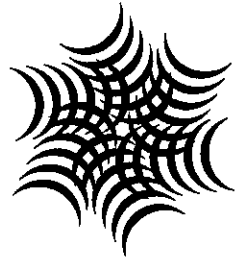


Food Webs at the Landscape Level



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The Variation of Lake Food Webs across the Landscape and Its Effect on Contaminant Dynamics

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Persistent contaminants such as organochlorines, methyl mercury, and radiocesium have become widespread atmospheric pollutants and constitute important allochthonous inputs to aquatic ecosystems (Eisenreich et al. 1981; Patton et al. 1989). Even in areas remote from industrial activities and other anthropogenic sources, such as the open sea and extreme polar regions, dangerously high concentrations of these substances can be found in biota (Bidleman et al. 1989; Kidd et al. 1998). In addition to being widely distributed by atmospheric processes, these substances are concentrated within watersheds and transported along streams and rivers to lakes, estuaries, and oceans. Within food webs, trophic transfer can result in dangerously high exposures for high-level consumers, even though input concentrations may be barely detectable. At the base of the aquatic food chain, phytoplankton bioaccumulate these substances, and in so doing, concentrate them by several orders of magnitude. This bioaccumulation represents an important avenue of contamination for animal consumers, and because significant biomagnification usually occurs at each trophic link, concentrations can build up through the food web and pose significant health risks to both humans and wildlife, especially if food chains consist of many trophic levels (Oliver and Niimi 1988; Rowan and Rasmussen 1992, 1994).

Ever since these risks began to be recognized, we have also been impressed by the enormous between-system variation in contaminant levels in top predators that exists across the landscape, even within relatively homogeneous regions such as the Canadian Shield (Rasmussen et al. 1990; Vander Zanden and Rasmussen 1996). Generic approaches to fisheries and environmental management tend to focus on "average" conditions and will naturally tend to ignore exposure risks associated with this variation unless the processes that generate it are understood and the likelihood of spatial transport is recognized. For example, lakes and oceans with long food chains can have highly contaminated top piscivores that migrate long distances, thus serving as important transport vectors on the landscape (Scudato and McDowell 1989; Eggold et al. 1996). This is a problem of importance to ecosystem management, and one that is readily incorporated into a broad landscape framework (Turner 1989).

Both the processes that generate variation and the transport processes that broadcast it pose daunting problems for scientific study because of the large spatial scales involved and the obvious limits to experimentation. These problems have led to an emphasis on comparative methods that focus on among-system variation (Cabana et al. 1994; Vander Zanden and Rasmussen 1996) and the use of widely disseminated geochemical tracers (e.g., stable isotopes and radioisotopes) to study trophic transfer within food webs and transport processes on the landscape (Cabana and Rasmussen 1994, 1996; Vander Zanden, Casselman, and Rasmussen 1999; Vander Zanden, Shuter et al. 1999; Trudel and Rasmussen 2001). Tracer methodologies provide cost-effective measures that can be used to characterize local food webs in a manner that is not only accurate and replicable, but also time-integrative, and therefore very useful in large-scale comparative studies. In this chapter we will outline how such approaches have been used to examine variation among lake food webs, its relationship to contaminant biomagnification, and the transfer of biomagnified contaminants across the landscape by migrating fish.

UNDERLYING FACTORS CONTRIBUTING TO THE SPATIAL VARIATION OF LAKE FOOD WEBS

The variation among lake food webs in eastern Canada appears to depend mainly on the mix of species that have had the opportunity to colonize the postglacial landscape (Carter et al. 1980; Roff et al. 1981; Dadswell 1974; Sprules and Bowerman 1988). Since glaciers covered the entire region as little as 10,000 years B.P., it is not speciation and endemism that result in

lake-specific differences, but rather biogeographic factors affecting postglacial dispersal. Of importance in this regard are the physical relationship of a lake to major proglacial lake basins and the sea, the drainage patterns that were reestablished on the landscape after glacial retreat, and the "watershed capture" events that accompanied continental rebound and allowed species from southern and eastern drainages to move northward (Martin and Chapman 1965; Dadswell 1974). Similarly, Hershey et al. (1999) have linked food web structure in North Slope Alaskan food webs to geomorphological history and biogeographic factors operating on the postglacial landscape. The biogeographic distributions of a great many of the fish and invertebrate species that constitute lake food webs are far from equilibrium, and many important species are confined to lakes situated along drainages that served as major avenues of postglacial dispersal. The extent of this "biogeographic disequilibrium" has neither been completely documented—especially in regard to invertebrate taxa—nor has its importance to food web structure been generally appreciated.

Superimposed on the postglacial lottery has been the rapidly accelerating onslaught of modern-day introductions, many of which are unintentional, or at least poorly recorded, with the consequence that we sometimes know little more about them than about the postglacial invasions (Evans and Loftus 1987). In many other cases, these introductions have been intentional efforts to create or enhance fisheries. The Great Lakes have received the greatest influx of exotic introductions. Among the most noteworthy of these invaders are the Pacific salmonids, which have not only dramatically altered the lake food webs, but have also established spawning migrations that span considerable distances inland (Crawford 2001). These introductions, as well as subsequent lake management protocols, have also contributed to the variation and uniqueness of individual lake food webs in the region, although introductions, if widespread enough, can ultimately lead to broad-scale uniformity.

PELAGIC FOOD WEBS

The pelagic food webs of eastern Canadian lakes generally contain lake trout (*Salvelinus namaycush*) if the lakes are deep enough for stable thermal stratification and the hypolimnia have sufficient levels of dissolved oxygen during the summer months (Goddard et al. 1987). Lake trout are native to the area, although they have been stocked in some headwater lakes that lacked populations naturally. These fish are generally confined to the hypolimnion during the summer months, where they feed on pelagic forage

fishes (e.g., rainbow smelt, cisco, lake whitefish, sculpins), benthic invertebrates, or zooplankton (including *Mysis*) (Trippel and Beamish 1993; Vander Zanden and Rasmussen 1996). During the winter months lake trout feed actively throughout the lake and often feed extensively on littoral fishes and invertebrates (Martin 1954). In lakes lacking pelagic forage fishes (class 1 lakes), lake trout typically consume zooplankton and benthic invertebrates during summer and a broader spectrum of foods during the winter months (Martin 1952, 1954; Vander Zanden and Rasmussen 1996). These lakes are typically small headwater lakes that were isolated from the main drainage channels that were used as dispersal corridors following glaciation. Lakes situated along major drainages and glacial spillways typically have a richer pelagic community characterized by multiple species of pelagic forage fishes. Lakes that fall within the boundaries of former proglacial lakes typically contain glacial relict crustaceans, such as *Mysis relicta* and *Diporeia hoyi* (Dadswell 1974). Although *Mysis relicta* has been notoriously introduced to lakes throughout the world (for example, Lake Tahoe, California-Nevada; Flathead Lake, Montana), populations of *Mysis* in eastern Canada are strictly native, glacial relict populations (Dadswell 1974). Lakes containing these species have the longest and most complex food webs, and we refer to them as class 3 lakes (Rasmussen et al. 1990; Vander Zanden and Rasmussen 1996). Class 2 lakes are those that include pelagic forage fishes, but no megazooplankton.

We have compared the trophic positions of lake trout from class 1, 2, and 3 lakes using both stable isotope measures (Cabana and Rasmussen 1994; Vander Zanden, Casselman, and Rasmussen 1999; Vander Zanden, Shuter et al. 1999) and stomach contents analyses (Vander Zanden and Rasmussen 1996). Both methods reveal that trophic position increases significantly with lake class. An important factor contributing to the between-system variation in food web structure, and to the variation in the trophic positions of most common fish species, is the generalist nature of these consumers. Indeed, most lake trout feed on a broad spectrum of prey species, sizes, and functional groups, and most include prey that vary widely in trophic position within their diet (Vander Zanden and Rasmussen 1996). Thus omnivory is an important general feature of lake food webs, and lakes with similar species composition can differ considerably in trophic structure (Vander Zanden, Shuter et al. 1999).

While the distinction between class 1, 2, and 3 lakes is based largely on zoogeographic history, pelagic communities have often been influenced by introductions of lake trout, brook trout, Atlantic salmon, walleye, lake whitefish, cisco, alewife, and rainbow smelt (Evans and Loftus 1987; Scott and

Crossman 1973). The pelagic communities of the Laurentian Great Lakes have been altered the most through introductions of forage fishes such as rainbow smelt, alewife, and emerald shiner, top predators such as chinook salmon, coho salmon, pink salmon, rainbow trout, and brown trout, and hybrid species such as the splake (Martin and Baldwin 1960; Fraser 1980; Crawford 2001). These invaders not only have completely restructured the Great Lakes food webs, but also, by virtue of their extensive spawning runs, have invaded most of the major waterways draining into the lakes.

Although lake trout are still present in most of the Great Lakes basins, their numbers are often far below historical levels due to a combination of overfishing, the effects of marine lampreys, and competition and predation from exotic species (Christie et al. 1987). Furthermore, the spawning stock of lake trout in each of the lakes is a fraction of what was formerly present, indicating a loss of genetic diversity.

Although the rainbow smelt is native to some lakes in this area, usually those that were at one time part of Champlain Sea (a marine intrusion during the last glaciation), this species has been stocked into a great many lakes in Ontario and Quebec, usually illegally, and has subsequently colonized much of the region (Evans and Loftus 1987). This species feeds heavily on young-of-the-year fish and can become highly cannibalistic in certain lakes (Vander Zanden and Rasmussen 1996; Evans and Loftus 1987). This behavior is rarely encountered in coregonids. Consequently, the trophic position of lake trout is typically higher in lakes containing rainbow smelt, and this higher trophic position corresponds with increased levels of contaminant bioaccumulation in lake trout (Vander Zanden and Rasmussen 1996).

While large lakes typically have a well-developed pelagic food web, including piscivorous fishes such as lake trout, walleye, and burbot, medium-sized and smaller lakes, especially those situated higher in drainage systems (e.g., headwater lakes), often lack a "true" offshore fish community. In such lakes a wide variety of littoral species make part-time use of the pelagic zone.

An important factor that introduces variation into food webs in eastern Canada is the rapid rate at which exotic species are invading and spreading throughout the region. Some of these invasions are intentional and authorized—historically, introductions of smallmouth bass have been carried out throughout the region with the aim of enhancing the sport fishery (Vander Zanden, Casselman, and Rasmussen 1999). Other species are expanding by virtue of their remarkable capacities for dispersal; the northern pike and rock bass appear to be examples. The most significant factor in the spread of littoral fish species throughout the region, however, appears

to be the "bait bucket brigade," whereby fisherman purchase what they generally refer to as "minnows," but which actually are a mixture of sunfish, rock bass, bullheads, cyprinids, and perch, and at the end of their day of fishing dump the bucket into the lake they are fishing (Litvak and Mandrak 1993). Although policies are being introduced to deal with this problem in Ontario and Quebec, other states and provinces do not adequately restrict the use of live bait and are at risk of future species invasions emanating from the bait bucket. Although the public is becoming gradually more aware of the problems that species introductions can present, introductions of this type will continue.

FOOD WEB VARIATION AND FISHERIES MANAGEMENT

The tremendous variation in food web structure has important implications for fisheries management. Consider that variation in the length of food chains leading to piscivores often spans nearly two entire trophic levels. From a trophic-dynamic perspective, assuming ecological efficiencies of 10%, each additional trophic level should correspond to an order of magnitude decrease in fisheries production. A trophic-dynamic approach to predicting fisheries production has not been well developed in freshwater systems, possibly because of the extreme variation of trophic positions and the amount of omnivory in these food webs. For lake trout, two studies observed that yield was independent of community composition, which reflects the number of trophic levels (Kerr and Martin 1970; Goddard et al. 1987). Furthermore, many factors other than the amount of available energy will affect the potential fisheries yield. For example, Kerr and Martin (1970) concluded that piscivorous lake trout achieved greater foraging efficiency than planktivorous lake trout populations, resulting in similar levels of production for the two populations.

The life history characteristics of lake trout (maximum size, age and size at maturity, reproductive output, natural mortality rates, and growth rates at various life stages) are highly variable across lakes. Sustainable yield and sensitivity to exploitation should vary as a function of the life history pattern of the population. This variation makes managing lake trout (as a species) a difficult prospect, particularly considering that lake trout occur in thousands of lakes across Canada and that they are commonly affected by overexploitation. One approach would be to uncover some correlates of life history patterns and use these surrogate variables as a basis for management. Early studies reported that life history was influenced primarily by differences in diet (Martin 1966). Shuter et al. (1998) found that lake

area and total dissolved solids correlated with lake trout life history patterns. They proposed that these environmental correlates be used to develop fisheries exploitation guidelines, particularly in situations in which lake-specific data are not available.

Martin (1966) reported that the growth, size, reproduction, and life history of lake trout were driven by the relative contributions of zooplankton and fish to lake trout diet. This finding is a strong indication that food chain structure can play an important role in shaping lake trout life history. We found that lake area and fish species richness were close determinants of food chain length, explaining more variation in food chain length than the lake class variable (Vander Zanden, Shuter et al. 1999). This close relationship between food chain length and lake area suggests that lake area, although correlated with life history patterns, serves as a surrogate for trophic structure. Further studies should examine the role of trophic structure in influencing fish life history and its implications for fisheries management.

THE APPLICATION OF FOOD WEB APPROACHES TO CONTAMINANT STUDIES

Many persistent contaminants are atmospherically dispersed and deposited on the landscape through precipitation and dry deposition (Blais et al. 1998). The pattern of distribution is often complex, and the long-range dispersal of these contaminants often obscures any relationship between the pattern of deposition and their original source. Persistent contaminants of this kind are bioaccumulated by fish and other biota, and concern over human health risks has led to outright consumption bans and the closure of fisheries, or more often, to consumption advisories on many species of fish and wildlife. Contaminants of interest in this regard include PCBs, DDT and other organochlorine pesticides, methyl mercury, and ¹³⁷Cs. Surveys carried out by federal and provincial agencies during the 1970s revealed not only major differences in the degree of contamination among fish species, but more interestingly, major differences among lakes in contamination levels of the same species that could not be explained by local pollution sources (Crawford and Brunato 1978).

Although the cycling of all of these contaminants can be influenced in important and complex ways by biogeochemical processes, trophic transfer is the major pathway of exposure to these contaminants. Indeed, for Great Lakes fish, in which a great many organochlorines and other contaminants have been measured, it could be easily shown that levels of these contaminants were many times higher than the levels predicted by bioconcentration

models (through direct uptake from water) based on laboratory contaminant exposures (Oliver and Niimi 1988; Rowan and Rasmussen 1992). The higher the trophic position of the fish, the greater was the discrepancy, and for large piscivorous salmonids, the levels of contaminants in tissues could be up to a hundred times as much as could be accounted for by direct uptake from water (Oliver and Niimi 1988). For this reason, we hypothesized that a great deal of the variation in contamination levels, both among species and among systems, was related to the trophic structure of the food web and that the trophic position of a fish was a reflection of the amount of bio-magnification occurring in the food web leading to that fish (Rasmussen et al. 1990). In this way, we felt that ecological approaches oriented around the food web could make important contributions to the understanding of exposure risk to humans and wildlife—an area traditionally dominated by chemists and toxicologists. In addition, the study of contaminants in fish and wildlife could potentially provide us with possible tracers useful in the study of food webs.

Detailed analyses of food webs using stomach contents analysis require the sacrifice of a great many fish, making this approach costly and labor-intensive. Thus, for most ecosystems, there are too few food web data available to allow convincing comparative studies to be carried out. In order to test the hypothesis that food web structure—and more specifically, the length of the food chain—was an important determinant of contaminant levels, we needed to develop efficient surrogate variables that could be measured in many lakes and, at the same time, were convincingly related to food web structure.

The most extensive fish contaminant surveys had been carried out by the Ontario Ministry of the Environment during the 1970s, and the most complete data were available for PCBs and methyl mercury in lake trout (Crawford and Brunato 1978). Although no food web data were available for the eighty or so lakes in which trout had been examined for contaminants, a database on fish species composition had been compiled by the Ontario Ministry of Natural Resources. We were thus able to assign the lakes for which we had lake trout contaminant data to class 1, 2, or 3, reflecting food chain length based on pelagic community composition (Rasmussen et al. 1990). Using lake class as a predictor variable in multiple regression models, we demonstrated that food chain length was a strong determinant of PCB and mercury concentrations in lake trout (Rasmussen et al. 1990; Cabana et al. 1994). Other significant predictors of lake trout PCB concentrations were the lipid content of the trout and the distance north from major Great Lakes cities.

We were confident that this simple lake classification scheme reflected broad-scale patterns in food chain length: class 1 lakes should have the shortest food chains because they lacked pelagic forage fishes and *Mysis*, while class 3 lakes should have the longest food chains because both of these trophic levels were present. Yet this simple classification based on the concept of discrete trophic levels certainly overlooked many intricacies of trophic structure. To address this problem, we examined the food web structure of these systems in a series of stable isotope and dietary studies.

The $\delta^{15}\text{N}$ values measured in lake trout, pelagic forage fishes, and *Mysis* from a sample of lakes in each food web class indicated that although $\delta^{15}\text{N}$ increased with lake class, the increase between classes was typically less than a full trophic level equivalent (Cabana and Rasmussen 1994), suggesting high levels of omnivory in the food chain (Cabana and Rasmussen 1994). This study also demonstrated that $\delta^{15}\text{N}$ was a strong predictor of mercury concentrations in lake trout—in fact, a much stronger one than lake class. The isotopic analysis also revealed significant among-lake variation in $\delta^{15}\text{N}$ values in lake trout within each class of lakes, although it was uncertain whether this variation reflected underlying among-lake differences in $\delta^{15}\text{N}$ at the base of the food web (Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999b), or whether it was a result of actual among-lake differences in the food webs leading to lake trout. We have since developed the means to correct for baseline variation at the among-lake (Cabana and Rasmussen 1996; Vander Zanden et al. 1997) and within-lake levels (Vander Zanden and Rasmussen 1999b). Development of this baseline correction permitted us to examine broad-scale patterns in trophic structure and food chain length at the individual lake level (Vander Zanden, Shuter et al. 1999); indeed, both baseline and trophic differences contributed to variation in $\delta^{15}\text{N}$ signatures among lake trout and other biota. This work demonstrated that lakes with similar community composition can exhibit dramatic differences in trophic structure and that other variables, such as fish species richness and lake area, provide better predictors of food chain length than simple measures of food chain length based on the number of trophic levels (Vander Zanden, Shuter et al. 1999).

We also carried out another comparison of class 1, 2, and 3 food webs based on published and unpublished lake trout and pelagic forage fish diet data (Vander Zanden and Rasmussen 1996). In this study, we calculated trophic positions for more than two hundred lake trout and pelagic forage fish populations. Trophic position is a continuous variable calculated from the weighted mean trophic position of stomach contents. To do this calculation, we had to make the approximation that invertebrates as zooplankton

and noncarnivorous benthos were primary consumers (trophic position = 2). Our dietary food web reconstruction corroborated the stable isotope results in that lake trout ranged in trophic position from 3.0 to 4.6, lake trout from class 3 lakes had the highest trophic position (mean = 4.4), those from class 1 lakes had the lowest trophic position (mean = 3.6), and those from class 2 lakes had intermediate values (mean = 3.9). Despite this qualitative correspondence with lake class, omnivory was prevalent at certain food web linkages. For example, lake trout from class 3 lakes exhibited a trophic position significantly lower than the value of 5.0 predicted from the lake class variable. Although class 3 lake trout were almost completely piscivorous, the forage fishes that they were utilizing were highly omnivorous, with *Mysis* rarely dominating their diets. Stable isotope analysis showed that *Mysis* were also quite omnivorous and that only the adults were completely carnivorous (Braunstrator et al. 2000).

Dietary and stable isotope studies indicated that class 1 lake trout, although highly variable in their trophic position, were typically much more piscivorous than we had initially expected, given the absence of pelagic forage fishes in these lakes (Vander Zanden and Rasmussen 1996). In fact, lake trout from such lakes can rely heavily on littoral fishes, particularly during the cold-water period of the year (Vander Zanden and Rasmussen 1996). Subsequently, we were able to determine that the extent to which lake trout used littoral forage fishes was mediated by the presence of introduced small-mouth bass and rock bass (Vander Zanden, Casselman, and Rasmussen 1999). This bass-induced trophic shift on the part of lake trout is hypothesized to lead to reduced contaminant burdens in lake trout as a result of their depressed trophic position.

Lipids have long been known to be highly correlated with PCB levels in fish, and this has often led to confusion about the nature of the biomagnification process in fish, since many chemical toxicologists have argued that the relationship to lipids was evidence that the contaminants were being taken up directly from the water (Hamelink et al. 1971). While our analyses always showed that trophic position was strongly linked to lake trout PCB levels, even when lipid-adjusted (or lipid-partialed) data were used (Rasmussen et al. 1990; Vander Zanden and Rasmussen 1996), the lipid patterns were still very interesting, since the lipid content of the flesh also strongly increased with trophic position. Many of the lipids found in fish tissues contain polyunsaturated fatty acids, which are synthesized only by plants and algae. These fatty acids are biomagnified through the food chain, stored in body tissues, and ultimately play an important role in reproduction. The relationship between lipid content of lake trout and trophic position suggests

that there may be an important food web dimension to lipid metabolism that has been little studied by aquatic ecologists. Although other persistent contaminants do not typically exhibit biomagnification factors as high as those of the highly lipophilic organochlorines (Vander Zanden and Rasmussen 1996), clear enrichment patterns in relation to food chain length could be seen for methyl mercury and for radiocesium (Cabana et al. 1994; Rowan and Rasmussen 1994).

POTENTIAL FOR TRANSFER OF BIOMAGNIFIED CONTAMINANTS ACROSS THE LANDSCAPE

Wild salmonids grow very large, reach high trophic positions, have high lipid concentrations, and thus bioaccumulate very large body burdens and concentrations of organic contaminants. Thus Great Lakes salmonids are among the most contaminated fish in the world (Rowan and Rasmussen 1992; Oliver and Niimi 1988). Many of the introduced Pacific salmonids have established major runs in river systems leading to the Great Lakes. Many fish and invertebrates in these river systems become contaminated when they consume the eggs of these migrating salmonids (Merna 1986). In addition, since most Pacific salmonids die immediately after spawning, and their carcasses decompose and are consumed by insect larvae and crustaceans, salmonid spawning runs have significantly increased the loadings of Mirex, PCBs, and other organochlorines in these tributaries (Scrudato and McDowell 1989; Eggold et al. 1996). There is also evidence that Mirex transported by introduced salmonids enters the terrestrial food web when blowfly larvae consume rotting carcasses (Johnson and Ringler 1979).

On the west coast of North America, salmonids complete their life cycles over enormous distances and home very precisely to their place of origin. These fishes biomagnify contaminants that they accumulate through the Pacific ocean food web before returning to spawn and die in freshwater systems far inland. While documentation of organochlorine levels in Rocky Mountain lakes is very sketchy, there are some lakes in which levels of contamination in the biota and sediments (Kidd et al. 1995) greatly exceed the levels (by orders of magnitude) expected from atmospheric inputs and runoff, which are generally very low in the Northwest. Although this ecosystem transfer link has yet to be clearly demonstrated, it is reasonable to speculate that systems supporting large populations of anadromous salmonids high in trophic position should have significantly enriched contaminant budgets. Many of the more important organochlorines have bioconcentration factors on the same order as key nutrients such as N and P (up to 10^6),

and it is well known that the decomposing carcasses of Pacific salmonids are so numerous and large that they often contribute greatly to the nutrient budgets and isotopic signatures of West Coast lakes and rivers (Cederholm et al. 1999; Milner et al. 2000; Gresh et al. 2000; MacAvoy et al. 2000).

THE IMPORTANCE OF BIOENERGETIC VARIABLES TO BIOMAGNIFICATION OF PERSISTENT CONTAMINANTS

Because we were able to develop precise first-order elimination models for cesium (Rowan and Rasmussen 1995) and methyl mercury (Trudel and Rasmussen 1997), and because their uptake and elimination are not complicated by a complex interplay with the lipid pool, we pursued mass balance studies on these contaminants with the aim of testing biomagnification models and evaluating the importance of the bioenergetic budget to biomagnification (Trudel and Rasmussen 2001). Most discussions of biomagnification are chemically oriented, and the biomagnification factor is generally considered to be solely an attribute of the contaminant in question, ignoring biological variables. Our modeling studies were very successful in demonstrating that the activity budget of fish was an important determinant of the biomagnification factor (Trudel and Rasmussen 2001) and that the energy spent on activity varied by twofold or more among systems for the same species (Rowan and Rasmussen 1996; Trudel et al. 2000). These models show that fish with high consumption rates coupled to high activity costs build their contaminant burdens much more rapidly than they grow, since intake greatly exceeds the rate of elimination.

The precision that was possible in measuring and modeling the mass balance of cesium and methyl mercury made it possible to invert the models and calculate feeding rates from the increase in body burden over an age class (adjusted for elimination using a temperature-specific allometric model). This approach allowed us to work out the *in situ* bioenergetic budgets for a wide spectrum of fish and to study variation among systems in the energy they spent on activity (Rowan and Rasmussen 1996; Trudel et al. 2001). Just as the growth curves of two widespread species, the yellow perch and the lake trout, were highly variable, so was the activity component of the energy budget. This variation appears to be explainable by ecological variables such as the transparency of the water and the relative size of the prey being consumed (Boisclair and Rasmussen 1996; Pazzia et al. 2002; Trudel and Rasmussen 2001).

Using this radiotracer method, we have shown that metabolic and activity costs can be highly site-specific for fish and that these costs are sensitive to

environmental variables. In certain lakes, lake trout feed almost exclusively on invertebrates, and these fish grow much more slowly than piscivorous populations (Martin 1952, 1966). Recent work shows that this growth deficiency is not related to below-normal food consumption, but rather to greatly elevated metabolic costs, which lead to reduced growth efficiency (Pazzia et al. 2002).

Even different subpopulations of a species within a lake can exhibit significantly different activity costs. Dwarf lake whitefish (zooplanktivores) have daily rations similar to those to normal lake whitefish (zoobenthivores), but expend far more energy (Trudel et al. 2001). This increased energy expenditure appears to result from the need to assemble the daily ration from a large number of individually consumed small prey (zooplankton). Thus, bioenergetically, the energy budgets of dwarf whitefish resemble those of stunted yellow perch or lake trout, in that the energy investment required for a fish to obtain a normal ration is much greater when the ration is composed of many small prey than when it is made up of a few larger ones. Dwarf whitefish have tissue concentrations of mercury several times higher than those of normal whitefish, although they feed at similar trophic positions on prey with similar levels of mercury contamination (Trudel et al. 2001).

These studies on the effect of bioenergetic factors on biomagnification show that variation among food webs in the degree of biomagnification is not simply a result of differences in food chain length (trophic position) from system to system, but also results from considerable among-system variation in energetic conversion efficiencies, which ultimately determine the tissue concentrations of contaminants in organisms.

We have also used this tracer approach to estimate the bioenergetic costs of living in a metal-contaminated environment. Yellow perch inhabiting metal-contaminated lakes in the Noranda region of northern Quebec have significantly lower growth efficiencies and higher activity costs than perch from reference lakes. These effects are probably a combination of direct metal toxicity effects on fish and the indirect effects of metal contamination on communities of benthic invertebrates. Metal-contaminated lakes have very few prey-sized fish and also lack many of the macroinvertebrates that yellow perch normally consume during their transition to piscivory (Sherwood et al. 2000).

Thus, while it is indeed unfortunate that our environment is polluted with hazardous compounds that poison wildlife and force us to restrict consumption of wild fish and game, we at least can make the best of a bad situation by utilizing these substances as tracers to learn more about the bioenergetic and trophic variation of wild populations.

CONCLUSIONS

It is important to recognize that persistent contaminants such as organochlorines, mercury, and radiocesium are widespread atmospheric pollutants and that they constitute potentially important allochthonous inputs to ecosystems, putting both humans and wildlife at risk, even in parts of the world very remote from industrial activities and anthropogenic point sources. In order to draft policies that adequately deal with the risks to humans and wildlife that persistent contaminants pose, it is necessary that we understand the factors that magnify their concentrations and how those factors vary across the landscape. Food web processes play an important but poorly recognized role in biomagnification, and an impressive amount of variation exists among food webs in the degree to which persistent contaminants are biomagnified. Much of this variation results from the zoogeographic processes that have occurred on the landscape in the past together with the species invasions that are occurring at present.

Management policies cannot be uniquely constructed for each lake or river system, but rather need to operate within management plans derived for larger regional scales. Generic approaches to fisheries and environmental management tend to focus on "average" conditions, and they will naturally tend to ignore exposure risks associated with variation unless the processes that generate it are understood and the likelihood of spatial transport is recognized. Humans and wildlife that consume fish can be exposed to serious risks if they concentrate their foraging in high-risk areas. It is also important to recognize that lakes and oceans with long food chains can have highly contaminated top piscivores that migrate long distances, thus serving as important transport vectors on the landscape.

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