e.g. Lammens et al. 1985).

In summary, rainbow smelt are generalist feeders with broad temperature tolerances that exhibit diel vertical migrations. Consequently, they interact with numerous trophic levels in multiple habitats. Rainbow smelt are therefore capable of affecting invaded lakes at the level of individuals, populations, communities, and the whole ecosystem (Simon and Townsend 2003). Commonly, researchers focus on the direct effects of rainbow smelt invasion on the abundance and condition of piscivores, planktivores, and zooplankton, and on the composition and structure of invaded communities. Rainbow smelt invasion may also affect nutrient cycling between and productivity within different trophic levels and ecosystem components (Vitousek 1990). Predation pressure by rainbow smelt may also result in a cascade of trophic effects with consequence for phytoplankton and abiotic variables within a lake. These indirect and subsidiary effects can be significant. Future research into the effects of exotic rainbow smelt should focus on impacts at multiple scales within an invaded lake.

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