Sewage and the ecology of the St. Lawrence River

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ABSTRACT

This thesis examines the ecological consequences of sewage disposal in aquatic ecosystems. Sewage simultaneously represents a form of enrichment and a source of stress to a receiving system. Enrichment effects dominate when sewage loading does not exceed the capacity of the system to assimilate waste, as is presently the case in the St. Lawrence River. We developed a method to quantify the assimilation of sewage-derived organic matter by riverine biota, then used this method to examine the pathways by which sewage enhances secondary production in the St. Lawrence. We showed that the relative importance of dissolved nutrients and particulate organic matter to the river food web is to a large degree dictated by the physical and biological characteristics of the local environment. The effects of this enrichment on the receiving water community were also influenced by habitat characteristics. Analysis of body size distributions revealed that only the largest organisms had higher densities at enriched sites, and that the identity of these organisms depended on habitat structure. Densities of smaller organisms were controlled by a combination of habitat characteristics and feeding interactions. This pattern was consistent with food web models of top-down (consumer) control. At each trophic level, relatively invulnerable (large) prey achieved higher densities, whereas densities of more vulnerable (small) prey were controlled by their predators. Finally, we synthesized the ideas outlined above to predict how conditions in the St. Lawrence will change in the future as a result of lower water levels. More extensive macrophyte cover, slower current, and warmer temperatures in a shallower St. Lawrence will all enhance the ability of the system to physically retain and biologically process sewage nutrients, but will also increase the likelihood of negative effects such as anoxia.

RÉSUMÉ

Cette thèse examine les conséquences écologiques du rejet d'eaux d'égout dans des écosystèmes aquatiques. Pour ces systèmes, les eaux d'égout représentent simultanément une forme d'enrichissement et une source de stress. Les effets d'enrichissement dominent lorsque la charge d'eaux d'égout n'excède pas la capacité du système d'assimiler les déchets, le cas actuel du fleuve St-Laurent. Nous avons développé une méthode pour mesurer l'assimilation de la matière organique provenant de l'eau d'égout par la biota fluviale, qui a eté par la suite utilisée pour examiner les voies par lesquelles les eaux d'égout mettent en valeur la production secondaire dans le fleuve St-Laurent. Nous avons démontré que les caractéristiques physiques et biologiques de l'environnement local déterminent en grande partie l'importance relative des nutriments dissous et de la matière organique particulaire au réseau trophique de ce fleuve. Les caractéristiques de cet habitat influencent aussi les effets de cet enrichissement sur la communauté biologique du fleuve. L'analyse des distributions de tailles a indiqué que seulement les plus grands organismes possèdent des densités plus élevées aux sites enrichis, et que l'identité de ces organismes dépend de la structure de l'habitat. Les densités de plus petits organismes ont été contrôlées par une combinaison de caractéristiques d'habitat et des interactions trophiques. Ces observations se conforment aux modèles de réseau trophique du contrôle “top-down” (du consommateur). À chaque niveau trophique, la (grande) proie relativement invulnérable a réalisé des densités plus élevées, tandis que des densités d'une (petite) proie plus vulnérable ont été contrôlées par leurs prédateurs. Finalement, nous avons synthétisé ces idées pour prévoir les conditions dans le fleuve St-Laurent pour des niveaux plus bas de l'eau. Une couverture plus étendue de macrophyte, un courant plus lent, et des températures plus chaudes dans un fleuve un peu moins profond mettront en valeur la capacité du système de retenir physiquement et de traiter biologiquement des nutriments d'eaux d'égout, mais augmenteront également la probabilité d'effets négatifs tels que la anoxia.

TABLE OF CONTENTS

LIST OF TABLES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

LIST OF FIGURES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

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This thesis contains five chapters, each of which has been prepared for publication in peer-reviewed scientific journals. The first chapter has been submitted to Ecological Applications, the second to Limnology and Oceanography, and the third and fifth to Canadian Journal of Fisheries and Aquatic Science. The fourth has been prepared for submission to American Naturalist.

This thesis represents the results of my own independent research. All five chapters have been co-authored by my thesis supervisor, Dr. Joseph B. Rasmussen. Dr. Rasmussen contributed substantially to the design, execution, analysis, and presentation of the results presented herein. Dr. David Marcogliese (Environment Canada) was involved in the research presented in Chapters 2 and 3, and is co-author of these chapters.

CONTRIBUTIONS TO ORIGINAL KNOWLEDGE

Chapter 1

This is the first study to demonstrate the utility of stable nitrogen isotopes for tracing the ecological fate of sewage-derived particulate organic matter (POM). To my knowledge, it is also the first work to consider the fate of sewage in a system that does not show obvious accumulation of sewage-polluted sediment. I demonstrate that substantial amounts of sewage-derived POM may be assimilated by benthic primary consumers in the absence of sediment accumulation, and that the fraction of primary consumers' carbon and nitrogen which is of sewage origin may be disproportionately large relative to the concentration of sewage-derived POM in the bulk seston.

Chapter 2

Much of the general theory in river ecology was developed in forested, relatively undisturbed catchments. This chapter extends these theories by considering the nearly ubiquitous influence of sewage. I develop a conceptual model of how the physical and biological characteristics of an aquatic system dictate how that system will respond to enrichment with various forms of nutrients. I then use estimates of fish biomass and growth rates to show that sewage enhances secondary production in the St. Lawrence River, and to quantify the rate at which sewage nutrients and POM are assimilated by the food web of the river. Furthermore, I show that local habitat characteristics influence the uptake of dissolved nutrients, and thus the relative importance of dissolved and particulate forms of enrichment to the food web. Previous work on organic enrichment has usually been in systems so heavily eutrophied that sediment or water column anoxia was a dominant environmental factor. What work has been done on modest levels of organic enrichment has largely been in marine systems, and most has considered only the response of benthic macroinvertebrate community structure. This chapter develops general ideas about higher-level ecological consequences of enrichment, and relates these consequences to characteristics of the receiving system.

Chapter 3

This is the first study to show that sewage enrichment alters the size distribution of the receiving-water community. Furthermore, it works toward reconciling two alternative approaches to studying size distributions.

Chapter 4

This is the first experimental field test of the importance of consumer control in food webs with heterogeneous prey. The role of prey heterogeneity in mediating consumer control has been shown theoretically, but has heretofore been tested only in model (micro- and mesocosm) food webs. I show that invulnerable prey are effectively another top trophic level, and are thus free to respond to increases in basal productivity along with top predators. These effects cascade to the next lower trophic level.

Chapter 5

This chapter is intended to draw attention to an incipient problem in aquatic ecology: lower river discharge (a likely outcome of climate change in Canada) will reduce the capacity of many rivers to assimilate sewage loading. This chapter presents few new data, but it develops important new ideas. It extends a model (first presented in Chapter 2) of how physical and biological characteristics dictate a system's response to sewage loading, considering what will happen when these characteristics change with reduced river discharge. The analysis outlined here for the St. Lawrence provides a framework for considering the future of other Canadian waters subject to sewage loading.

ACKNOWLEDGEMENTS

This thesis has the word “ecology” in its title largely because of the influence of my supervisor, Joe Rasmussen. Most of what I think I know about ecology, I learned from him. Thanks, Joe.

This work benefited from the involvement of many other wise and generous people. First, I wish to thank Rob Peters for inviting me to McGill and giving me the opportunity to work in this amazing place. Neil Price and Christiane Hudon (my supervisory committee) provided guidance and reality checks. Other members of the department, including Jaap Kalff, Kevin McCann, and Amanda Vincent, provided endless kind advice. David Marcogliese, Normand Bermingham, François Gagne, and François Boudreault (Centre St-Laurent, Environment Canada) provided expertise, contacts, samples, data, and a place to park my boat. Paul-Andre Leduc and Yves Lafleur (Station d’épuration, Communauté urbaine de Montréal) were generous with their time and expertise. Financial support came from NSERC, GRIL, the Canadian Water Resources Association, and the Vineberg family.

The people of the 6th floor and Joe’s Garage made my time at McGill a challenging and fun experience. Jessica, Neil, JennyK, Graham, Rees, Dave, Alice, Jake, Yvonne, Marc, and many others provided intellectual, moral, and social support. My deepest gratitude also goes out to the Thomson House regulars (including many of the previous list) and staff, for providing a welcoming home away from home. Thanks also to the dancers, Andrea, Darla, Malo, Sinead, Alison, and Joelle, and the birders, Christina and Angela, for helping preserve some vestige of my sanity. And of course, Amy. Thank you for being so patient.

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GENERAL INTRODUCTION

Cities have been discharging their waste into rivers since the Romans first dumped sewage into the Etruscan-built *Cloaca Maxima* (literally, "big sewer") in the 6th century B.C. Subsequent pollution of the Tiber, Rome's main source of drinking water, is believed to have contributed to the fall of the Roman Empire. Accelerating urbanization in Europe and North America during the Industrial Revolution led to similar problems: odours rising from the Thames during 1858 and 1859 made life in London almost intolerable, and the Chicago Drainage Canal became known as "Bubbly Creek", with a thick scum that people could safely walk on (Warren 1971). Chicago was discharging waste into Lake Michigan, which provided its water supply, even with epidemic typhoid prevalent (Warren 1971). Today, only 16% of the world's population has access to adequate sewage treatment (WHO/UNICEF 2000). The remaining 5.1 billion people discharge millions of tonnes of untreated sewage each day.

Historically, management and scientific interest have focused on the gross negative impacts of sewage loading: pathogenic bacteria cause disease epidemics and contaminate shellfish, organic matter stimulates oxygen depletion by heterotrophic bacteria, and inorganic nutrients trigger blooms of noxious algae. These impacts have direct repercussions for human health and human uses of aquatic systems, and thus attract attention and funding. In the vast majority of cases, however, such gross negative impacts are localized or absent. Aquatic systems have the capacity to assimilate a certain amount of sewage loading without undergoing dramatic changes. If this capacity is not exceeded, the nutrients and organic matter in sewage serve primarily to enrich the system.

Sewage can enrich a receiving system by stimulating local production, as inorganic nutrients and dissolved organic matter are taken up by algae and bacteria, or by providing a subsidy of particulate organic matter (POM) which is degraded by bacteria or fungi and consumed by metazoans. Inorganic nutrients in sewage can support increased growth of periphyton in Canadian rivers

(Scrimgeour and Chambers 2000; Chambers et al. 1997), and nutrient addition experiments in rivers have shown that this sort of enrichment can support higher production of consumers (Deegan and Peterson 1992; Hill et al. 1991; Johnston et al. 1990; Slaney et al. 1994). Particulate organic matter in sewage can also be a very important source of secondary production, especially in streams and large rivers, which are well suited to exploiting POM (Vannote et al. 1980; Minshall et al. 1983, 1985). King and Ball (1967) reported higher densities and faster growth of primary consumers downstream of a sewage outfall, and could attribute less than 10% of secondary production to autochthonous production. The potentially enriching role of sewage POM is supported by work in which experimental additions of grain or soybean have produced 1.5- to 2.9-fold increases in total invertebrate biomass in mid-sized rivers (Mundie et al. 1983; Johnston et al. 1990).

The seminal work of Pearson and Rosenberg (1978) on marine benthic communities suggests that sewage simultaneously represents a form of enrichment and a source of stress to a receiving system. Greater exposure to sewage produces a greater potential enhancement of community production, but also increases the frequency and severity of sediment and water-column anoxia. At low exposure, enhancement effects dominate and there is a net increase in community production, without any dramatic changes in the community. As exposure increases, negative effects become more important. The net change in community production is still positive, but the composition of the community shifts from subsurface- to surface-feeding primary consumers that are more tolerant of hypoxia and organic mud. At high exposure, these negative effects become overwhelming and more and more taxa are excluded, producing a net decrease in community production.

Work in fresh waters has mainly been concerned with anoxia-induced changes to the macroinvertebrate assemblage. For example, the well-known Saprobien system (Kolkwitz and Marsson 1909) describes a shift from "cleanwater" organisms to hypoxia-tolerant species, and ultimately to dominance by a few of the most tolerant species, with increasing organic pollution (reviewed by Cairns and Pratt 1993). Evidence for enrichment effects is scattered. Ellis and Gowing (1957) reported 2- to 4-fold higher densities of benthic invertebrates and only slight decreases in dissolved oxygen in a reach of Houghton Creek downstream of the sewage outfall of Rose City, Michigan (population 500). Katz and Howard (1955) found similar increases in a section of Lytle Creek immediately downstream of the outfall of Wilmington, Ohio (population 7000), but also reported extensive deoxygenation and dramatic changes to the fish community. Farther downstream, these negative effects diminished and fish were able to respond to sewage enrichment with faster growth. Several studies have reported increases in gut fullness (Ellis and Gowing 1957), condition (Ellis and Gowing 1957) and growth rate (Katz and Howard 1955; Eggers et al. 1978; Johnston et al. 1990) of fishes in sewage-enriched streams. Some authors have suggested that sewage discharges enhance fisheries yields (Hubbs 1933; Metcalf 1942; Cross 1950).

The goal of this thesis is to improve our understanding of how sewage influences the ecology of rivers, with special emphasis on the mechanisms and consequences of sewage enrichment. The St. Lawrence River downstream of Montreal, Quebec is an excellent model system for this work. Montreal's wastewater treatment plant discharges nutrients and organic matter at a higher rate than any other city in Canada, but the St. Lawrence seems to be protected by hydrodynamic forces from most adverse impacts. High current speeds and strong vertical mixing in this reach of the river prevent net sedimentation and the familiar problems associated with the accumulation of organic mud. Water column oxygen depletion is prevented by strong dilution and vertical mixing that replenishes oxygen consumed in the degradation of organic matter. Consequently, the primary effect of the sewage discharge is sustained enrichment of this reach.

I have assembled this thesis in manuscript format with five chapters, each of which has been prepared for publication in a peer-reviewed journal. Each manuscript addresses a different aspect of the role of sewage in the ecology of the St. Lawrence River. I believe that this thesis has value as a case study of this ecologically and economically important river, but at the same time I have tried as much as possible to draw generalizable conclusions from the work. The human population of the planet continues to grow, and is becoming increasingly urban (ICWE 1992; WHO/UNICEF 2000). Almost every large river in the world already receives sewage discharges from urban centres (Meybeck and Helmer 1989). It is work like that presented here that will allow us to understand and cope with the inevitable effects on the aquatic systems that assimilate our waste.

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CHAPTER 1: QUANTIFYING THE ASSIMILATION OF SEWAGE ORGANIC MATTER BY RIVERINE BENTHOS

deBruyn, A.M.H. and J.B. Rasmussen. Quantifying the assimilation of sewage organic matter by riverine benthos. submitted to Ecological Applications

Abstract

Fresh waters worldwide receive substantial loadings of particulate organic waste from municipal sewage collection and treatment works. This material may transport a wide variety of particle-associated contaminants. Using stable isotopes of carbon and nitrogen, we detected the influence of a nearby primary sewage treatment plant on the benthic foodweb of a large temperate river. Despite the low concentration of wastewater and the absence of accumulated sediment, > 60% of carbon and nitrogen in benthic organisms near the outfall was of sewage origin. This fraction is disproportionately high relative to the fraction of sewage-derived suspended particulate matter in the seston, suggesting preferential assimilation. Assimilation of sewage-derived particulate organic matter exposes benthos to high levels of contamination and may represent an important source of contaminants to higher trophic levels.

Introduction

The majority of the world's population lives in close proximity to fresh water, and increasing urbanization places ever greater stresses on aquatic ecosystems (ICWE 1992). Advances in sewage treatment technology have greatly reduced the loads of organic matter, inorganic nutrients and contaminants discharged by many urban centers. These improvements have reduced the occurrence of obvious impacts such as oxygen depletion, gross eutrophication, and acute toxicity. Contaminants are still frequently observed in municipal wastewaters and their receiving systems, however. These include estrogenics (Gagne and Blaise 1998), radionuclides (Long et al. 1998), genotoxins (White et al. 1998), aromatic hydrocarbons (Pham et al. 1999), organochlorine pesticides (Scrimshaw and Lester 1995) and metals (Bascom 1982; Mugan 1996). Many of these contaminants are typically associated with the particulate phase, and therefore present a threat to organisms in the receiving system. Sewage-derived particulate organic matter (SDPOM) is a mixture of organic detritus and microorganisms such as bacteria and algae. This is a high-quality food source which can represent an important vector for transfer of sewage-associated contaminants to aquatic consumers (Bascom 1982; Costello and Read 1994; Spies 1984).

To assess the potential hazard of SDPOM, previous work has addressed the dispersal and accumulation of this material in receiving systems. Physical exposure to SDPOM-contaminated sediment may be only a minor uptake route for contaminants, however. Consumption of sediment is the dominant exposure route of detritivores to hydrophobic organics and many metals (Forbes et al. 1998; Wang and Fisher 1999; Lee et al. 2000). Accumulation of SDPOM in sediment does not necessarily indicate consumption of that material by the benthos. Conversely, the absence of accumulated SDPOM does not preclude important entry of that material into a benthic foodweb, for example through suspension feeding or deposit feeding on temporarily settled material.

Stable isotope techniques are widely employed to elucidate feeding relationships. Because SDPOM often has stable isotopic ratios distinct from those of organic material produced in situ, $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ have been used to trace SDPOM accumulation (Vivian 1986; Macko and Ostrom 1994) and to detect the entry of SDPOM into marine foodwebs. Studies in mesocosms (Gearing et al. 1991) and marine sediments subjected to long-term burial by sewage sludge (Rau et al. 1981; Van Dover et al. 1992; Spies 1984; Spies et al. 1989; Tucker et al. 1999) have reported shifts in the stable isotopic signatures of primary and secondary consumers, reflecting important assimilation of SDPOM. More recently, relative abundances and carbon isotopic compositions of membrane fatty acids have revealed the importance of sewage sludge in the diet of urchins at a "marginally affected" location near a marine dumpsite (Rieley et al. 1997). No comparable work has been done in freshwater systems. Sewage loading may explain the high $\delta^{15}N$ of primary consumers in lakes with densely populated watersheds (Cabana and Rasmussen 1996) and juvenile striped bass in the Delaware River (Wainright et al. 1996), but this shift is thought to be via incorporation of inorganic nitrogen at the base of the foodweb.

Rivers typically receive much smaller loads of SDPOM than the highly polluted marine systems addressed by earlier work. As well, large rivers may have no permanent sedimentation zones, making it difficult to even qualitatively assess exposure of biota to SDPOM. If riverine production is low, even a moderate discharge represents an important local subsidy of high-quality organic matter. Uptake of SDPOM could represent a major pathway of contaminant transfer to higher trophic levels.

Here we report evidence that benthic riverine invertebrates can assimilate substantial amounts of SDPOM in the absence of obvious sediment accumulation. Furthermore, sewage-derived carbon and nitrogen in invertebrate tissue may be greater than the fraction of suspended particulate matter which is of sewage origin, suggesting preferential assimilation of SDPOM. We discuss how this information may be used to delineate the spatial extent of sewage impact in the St. Lawrence River, and to estimate contaminant bioaccumulation within this area.

Methods

Receiving system. The St. Lawrence is a large, fast-flowing, temperate river. At the island of Montreal, the river has two distinct, adjacent water masses: the clear, hard, "green water" of the Great Lakes (80% of the total discharge) and the humic, soft, "brown water" of the Ottawa River (St. Lawrence Centre 1996). Neither water mass has high nutrient levels (dissolved P < 30 μg/L; dissolved N < 0.5 mg/l) and neither is very productive (median summer chlorophyll-*a* < 2.5 μg/L) (Hudon and Sylvestre 1998). Flow rates are typically 2-3 m/s in the main channel, and net sedimentation of suspended material is restricted to the deepest areas outside the main channel. Permanent deposition is a small component of the suspended solids budget of this river (Carignan and Lorrain 2000).

Wastewater Treatment Plant: The Montreal Urban Community (MUC) wastewater treatment plant is a primary treatment facility serving 1.8 million people on the Island of Montreal (Purenne 1998). Most of the approximately 8000 commercial establishments and industrial plants on MUC territory also discharge their wastewater directly into the sewer system, contributing 15% of its total flow (Pham et al. 1999). This wastewater is treated to promote coagulation, passed through settling ponds, and discharged directly to the St. Lawrence River via an underwater pipe at a depth of 7 m and a distance of 4.5 km from the Island of Montreal. Residence time in the settling ponds is about 2-3 h, and effects an 85% reduction in suspended solids.

Effluent is discharged at an average rate of $2x10^6$ m^3/d, with an average of approximately 20 mg/l of suspended particulate matter, 0.5 mg/l total phosphorus, and 9 mg/l total nitrogen (Deschamps et al. 1998; Purenne 1998). On an annual basis, this discharge contributes $1.8x10^4$ tonnes of particulate matter to the weakly productive waters of the St. Lawrence River (Purenne 1998). Particle-associated contaminants that have been detected in this wastewater include polychlorinated biphenyls, polycyclic aromatic hydrocarbons and a variety of heavy metals (Deschamps et al. 1998; Purenne 1998; Pham et al. 1999).

The general trajectory of the MUC wastewater plume has been described using a Rhodamine dye dispersion study (Boulanger 1984). Lateral mixing in this section of the St. Lawrence is very slow, and the narrow mixing zone between the two water masses persists at least to the mouth of Lake St-Pierre, about 60 km downstream of Montreal (Verrette 1990). The MUC wastewater is discharged into the middle of this mixed water mass, and seems to widen very gradually downstream. The discharge rate of wastewater has increased from 5 to 30 m^3/s since the dye tracer study was conducted, and the current extent of the plume is not well known. More recent studies have used intrinsic tracers such as conductivity to locate the plume (Pham et al. 1999), but these are instantaneous readings and consequently imprecise. Both the Ottawa and St. Lawrence rivers are regulated, and both can therefore exhibit large daily, seasonal, and interannual variation in water levels which affect the width and concentration of the plume.

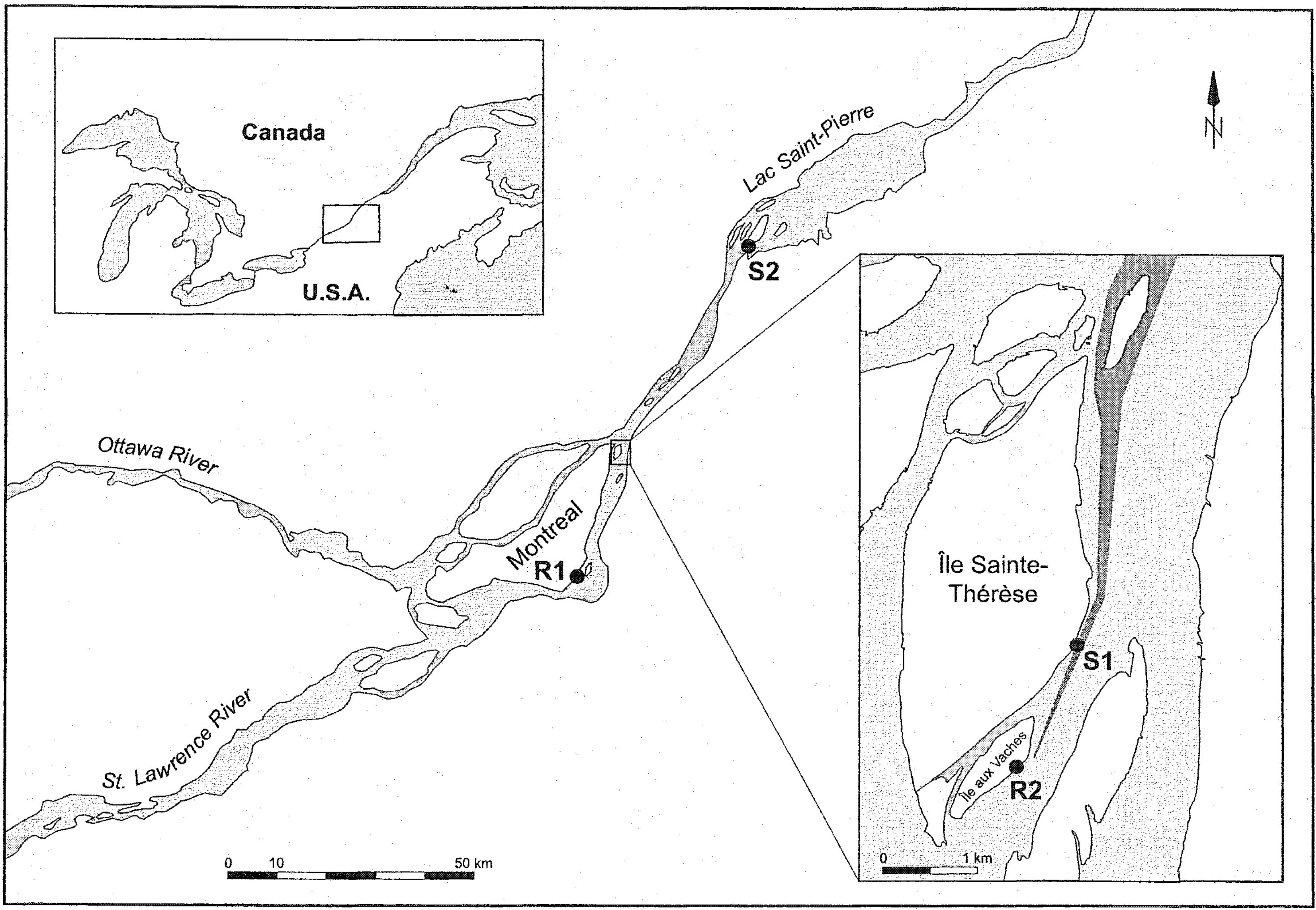
Sample sites. Biota were collected at two reference sites and two sewage-exposed sites along the fluvial section of the St. Lawrence River (Fig. 1). Reference site 1 (R1) was 29 km upstream of the outfall, on the south shore of the island of Montreal at LaSalle (45°25'N 73°35'W). Reference site 2 (R2) was 200 m upstream of the outfall at Île aux Vaches (45°40'N 73°28'W). Flow in this area is ≥ 1 m/s, so both reference sites are far enough upstream that they are never exposed to the MUC wastewater. It is important to note that there are many discharges of sewage to the waters upstream of our study reach. Our "reference" sites therefore serve as a reference only with respect to the primary-treated effluent from Montreal's wastewater treatment plant. Upstream sources of POM and inorganic nutrients provide the background against which we try to detect the influence of this effluent.

A heavily sewage exposed site (S1) was chosen approximately one kilometer downstream of the outfall, where the plume passes near a navigational beacon (45°41'N 73°27'W) about 50 m off the shore of Île Sainte-Thérèse. Samples were taken from the rocky base of the beacon tower. Conductivity measurements indicate that S1 is exposed to 5 - 10% sewage by volume. Samples were also taken from a small island of concrete rubble near Sorel (S2; 46°04'N 73°04'W), 56 km downstream. This site was chosen to be at the edge of the mixed water zone, where exposure to the MUC wastewater plume is low. Conductivity measurements indicate that S2 is exposed to about 1% sewage by volume. All four sites are in the mixing zone between the Great Lakes and the OttawaRiver water masses, although the relative proportions of each water mass vary among sites.

Sampling. Biota were collected on a single visit to each site between June 26 and August 3, 1999. At each site, rocky habitat was searched for zebra mussels (*Dreissena polymorpha*, an obligate suspension feeder), amphipods (*Gammarus fasciatus,* a detritivore/deposit feeder), snails (*Bithynia tentaculata*, a detritivore/deposit feeder and facultative suspension feeder) and filamentous periphyton. Sewage-derived particulate matter was collected at the wastewater treatment plant on April 9, June 17, and August 3, 1999. On June 26, particulate matter was collected upstream of the wastewater outfall (adjacent to R2) and downstream of the outfall, in the plume adjacent to S1. Particulate matter was collected on precombusted Whatman GF/C filters.

Sample preparation and analysis. Invertebrates were held for a few hours to allow gut clearance. All samples were stored at -20°C and subsequently dried for 48 hours at 70°C. Molluscs were removed from their shells and inspected closely for shell fragments before drying. Filamentous algae samples were rinsed with distilled water to remove loosely attached particulate matter. Algal filaments from S1 (the heavily sewage-exposed site) were encrusted with particulate matter which could not be completely rinsed off, possibly due to residual coagulant in

Figure 1. Locations of study sites on the St. Lawrence River (R1: LaSalle; R2: Île aux Vaches; S1: beacon tower; S2: Sorel). Dark area in expanded inset is approximate location of wastewater plume, with outfall at southernmost point of this dark area.


Canada
U.S.A.
N
Lac Saint-Pierre
S2
Ottawa River
Montreal
R1
St. Lawrence River
0
10
50 km
Île Sainte-
Thérèse
S1
Île aux Vaches
R2
0
1 km

the treated wastewater. Whole amphipods (5 per site), snails (3-7 per site) and zebra mussels (1-3 per site), and approximately 5 g wet weight of filamentous algae were pulverized and subsampled for analysis. POM was recovered by scraping the surface of the glass-fibre filter after drying. Stable isotope ratios of carbon and nitrogen were determined on a mass spectrometer at the Hatch Isotope Laboratory, University of Ottawa. Eighteen samples prepared and submitted in duplicate indicated good technical precision ($\delta^{13}C$ sd = 0.40; $\delta^{15}N$ sd = 0.33).

Data analysis. Stable isotope signatures of consumers from the two reference sites were used to infer the signatures of their non-sewage diets. The extent of sewage assimilation was then calculated for each taxon collected at the sewage-exposed sites. We used a model describing a mixture of SDPOM and the inferred non-sewage diet:

$$\delta X_{\text{consumer}} = P_{\text{SDPOM}} \bullet (\delta X_{\text{SDPOM}} + F_{\text{SDPOM}}) + (1 - P_{\text{SDPOM}}) \bullet (\delta X_{\text{non-sew}} + F_{\text{non-sew}})$$

where δX is the mean isotopic ratio ($\delta^{13}C$ or $\delta\ ^{15}N$) of the consumer, SDPOM endmember, or non-sewage endmember (Tables 1 and 2), P_{SDPOM} is the proportion of SDPOM in the diet of the consumer, and F is the trophic fractionation shift of primary consumers vs SDPOM and the non-sewage endmember. We assumed no trophic fractionation of carbon (DeNiro and Epstein 1978; France and Peters 1997) and considered a range of trophic fractionation of nitrogen. Adams and Sterner (2000) present evidence that fractionation of N by primary consumers varies with the C : N ratio of their diet. For the non-sewage endmembers, we replaced the term ($\delta X_{\text{non-sew}} + F_{\text{non-sew}}$) with the mean isotopic signature of consumers at the appropriate reference site (Table 2). For the SDPOM endmember, we used the measured isotopic signature of SDPOM and the mean reported trophic N fractionation shift of +3.4‰ (Minigawa and Wada 1984; Cabana and Rasmussen 1994), bracketed by the values +2 and +4‰, taken from Adams and Sterner (2000) to encompass most of the range of dietary C : N.

Using stable isotope analysis to determine diet depends on adequate knowledge of endmembers. For the non-sewage endmembers, our approach was to infer the overall isotopic signature of the diet from consumers at reference sites. Freshwater POM shows large temporal variance in $\delta^{15}N$ (Cabana and Rasmussen 1996; Leggett et al. 1999; inferred from variance in zooplankton $\delta^{15}N$ in Branstrator et al. 2000); the mean isotopic signature inferred from relatively large consumers integrates this variation over time and reflects only that portion of the POM which is assimilated. This approach assumes that there are similar proportions of non-sewage foods at the sewage-exposed sites, but avoids the difficulty of estimating the proportions of various foods in the consumer's diet, and measuring isotopic ratios of all diet components. Where the food source is discrete, like SDPOM, direct measurement is preferable. The isotopic signature of the SDPOM endmember was measured directly, using the samples from the treatment plant.

Results

Reference sites: Stable isotope ratios of periphyton at the two reference sites differed somewhat in $\delta^{13}C$ (-14.2 and -11.8‰) but less in $\delta^{15}N$ (+7.4 and +8.2‰; Table 1; Fig. 2). *Gammarus* and *Bithynia* also had remarkably constant isotope ratios within sites, between sites, and between the two species (Table 1; Fig. 2). The only substantial variation in snail and amphipod signatures was a difference in $\delta^{13}C$ of about +1‰ (*Gammarus*) or +2‰ (*Bithynia*) between R1 and R2. Zebra mussels showed more of a difference in $\delta^{13}C$ between reference sites, from -24.7 at R1 to -20.1‰ at R2, but had similarly low variation in $\delta^{15}N$ (Table 1; Fig. 2). Particulate organic matter collected on June 26 near R2 was similar in $\delta^{13}C$ to zebra mussels from this reference site (-20.4‰), and lighter in $\delta^{15}N$ (+3.4‰).

Sewage-exposed sites: Sewage-derived POM collected from the MUC wastewater treatment had similar $\delta^{13}C$ on the three sampling dates (mean -21.8‰; sd 0.5‰) but $\delta^{15}N$ became progressively more negative over the course of the summer (+0.54‰ on Apr 9, -2.0‰ on Jun 17, and -2.8‰ on Aug 3). All taxa collected at S1 reflected substantial sewage influence in their stable isotopic signatures (Table 1; grey area in Fig. 2). Periphyton (with encrusting particulate matter) had $\delta^{13}C$ of -20.4 and $\delta^{15}N$ of -2.0‰, reflecting a shift of -7.5‰ $\delta^{13}C$ and -9.8‰ $\delta^{15}N$ versus the mean value for reference sites. Snails and amphipods were both shifted approximately -2.5‰ $\delta^{13}C$, but *Bithynia* displayed a greater shift in $\delta^{15}N$ than *Gammarus* (-6.7‰ and -4.7‰, respectively). *Dreissena* were shifted -6.8‰ in $\delta^{15}N$, but had $\delta^{13}C$ similar to both SDPOM and mussels from the nearby reference site at R2. Particulate organic matter collected on June 26 near S1 was similar in $\delta^{13}C$ to all taxa collected at this site (-20.5‰), and lighter in $\delta^{15}N$ (-3.4‰).

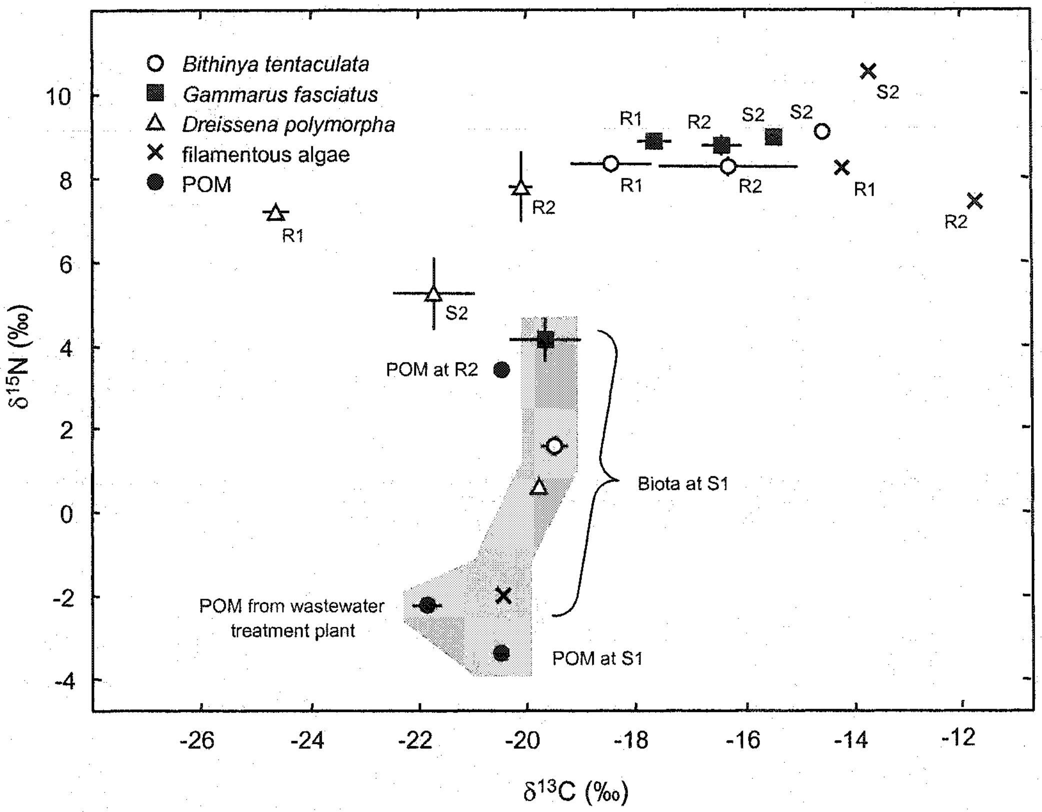
The marginally exposed site (S2) showed a very different pattern of isotopic shifts. Periphyton was intermediate in $\delta^{13}C$ between the two reference sites, but was 2.7‰ enriched in ^{15}N versus the mean of the two. *Gammarus* and *Bithynia* displayed the same progressive downstream difference in $\delta^{13}C$ that was observed at the reference sites (+1 and +2‰, respectively), but *Bithynia* also displayed a small enrichment in ^{15}N (+0.8‰). *Dreissena* was intermediate between the two reference sites in $\delta^{13}C$, but showed a -2.2‰ shift in $\delta^{15}N$ versus the mean of the two, the same direction as that observed at S1.

Assimilation of SDPOM: Estimated proportions of SDPOM in the diets of primary consumers at the sewage-exposed sites are presented in Table 2. Sewage-derived POM comprised 61% of the carbon assimilated by *Gammarus* at S1, and from 52 to 66% of the nitrogen. *Bythinia* at S1 had switched to suspension feeding (see Discussion), so the non-sewage diet of both *Dreissena* and *Bithynia* at S1 was POM. $\delta^{13}C$ of riverine POM was poorly separated from that of SDPOM. Furthermore, $\delta^{13}C$ of the consumers suggested that the bulk SDPOM signature was not a good reflection of the true endmember (due to selective feeding, see Discussion). $\delta^{15}N$, however, indicated a diet dominated by SDPOM

Table 1. Stable isotopic ratios (mean ± sd) of samples collected at two reference sites and two sites exposed to the Montreal Urban Community municipal wastewater in the St. Lawrence River. SD not available for samples analyzed as composites.

		Reference sites		Sewage-exposed sites	
Taxon	Isotope	R1 (LaSalle)	R2 (Île aux Vaches)	S1 (beacon)	S2 (Sorel)
Gammarus fasciatus	$\delta^{13}C$	-17.64 ± 0.73	-16.42 ± 0.65	-19.70 ± 1.21	-15.44
	$\delta^{15}N$	+8.83 ± 0.27	+8.75 ± 0.48	+4.11 ± 0.92	+8.97
		n = 5	n = 5	n = 5	n = 5
Bithynia tentaculata	$\delta^{13}C$	-18.40 ± 1.31	-16.28 ± 2.21	-19.46 ± 0.74	-14.56
	$\delta^{15}N$	+8.33 ± 0.41	+8.25 ± 0.41	+1.55 ± 0.62	+9.08
		n = 3	n = 3	n = 7	n = 3
Dreissena polymorpha	$\delta^{13}C$	-24.64 ± 0.35	-20.07 ± 0.39	-19.75	-21.70 ± 1.09
	$\delta^{15}N$	+7.07 ± 0.21	+7.78 ± 1.42	+0.59	+5.24 ± 1.20
		n = 2	n = 3	n = 1	n = 2
periphyton	$\delta^{13}C$	-14.20	-11.75	-20.43	-13.71
	$\delta^{15}N$	+8.22	+7.39	-2.00	+10.50
POM	$\delta^{13}C$		-20.45		-20.48
	$\delta^{15}N$		+3.40		-3.35

Figure 2. Mean $\delta^{15}N$ vs. mean $\delta^{13}C$ (± 1 SE) for benthic primary consumers and filamentous algae at two reference sites (R1: LaSalle; R2: Île aux Vaches) and two sewage-exposed sites (S1: beacon tower; S2: Sorel) on the St. Lawrence River. Samples from the heavily sewage-exposed site S1 are enclosed in grey. Standard errors are not available for samples analyzed as composites of several individuals (*Gammarus* and *Bithynia* from S2). Particulate organic matter (POM) was collected from the MUC wastewater treatment plant on 3 dates, and from sites upstream (R2) and downstream (S1) of the outfall on a single date.



Bithinya tentaculata
Gammarus fasciatus
Dreissena polymorpha
filamentous algae
POM
R1
R2
S2
POM at R2
Biota at S1
POM from wastewater treatment plant
POM at S1
δ15N (‰)
δ13C (‰)
10
8
6
4
2
0
-2
-4
-26
-24
-22
-20
-18
-16
-14
-12

for both taxa at this site (>80% for *Bithynia*, >90% for *Driessena*). At S2, neither detritivore reflected any substantial assimilation of SDPOM. The $\delta^{13}C$ of non-sewage POM at S2 could not be estimated, but $\delta^{15}N$ indicated 29 - 39% SDPOM nitrogen in the diet of *Dreissena* at this site.

Discussion

Sewage-derived POM: Isotopic values for sewage solids reported in the literature vary considerably in both $\delta^{13}C$ (mean -23.4‰; range -28.5 to -16.5‰; n=13) and $\delta^{15}N$ (mean +3.2‰; range -1.1 to +7.2‰; n=7) (compilation in Van Dover et al. 1992; Gearing et al. 1991, 1994; Andrews et al. 1998). Sewage-derived POM collected from the MUC wastewater treatment plant was similar in $\delta^{13}C$ to the literature mean value (-21.8‰) but $\delta^{15}N$ was somewhat lower on average (-2.0‰) and became progressively more negative over the course of the summer. This progressive change was correlated positively with retention time of the treatment plant (r^2=0.98; n=3) and with temperature in the settling ponds (r^2=0.97; n=3), suggesting that the change may be a biologically mediated process.

Fractionation processes in sewage tend to increase $\delta^{15}N$ of the total dissolved inorganic nitrogen (DIN) pool as $^{14}NH_3$ volatilizes more readily than $^{15}NH_3$, and $^{14}NO_3^-$ is reduced more quickly than $^{15}NO_3^-$ by denitrifying bacteria (Kendall 1998). Over 90% of inorganic nitrogen in the MUC settling ponds is NH_3-NH_4^+, but the concentration of NH_3-NH_4^+ in the effluent is similar to that of the untreated wastewater and NO_2-NO_3^- is slightly higher (Deschamps et al. 1998), suggesting that the residence time of these ponds is not sufficient to permit substantial volatilization or denitrification. Fractionation during nitrification (transormation of NH_4^+ to NO_3^-) produces isotopically lighter NO_3^- (Kendall 1998). In addition, algal uptake of DIN may discriminate against ^{15}N by up to -27‰ under such N-replete conditions (6 mg/l DIN; Deschamps et al. 1998), resulting in an isotopically light particulate phase (Fogel and Cifuentes 1993). A progressive seasonal increase in algal growth in the nitrogen-rich settling ponds

Table 2. Proportion of sewage-derived carbon and nitrogen in primary consumers at two sites downstream of the Montreal Urban Community municipal wastewater outfall. Non-sewage endmember values are inferred diets of consumers at reference sites.

Consumer	Site	Non-sewage endmember	Estimate from $\delta^{13}C$	Estimates from $\delta^{15}N^{a}$		
				2‰	3.4‰	4‰
Gammarus fasciatus	S1	diet of *Gammarus* at R2	0.61	0.52	0.61	0.66
Bithynia tentaculata	S1	diet of *Dreissena* at R2	-[b]	0.83	1.00	1.10
Dreissena polymorpha	S1	diet of *Dreissena* at R2	-	0.90	1.09	1.20
D. polymorpha	S2	mean diet of *Dreissena* at reference sites	-	0.29	0.35	0.39

[a] assuming the indicated trophic fractionation values

[b] unable to calculate a meaningful value

would produce the seasonal pattern in SDPOM $\delta^{15}N$ observed here. This isotopically light pool of sewage-derived phytoplankton may also be the fraction of SDPOM preferred by suspension feeders (see below).

Periphyton and inorganic nutrients: $\delta^{13}C$ of filamentous periphyton at the reference sites (mean -13.0‰) was heavier than mean values reported elsewhere (-29‰ in France 1995), consistent with observations that the DIC pool of Great Lakes water is about 10‰ enriched in ^{13}C over other large rivers (Leggett 1999; Yang et al. 1996). This enrichment is produced by equilibration with the atmosphere during the long residence time of the Great Lakes (Yang et al. 1996), and maintained by the very large pool of HCO_3^- in this water mass (Leggett 1999). ^{13}C enrichment in excess of this difference in the DIC pool may be due to boundary-layer CO_2 limitation enhanced in microhabitats with weak mixing. $\delta^{15}N$ of filamentous periphyton at the reference sites (+8.2 and +7.4‰ at R1 and R2) was similar to that reported elsewhere (+5 to +7‰ in summer; MacLeod and Barton 1998).

The strong shift in periphyton at S1 toward lighter values of $\delta^{13}C$ and $\delta^{15}N$ was at least partly due to encrusting SDPOM which could not be rinsed off. In addition, this shift may reflect a lighter source of DIC (e.g. CO_2 from respired organic carbon, Fry and Sherr 1984) and stronger fractionation of replete nitrogen (Fogel and Cifuentes 1993). Periphyton at S2 was intermediate in $\delta^{13}C$ to the reference sites, but 2.5‰ enriched in ^{15}N versus the mean of the two, indicating an isotopically heavier DIN pool than at the other sites. S2 is about 56 km downstream of the sewage outfall, corresponding to a flow time of about 20 hours. This delay is sufficient to permit substantial fractionation in the plume as sewage NH_3 volatilizes after discharge. The shift in $\delta^{15}N$ of periphyton at S2 suggests that this site is at least intermittently exposed to this isotopically heavy source of DIN.

Zebra mussels and POM: *Dreissena* is an obligate suspension feeder, and is known to preferentially retain higher quality particles, rejecting other particles as pseudofeces (Winkel and Davids 1982; Baker et al. 1998). Isotopic signatures of mussels at the reference sites indicate that this higher quality fraction of POM in the St. Lawrence has $\delta^{13}C$ between -20.1 and -24.6‰. Mussels from the upstream reference site (R1) had the more negative values of $\delta^{13}C$ (-24.6‰), similar to values reported for POM in eastern Lake Ontario (-28.7 to -24.3‰ in summer; Leggett et al. 1999) and the eastern St. Lawrence (-24.1‰; Tan and Strain 1983). This probably reflects the isotopic signature of the bulk of POM in the Great Lakes water mass, although there appear to be local differences at the other sites. Mussels at R2 were 4.5‰ enriched in ^{13}C relative to this value, reflecting a slightly different mix of Great Lakes and Ottawa River POM. Also, R2 is immediately downstream of the island of Montreal, and may therefore receive POM from combined sewer outfalls on the south shore of the island. The sample of POM collected at this site on June 26 had $\delta^{13}C$ of -20.4‰, also about 4‰ enriched relative to reported values and the inferred diet of mussels at R1.

$\delta^{15}N$ of mussels at the reference sites (+7.1 and +7.8‰ at R1 and R2) indicated a diet around +4‰, similar to eastern Lake Ontario POM (+3.5 to +8.5‰; Leggett et al. 1999), riverine POM $\delta^{15}N$ reported in the literature (+2 to +7‰: Owens 1987; Gearing et al. 1994; Riera 1998) and POM measured here at R2 (+3.4‰). R2 is immediately upstream of the sewage outfall and S1, so we used POM inferred from mussel signatures at this site as the non-sewage endmember to estimate assimilation of SDPOM by mussels at S1. The downstream sewage-exposed site (S2) is in a mixture of green water (R1) and Montreal-influenced mixed water (R2), so we used the average inferred POM of the two reference sites as the non-sewage endmember for *Driessena* at S2.

Amphipods and benthic production: The constancy of *Gammarus* $\delta^{15}N$ over the 29 km reach suggests that populations at the two reference sites are feeding from the same pool of material, a combination of benthic production and advected POM, accessed in microhabitats that enhance temporary deposition. The $\delta^{15}N$ of this pool (about +5‰) is intermediate between our values for POM (+4‰) and periphyton (+8‰). The $\delta^{13}C$ of this pool (about -17‰) is up to 7‰ heavier than St. Lawrence POM. Benthic production in freshwaters is typically enriched about 7‰ in ^{13}C over pelagic production because boundary-layer CO_2 limitation reduces photosynthetic fractionation (France 1995; Hecky and Hesslein 1995; Vander Zanden and Rasmussen 1999). Thus, we infer that *Gammarus* at these reference sites are assimilating a large fraction of isotopically heavy benthic production. We used the diet of *Gammarus* from the nearest reference site (R2) as the non-sewage endmember for amphipods at S1. *Gammarus* at S2 did not appear to be assimilating SDPOM.

The trend in *Gammarus* $\delta^{13}C$ toward heavier values at downstream sites (with the exception of SDPOM-dominated S1) may reflect a large-scale change in carbon dynamics along this reach of the river. The upstream reference site (R1) is immediately below the Lachine rapids, where turbulence provides benthic algae with ample dissolved CO_2 and photosynthetic fractionation is small. Beyond this point the flow is slower and more laminar, which enhances boundary-layer CO_2 limitation at the surface of algal cells. Consequently, this material has a $\delta^{13}C$ that ranges from -18‰ at R1 to -15‰ at S2.

Snails: The very close match between *Gammarus* and *Bithynia* isotopic signatures indicates that these taxa assimilate similar material at the reference sites, but *Bithynia* at S1 appeared to be feeding on suspended material (discussed below). We therefore used the same endmember for *Bithynia* as for *Dreissena* at S1 (R2 mussels). As with *Gammarus*, *Bithynia* at S2 did not appear to be assimilating SDPOM.

Assimilation of SDPOM: All three consumer taxa showed a shift in isotopic signatures at S1, reflecting important assimilation of sewage-derived carbon and nitrogen (grey area in Fig. 2; Table 2). Variance in stable isotope signatures of *Bithynia* at S1 was much lower than at either of the reference sites, indicating a more uniform food source (Table 1; Fig. 2). In addition, the isotopic signatures of *Bithynia* were more similar to *Dreissena* than to *Gammarus* at S1, suggesting that *Bithynia* and *Dreissena* were feeding on a similar pool of suspended POM.

Grazing is generally assumed to be the primary feeding mode of *Bithynia* in the St. Lawrence River (Flessas et al. 2000; Désy et al. 2000), but this snail is a facultative suspension feeder, employing a ctenidial filter when suspended food is of higher quality than benthic food (Tashiro and Esposito 1985; Brendelberger and Juergens 1993). In addition, both *Bithynia* and *Dreissena* are known to be selective feeders. *Bithynia* has been observed to select N-rich foods in the laboratory (Brendelberger 1995) and to cease feeding when only low-quality food is available (Brendelberger 1997). *Dreissena* preferentially retains higher quality particles (Winkel and Davids 1982; Baker et al. 1998). Because these consumers are able to select an N-rich fraction of SDPOM, they show a smaller trophic N fractionation at S1 than at the reference sites (Adams and Sterner 2000) and consequently a relatively larger shift in $\delta^{15}N$ than in $\delta^{13}C$ at S1.

Dreissena at S2 had $\delta^{13}C$ intermediate between those of the reference sites, indicating a mixture of Montreal-influenced POM (R2) and upstream St. Lawrence POM (R1). This is consistent with the position of this site, on the boundary between the midchannel mixed water and the green water of the Great Lakes. Mussels at S2 were 2.2‰ depleted in ^{15}N relative to the mean of the reference sites, indicating assimilation of about 30 - 40% sewage-derived nitrogen. If the dietary fraction simply reflected the proportion of SDPOM in the total POM, this would correspond to about 4% effluent by volume. The concentration of effluent at S2 is closer to 1%, suggesting that mussels at this site preferentially assimilate SDPOM.

Dreissena at S2 may also be assimilating some sewage DIN taken up by phytoplankton downstream of the outfall. $\delta^{15}N$ of periphyton at S2 indicates that either the sewage DIN is isotopically heavy or concentrations are too low to produce strong discrimination against ^{15}N, at least when it reaches this downstream site. Phytoplankton utilizing this DIN should therefore be similarly heavy and this shift should be reflected in the mussels. The observed shift in mussels at S2 to lighter values of $\delta^{15}N$ indicates that either the opportunity for phytoplankton uptake of sewage DIN is small, or mussels obtain most of their N from SDPOM and the contribution of isotopically heavy phytoplankton is small.

For *Gammarus* at S1, both $\delta^{13}C$ and $\delta^{15}N$ were consistent with a diet of 61% SDPOM, assuming: a) +3.4‰ trophic fractionation of SDPOM nitrogen; and b) that the remainder of the diet was isotopically similar to that of amphipods at R2. The similarity of the two estimates lends support to both assumptions. It is important to note, however, that filamentous periphyton at S1 appeared to be isotopically similar to SDPOM. This was partly due to adhering SDPOM, but possibly also from uptake of isotopically light DIC and DIN in the sewage. If the locally produced benthic diet of *Gammarus* was also influenced by light DIC and DIN, then 61% may be an overestimate. As noted above, however, DIN in the effluent is probably not isotopically light. Also, a high proportion of SDPOM in the diet of *Gammarus* is consistent with the reported preference of this taxon for detritus over benthic algae (Summers et al. 1997).

The apparently large contribution of SDPOM to the diets of all three taxa at S1 is in part a reflection of the fraction of POM in the plume which is of sewage origin. Much of the seston of the St. Lawrence is clay and silt, so the concentration of suspended organic matter is substantially lower than the total suspended particulates. Total algal biomass is often less than 1 mg/l in the mixed waters of the St. Lawrence (Hudon et al. 1996; Hudon 2000), and peak bacterial densities are not especially high (3.5×10^6 cells/ml in midsummer; Basu et al. 2000). Coliform bacteria alone can exceed 10^6 cells/ml in the MUC wastewater

(Purenne 1998) and microscopic inspection of the SDPOM indicates that it is predominantly organic detritus and algal cells. Thus, while the concentration of effluent at S1 was less than 10%, SDPOM represented up to 30% of the suspended matter, and as much as 60% of the particulate organic matter (given 1.35 mg/l non-sewage POM and 2 mg/l SDPOM at 10% effluent). Consequently, the nonselective deposit feeder (*Gammarus*) had an isotopic signature roughly consistent with the fraction of sewage-derived suspended matter (61%). The selective suspension feeders (*Dreissena* and *Bithynia*) had isotopic signatures disproportionately high relative to this fraction (80 - 100%), suggesting preferential assimilation of SDPOM. At S2, SDPOM constituted 12% of the POM (given 1.48 mg/l non-sewage POM and 0.2 mg/l SDPOM at 1% effluent). The proportion of sewage-derived nitrogen in *Dreissena* at S2 was 2 - 3 times higher than this, again suggesting preferential assimilation of SDPOM.

Potential applications. In the absence of sediment accumulation, determining the spatial extent of a wastewater plume in a river typically requires dye injection studies or extensive (and expensive) sampling of the water column for intrinsic tracers. Furthermore, these studies must be repeated to assess changes in plume location with seasonal and interannual hydrological changes of the river. Stable isotope analysis of primary consumers, as employed here, provides a time-integrated measure of their assimilation of sewage-derived material.

Even perfect information about the spatial extent of a sewage plume is insufficient to assess the exposure of biota to sewage-associated contaminants. Uptake of particle-associated contaminants is primarily via consumption. As our results demonstrate, assimilation of SDPOM may be disproportionately high relative to the fraction of POM which is of sewage origin. Stable isotope analysis provides a quantitative estimate of the exposure of primary consumers to SDPOM-associated contaminants in their diets. Combined with sewage contaminant measurements, these dietary data could be used in bioaccumulation models (e.g. Morrison et al. 1997) to estimate contamination of biota over a large spatial scale. Additionally, this technique may be used to elucidate links to higher trophic levels, revealing the potential for contaminant biomagnification.

In summary, we draw the following conclusions:

1) Substantial amounts of SDPOM are assimilated by benthic primary consumers in the absence of sediment accumulation.

2) The fraction of primary consumers' carbon and nitrogen which is of sewage origin is disproportionately large relative to the abundance of SDPOM in the POM.

3) Stable isotope analysis is a powerful and sensitive tool for tracing the ecological fate of SDPOM and associated contaminants.

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Connecting Statement

In the first chapter of this thesis, I developed a method to quantify the assimilation of sewage-derived particulate organic matter (POM) by riverine benthos. I showed that substantial amounts of POM were assimilated by the biota of the St. Lawrence in the absence of sediment accumulation, and that this assimilation was disproportionately high relative to the fraction of suspended POM which was of sewage origin. In the next chapter, I use this method to examine the pathways by which sewage enhances secondary production in the St. Lawrence, and to quantify the fluxes of sewage nutrients and POM into the benthic foodweb. Furthermore, I show that the relative importance of dissolved nutrients and POM is to a large degree dictated by the physical and biological characteristics of the local environment.

CHAPTER 2: THE ROLE OF SEWAGE IN A LARGE RIVER FOODWEB

deBruyn, A.M.H., D.J. Marcogliese, and J.B. Rasmussen. The role of sewage in a large river foodweb. submitted to Limnology and Oceanography

Abstract

Current theories in river ecology predict that the consequences of enrichment will be constrained by characteristics of the receiving system. We present a conceptual model of how different kinds of rivers respond to enrichment with various forms of nutrients. In general, the degree to which nutrients can be exploited by the biotic community is a function of nutrient retention time within the system, the efficiency with which the local biota can use nutrients in that form, and the degree to which other factors (e.g. temperature, light, oxygen) limit that use. We test these predictions at sites in the St. Lawrence River exposed to the primary-treated sewage of Montreal, Quebec. Higher fish biomass and production at sewage-exposed sites indicate on average a more than 10-fold enhancement of benthic invertebrate production. We estimate that more than 2000 tonnes per year of sewage-derived particulate matter enters the littoral foodweb of the St. Lawrence River in our 10 km study reach, and that this organic subsidy accounts for 70% of the enhanced production observed in this area. This fraction is lowest at sites with abundant macrophytes, suggesting that the remainder is due to stimulation of epiphytic biofilm by dissolved nutrients in the sewage.

Introduction

River ecologists have developed a small but powerful body of general theory, central to which is the overriding importance of longitudinal (upstream-downstream) and lateral (watershed-river) connections. These connections interact with physical forces that change along the course of a river, producing a continuum of morphological and hydrological features. The result is a shift in the relative importance of basal resources, from allochthonous litterfall in headwater streams to autochthonous producers in mid-sized rivers (Hynes 1970; Vannote et al. 1980; Minshall et al. 1985). Larger rivers are dominated by fine particulates transported in the main channel, although autochthonous production in the littoral zone and allochthonous inputs from riparian vegetation and floodplains may be energetically more important (Thorp and Delong 1994; Junk et al. 1989). The structure and function of the biotic community of a river reach develops to match the physical environment and the nature of basal resources.

Most of the world's rivers are influenced to some extent by human activities (Meybeck and Helmer 1989). These activities alter the fundamental physical and biological characteristics outlined above, and thus provide an opportunity to test our general theories. For example, dams have been instrumental in testing ideas about longitudinal connections (Ward and Stanford 1983). Studies in nutrient-enriched systems can be used in a similar way to address questions of productivity and nutrient cycling. Sewage is a particularly widespread (ICWE 1992; WHO/UNICEF 2000) and interesting form of enrichment. Sewage combines particulate organic matter (POM), dissolved organic matter (DOM), and inorganic nutrients, and can thus provide insight into the relative importance of allochthonous and autochthonous resources to river foodwebs.

Most previous work on sewage in rivers has been on systems so heavily enriched that anoxia is a dominant environmental factor. Organic matter in sewage imposes a biochemical oxygen demand (BOD), stimulating the consumption of oxygen by heterotrophic bacteria. When oxygen is not replenished as quickly as it is consumed, metazoan consumers will suffer (e.g., Chambers et al. 1997). However, in most cases the rate of sewage loading does not exceed the capacity of the river to maintain sufficient dissolved oxygen. Adequate dilution (high river discharge relative to sewage loading) and strong vertical mixing protect rivers from these negative effects and permit the biota to exploit sewage nutrients and organic matter. Even in rivers that do experience anoxia, BOD is eventually consumed and downstream reaches are free to respond to sewage enrichment.

The degree to which nutrients and organic matter can be exploited by the biotic community is a function of nutrient retention time within the system, the efficiency with which the local biota can use these materials, and the degree to which other factors (e.g. temperature, light, oxygen) limit that use. Conditions that enhance retention (slow current, physical structures, high surface area of substrate; Minshall et al. 1983) will reduce flushing capacity, but will provide more opportunity for the system to exploit the nutrients (i.e., produce 'tight spirals' sensu Webster 1975). In general, autotrophic systems (well lit streams, mid-sized rivers, large river littoral zones and backwaters) should be well suited to exploit inorganic nutrients, whereas heterotrophic systems (shaded headwaters, turbid river channels) should more readily assimilate POM.

Large rivers, which receive most of the world's sewage discharges, represent a mosaic of autotrophic and heterotrophic habitats. Benthic foodwebs in large river channels are thought to be primarily heterotrophic. These areas are light-limited and rely heavily on longitudinal (Vannote et al. 1980) and lateral (Thorp and Delong 1994; Junk et al. 1989) inputs of POM. Development of the pelagic foodweb is limited by low residence times (Basu and Pick 1996; Pace et al. 1992) and low surface area of contact limits access of the benthos to planktonic production.

The littoral zones and backwater of large rivers, on the other hand, have the potential for a large contribution of autotrophy. These areas are more or less well-lit, depending on the nature of riparian vegetation and the slope of the substrate. Macrophytes provide abundant surface area for attached algae and heterotrophic bacteria, and increase the residence time of inorganic nutrients and DOM. As well, these habitats support abundant grazers and their predators (Thorp and Delong 1994), so excess production can be effectively transferred to higher trophic levels. Macrophytes in littoral areas also enhance particle trapping (Sand-Jensen and Mebus 1996; Vermaat et al. 2000), increasing nutrient concentrations in the sediment (Chambers and Prepas 1994). Wave action in shallow areas enhances resuspension, ensuring a continual resupply of fresh POM to the sediment (Rasmussen 1993). These forces increase access of the benthic biota to labile POM. POM collectors are abundant, as are predatory invertebrates and fish that consume them (Thorp and Delong 1994).

Thus, large river littoral zones combine the heterotrophic capacity of small, retentive streams with the autotrophic potential of well-lit, mid-sized rivers. Large rivers also provide strong dilution and rapid flushing, protecting the biota from the negative effects of BOD. In particular, we can make and test the following predictions: 1) in the absence of anoxia effects, large river littoral zones will very effectively translate sewage into production of higher trophic levels; 2) the types of consumers present will determine the ultimate fate of sewage enrichment at a site; 3) uptake of dissolved nutrients will be enhanced by abundant light and physical structure; and 4) uptake of POM will be enhanced by wave action and abundant retention structures. In addition, we can test the prediction of Thorp and Delong (1994) that local autotrophic production forms the primary energetic basis for large river littoral foodwebs.

We tested these predictions for the littoral zone of a large, constrained river by exploiting a natural experiment. The municipal wastewater treatment plant of Montreal, Canada, has been discharging >450 tonnes of phosphorus and

>90,000 tonnes of POM annually into the St. Lawrence River since 1988 (Purenne 1998). High current speeds and strong vertical mixing prevent deoxygenation and net sedimentation in this reach of the river, so the primary effect is sustained enrichment. We evaluated the impact of sewage on abundance, biomass and production of fish and benthic invertebrates, and we used stable isotope analysis to determine the relative importance of particulate and dissolved pathways of enrichment.

Methods

Study system. The St. Lawrence is a large, fast-flowing, temperate river with a constrained channel. At the island of Montreal, the river has two distinct, adjacent water masses: the clear, hard, "green water" of the Great Lakes (80% of the total discharge) and the humic, soft, "brown water" of the Ottawa River (St. Lawrence Centre 1996). Neither water mass has high nutrient levels (dissolved P < 30 µg/l; dissolved N < 0.5 mg/l) and neither is very productive (median summer chlorophyll-*a* < 2.5 µg/l) (Hudon and Sylvestre 1998). Flow rates are typically 2-3 m/s in the main channel, and net sedimentation of suspended material is restricted to the deepest areas outside the main channel. Permanent deposition is a small component of the suspended solids budget of this river (Carignan and Lorrain 2000).

The Montreal Urban Community (MUC) wastewater treatment plant is a primary treatment facility serving 1.8 million people and 8000 commercial establishments on the Island of Montreal (Purenne 1998; Pham et al. 1999). Wastewater is treated to promote coagulation, passed through settling ponds (2-3 h, reducing suspended solids by 85%), and discharged directly to the St. Lawrence River via an underwater pipe at a depth of 7 m. Effluent is discharged at an average rate of 2×10^6 m^3/d, and contains approximately 100 mg/l POM (wet wt.), 0.5 mg/l total phosphorus, and 9 mg/l total nitrogen (Deschamps et al. 1998; Purenne 1998). This discharge contributes 450 t/y total phosphorus and 90,000 t/y (wet wt.) sewage-derived particulate organic matter (SDPOM) to the weakly productive waters of the St. Lawrence River (Purenne 1998).

The general trajectory of the MUC wastewater plume has been described using a Rhodamine dye dispersion study (Boulanger 1984). Lateral mixing in this section of the St. Lawrence is minimal, and the narrow mixing zone between the two water masses persists at least to the mouth of Lake St-Pierre, about 60 km downstream of Montreal (Verrette 1990). The MUC wastewater is discharged into the middle of the mixed zone, and seems to widen very gradually downstream. However, the discharge rate of wastewater has increased from 5 to 30 m^3/s since the dye tracer study was conducted, and the current extent of the plume is not well known. More recent studies have used intrinsic tracers such as conductivity to locate the plume (Pham et al. 1999), but these are instantaneous readings and consequently imprecise. Both the Ottawa and St. Lawrence rivers are regulated, and both exhibit large daily, seasonal, and interannual variation in water levels which affect the width and concentration of the plume.

Sample sites. We sampled fish and invertebrates from twelve sites in the fluvial St. Lawrence River downstream of the island of Montreal, Quebec, Canada (Fig. 1). Three of these were known to be in the discharge plume of the municipal wastewater treatment plant, within 10 km of the outfall. Conductivity measurements indicated around 5% sewage by volume in this area. Four were reference sites, hydrodynamically isolated from the plume. The remainder were downstream of the outfall and of unknown exposure. Sites were selected to represent a gradient of macrophyte cover, and thus a gradient of surface area for epiphytic primary production. All sites were shallow (<2.5 m) and had sand-clay sediment.

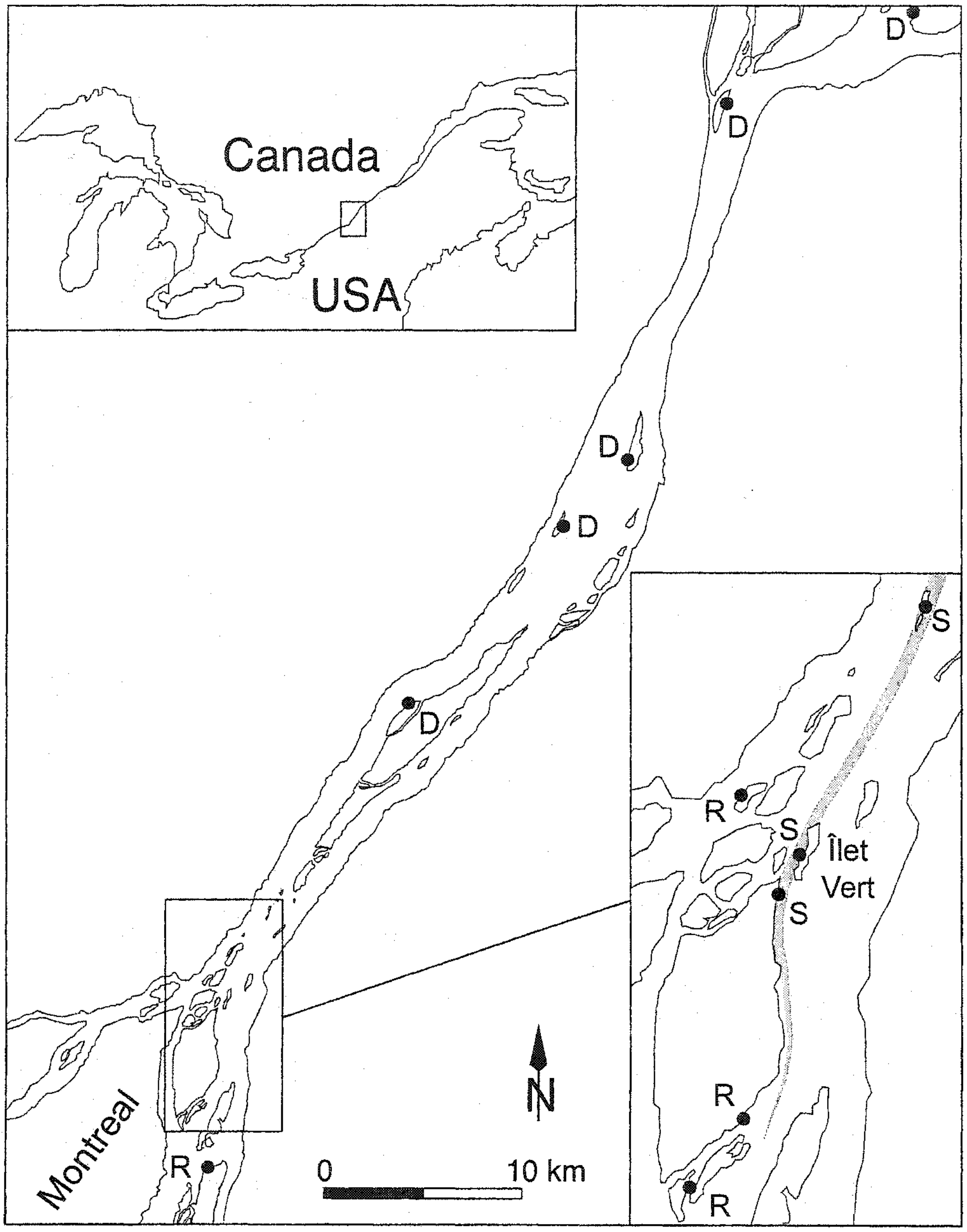
Sampling. Biota were collected on two visits to each site between July 17 and September 7, 2000. Fish were captured with a 40 m x 2 m seine (0.5 cm mesh). At least three seine hauls were taken on each visit, 50 to 100 m apart and successively upstream. One or two additional hauls were taken if low numbers of fish were obtained. The seined area was calculated from the shape of the deployed net (mean area/haul=320 m^2). Five to ten individuals of each species per visit (or as many as were available) were sacrificed and frozen for gut content analysis. All other fish were measured before release, and their wet weights were calculated using length-weight relationships derived from sacrificed fish. Gut contents were quantified as volume percent. Invertebrates for stable isotope analysis (chironomid larvae, trichopteran larvae and amphipods) were collected on each visit from grab samples of macrophytes and sediment which were sorted within a few hours of collection.

In order to establish a non-SDPOM endmember for stable isotope analysis of diet, we sampled an additional site exposed only to dissolved nutrients in the sewage. Benthic invertebrates were sampled on August 4 from a small bay at Îlet Vert, 4.5 km from the outfall. Water flowing through this site had passed through a long, dense macrophyte bed, and so we assumed that most of the SDPOM had been removed by interception and sedimentation (Sand-Jensen and Mebus 1996; Vermaat et al. 2000). We used this sample to estimate the isotopic signature of the non-SDPOM diet growing on sewage-derived dissolved nutrients. $\delta^{15}N$ of consumers at sites not exposed to the plume were all higher than these values, so this is a conservative assumption with respect to SDPOM assimilation.

Sewage-derived particulate matter was collected at the wastewater treatment plant on June 27, July 21, and August 11, 2000. Non-sewage suspended particulate matter was collected in the two water masses adjacent to the plume 8 times between 24 July and 7 September, 2000. Particulate matter was collected on precombusted Whatman GF/C filters and stored at -20°C until processing.

Stable isotope analysis. Invertebrates for stable isotope analysis were held alive for a few hours to allow gut clearance, stored at -20°C and subsequently dried for 48 hours at 70°C. Whole invertebrates (5-10 per species) were

Figure 1. Location of study sites on the St. Lawrence River (R: reference; S: sewage-exposed; D: downstream, unknown exposure). Shaded area in expanded inset is approximate location of Montreal's sewage plume.



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pulverized and subsampled for analysis. Particulate matter was recovered by scraping the surface of the glass-fibre filter after drying. Stable isotope ratios of carbon and nitrogen were determined on a mass spectrometer at the G.G. Hatch Isotope Laboratory, University of Ottawa.

Stable isotope signatures of consumers from Îlet Vert were used to infer the signature of the non-SDPOM diet at all sewage-exposed sites. The extent of sewage assimilation was then calculated for each taxon collected at the sewage-exposed sites. $\delta^{13}C$ was highly variable among reference sites, so we used a model describing a mixture of $\delta\ ^{15}N$ from SDPOM and the inferred non-sewage diet:

$$\delta\ ^{15}N_{consumer} = P_S \bullet (\delta^{15}N_S + F_S) + (1 - P_S) \bullet (\delta^{15}N_{non\text{-}S} + F_{non\text{-}S})$$

where $\delta\ ^{15}N$ is the mean nitrogen isotopic ratio of the consumer, SDPOM endmember, or non-sewage endmember, P_S is the proportion of SDPOM in the diet of the consumer, and F is the trophic fractionation shift of primary consumers vs SDPOM and the non-sewage endmember. For the non-sewage endmember, we replaced the term $(\delta^{15}N_{non\text{-}S} + F_{non\text{-}S})$ with the mean isotopic signature of consumers at the plume-exposed reference site. The isotopic signature of SDPOM was measured directly.

We estimated F_S from the relationship between $\delta^{13}C$ and $\delta^{15}N$ for all primary consumers at the sewage-exposed sites. If there is no trophic fractionation of carbon (DeNiro and Epstein 1978; France and Peters 1997), then extrapolating this relationship to the $\delta^{13}C$ of SDPOM provides an estimate of the $\delta^{15}N$ signature of a consumer eating 100% SDPOM. The difference between this consumer's $\delta^{15}N$ and that of SDPOM is F_S.

Secondary production. We estimated secondary production for each fish species at each site using growth increment summation (GIS) and instantaneous growth rate (IGR) methods (Rigler and Downing 1984). All fish weights were first corrected to a standard date to account for differences in sampling date among sites, by the following method. Each fish was assigned to an age class based on inspection of size-frequency distributions of pooled data for each species. Linear regression was used to describe the relationship between log weight and date for each age class of each species. The slope of this line was then used to project the weight of each individual fish in that age class backward or forward to August 1, removing any bias toward larger fish at sites that were sampled later in the season.

Growth increments between age classes were summed according to:

$$P_{GIS} = N_0 \bullet W_0 + \Sigma\, [((N_{i-1} + N_i)/2) \bullet (W_i - W_{i-1})]$$

where P is secondary production, N_i is the density of individuals in age class i (mean of two visits), W_i is the mean midsummer (Aug 1) weight of individuals in age class i, and the summed term is calculated for i = 1 to the oldest fish observed. This method estimates the total biomass added to each age class over the previous year by linear interpolation of N between adjacent age classes. In situations where 0+ fish are undersampled, this interpolation will slightly underestimate production of 1+ fish. When no members of an age class were captured at a site, the mean age class weight was replaced with the mean for that species at all other sites.

Instantaneous growth was summed according to:

$$P_{IGR} = \Sigma\, N_i \bullet W_i \bullet (10^{G_i} - 1)$$

where G_i is the slope of an age- and species-specific regression between log weight and date, calculated using data for age class i from all sites. This method estimates the biomass added to each age class on a single day (August 1). Because we could not calculate site-specific growth rates, variation in P_{IGR} only reflects variation among sites in total biomass and in the distribution of that biomass among age classes.

Total production of benthivorous fish biomass was calculated by multiplying the biomass of each age class of each species by the proportion of its diet comprising benthic invertebrates, then summing these products over all age classes of all species. Total production of piscivores was calculated in a similar manner. Total production of benthic invertebrates was back-calculated from fish production (Johnson et al. 1998). We assumed conversion efficiencies of 10% for benthivorous fish and 15% for piscivorous fish, reflecting differences in assimilation efficiency (1 - fecal and urinary losses) and growth efficiency (growth/consumption) between trophic levels (Sherwood et al. 2000; Trudel et al. 2001; Pazzia 2001).

Analysis of covariance (ANCOVA) was used to test for effects of weed cover (continuous), sewage exposure (categorical), and their interaction on the observed biomass density and estimated secondary production of each trophic level. Production estimates were log transformed to stabilize residual variance. Sewage-exposed and reference sites were analyzed separately by linear regression against weed cover if a significant main effect of sewage exposure was detected. The difference between these regression equations was used to describe the increase in biomass or production with sewage subsidy.

Pathways of enhanced production. Enhanced production of benthic invertebrates at the sewage-exposed sites is via both particulate (SDPOM) and dissolved (N, P and DOM) nutrients in the sewage effluent. To assess the relative importance of these two pathways, we calculated the fraction (A) of excess production at sewage-exposed sites that could be attributed to assimilation of SDPOM:

$$A_{SDPOM} = P_{SEW} \bullet D_{SDPOM} / (P_{SEW} - P_{REF})$$

where P is production of benthic invertebrates at a sewage-exposed (SEW) or reference (REF) site and D_{SDPOM} is the mean fraction of SDPOM in the diets of these invertebrates estimated from $\delta^{15}N$. Production values were calculated from the regression equations relating P to weed cover. The relative importance of inorganic and organic enrichment varied with weed cover, so we also calculated a weighted average for the entire plume area over our 10 km study reach.

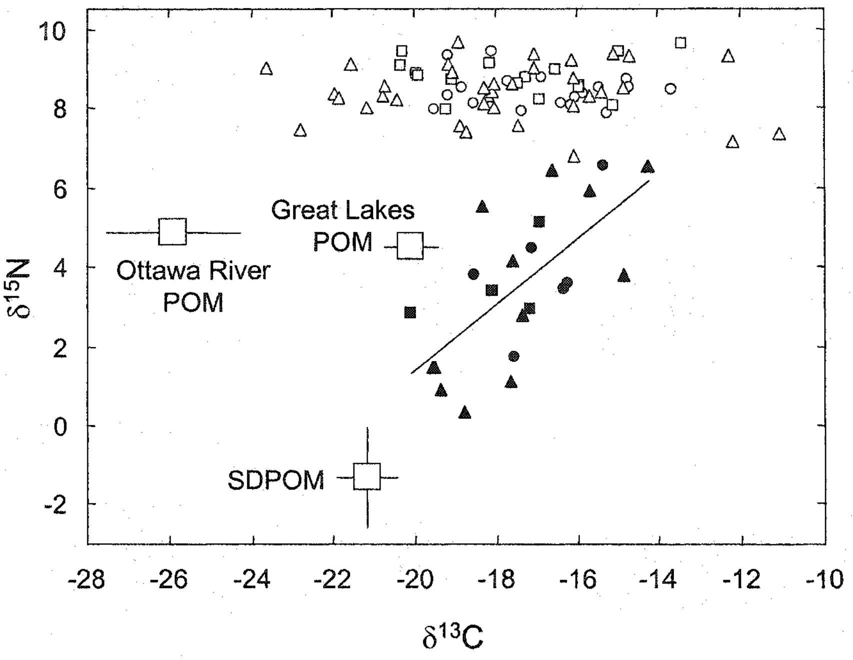
Fluxes of sewage nutrients. The total flux of SDPOM into the littoral foodweb of the St. Lawrence River was calculated as the product of area of littoral zone in the sewage plume, areal production of benthic invertebrates, and the proportion of that production which was based on sewage (D_{SDPOM}), divided by the efficiency with which SDPOM is converted into invertebrate biomass. The area of littoral zone in the plume was estimated using the 2.5 m depth contour (Hudon 1997) on hydrographic charts. We have no evidence that the plume intersects any islands beyond those sampled, so our analysis was constrained to the 10 km reach immediately downstream of the outfall. Conversion efficiency for benthic invertebrates was assumed to be 2%, similar to values observed for invertebrates consuming detritus (Benke 1996).

Results

Stable isotope analysis. $\delta^{13}C$ of primary consumers was highly variable within and among reference sites (-17.6 ± 2.6‰; Fig. 2), whereas $\delta^{15}N$ was much less variable (+8.6 ± 0.7‰). The signatures of all primary consumer taxa at reference sites covered similar ranges, indicating a common diet with $\delta^{13}C$ that varied among sites between -23.6‰ and -11.1‰, and a constant $\delta^{15}N$ of approximately +6.5‰.

Primary consumers at Îlet Vert also varied more in $\delta^{13}C$ (-15.4±1.2‰) than in $\delta^{15}N$ (+6.5±0.04‰). We assumed that the mean -2‰ shift in $\delta^{15}N$ at Îlet Vert versus reference sites was due to epiphytic uptake of dissolved inorganic

Figure 2. $\delta^{15}N$ vs. $\delta^{13}C$ of benthic primary consumers (circles: Amphipoda; squares: Trichoptera; triangles: Chironomidae) at sewage-exposed (closed symbols), reference and downstream (open symbols) sites on the St. Lawrence River. Particulate organic matter (open boxes, ± 1 SD) was collected from the MUC wastewater treatment plant (SDPOM), and from sites upstream of the outfall in the Great Lakes and Ottawa River water masses.

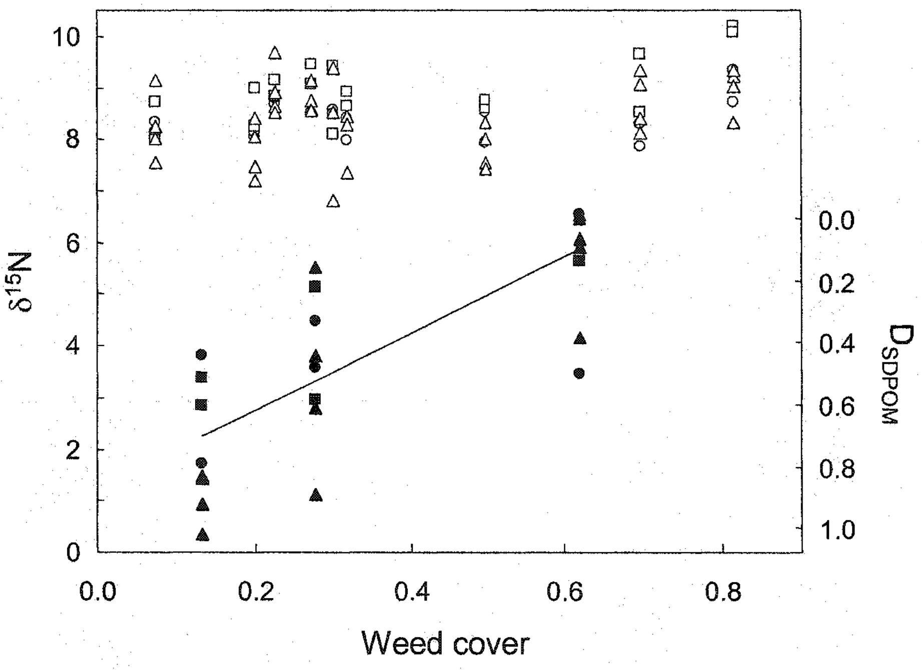

Great Lakes
POM
Ottawa River
POM
SDPOM
$\delta^{15}N$
$\delta^{13}C$
10
8
6
4
2
0
-2
-28
-26
-24
-22
-20
-18
-16
-14
-12
-10

nitrogen in the wastewater, and that greater shifts in consumer $\delta^{15}N$ indicated assimilation of SDPOM. Suspended particulate matter was relatively isotopically light, with $\delta^{13}C$ of –25.9 and –20.1‰ in the brown and green waters, respectively, and $\delta^{15}N$ of about +4‰ in both waters. SDPOM was within the range of the non-sewage sites in $\delta^{13}C$ (-21.2 ± 0.74‰), but was substantially lighter in $\delta^{15}N$ than the inferred diet of primary consumers at Îlet Vert (-1.3 ± 1.3‰, a 7.8‰ difference).

Isotopic signatures of primary consumers at the three sewage-exposed sites were shifted toward that of SDPOM. Regression of $\delta^{15}N$ versus $\delta^{13}C$ of sewage-exposed primary consumers was highly significant (r^2=0.45; $F_{1,20}$=16.6; p=0.0006); the regression equation ($\delta^{15}N = 0.82 \bullet \delta^{13}C + 17.8‰$), solved for the $\delta^{13}C$ of SDPOM, indicated a trophic fractionation value of +1.8‰. The mean fraction of SDPOM in the diets of primary consumers at these three sites, inferred from observed shifts in $\delta^{15}N$, decreased from 0.78 to 0.36 with increasing percent weed cover at the site (Fig. 3; r^2=0.62; $F_{1,24}$=39; p=0.000002). No shift in $\delta^{15}N$ was observed for any other site.

Consumer biomass densities. A total of 19,404 fish were captured, >95% of which were age 0+ to 1+. Benthivorous species included johnny darter (*Etheostoma nigrum)*, logperch (*Percina caprodes),* pumpkinseed (*Lepomis gibbosus),* rock bass (*Ambloplites rupestris)*, troutperch (*Percopsis omiscomaycus)*, banded killifish (*Fundulus diaphanus),* yellow perch (*Perca flavescens)*, smallmouth bass (*Micropterus dolomieui)*, largemouth bass (*Micropterus salmoides*), spottail shiner (*Notropis hudsonius)*, emerald shiner (*Notropis atherinoides)*, golden shiner (*Notemigonus crysoleucas),* blacknose shiner (*Notropis heterolepis*) , white sucker (*Catastomus commersoni)*, silver redhorse (*Moxostoma anisurum)*, and brown bullhead (*Ictalurus nebulosus*). Piscivores were northern pike (*Esox lucius)*, chain pickerel (*Esox niger*), muskellunge (*Esox masquinongy*), and yellow walleye (*Stizostedeon vitreum vitreum)*.

Figure 3. Effect of submerged macrophyte cover on the dietary importance of sewage-derived particulate organic matter (D_{SDPOM}), inferred from $\delta^{15}N$ of primary consumers (symbols as in Fig. 2).



10
8
6
4
2
0
$\delta^{15}N$
0.0
0.2
0.4
0.6
0.8
1.0
D_{SDPOM}
0.0
0.2
0.4
0.6
0.8
Weed cover

ANCOVA (Fig. 4) revealed that mean summer biomass densities (B) of piscivores were strongly correlated with percent weed cover ($F_{1,8}$=13.1; p=0.0068). There was a main effect of sewage exposure ($F_{1,8}$=9.8; p=0.014) but no significant interaction, indicating a constant ratio of B_{SEW}/B_{REF} across the gradient of weed cover. Benthivorous fish biomass densities were not well correlated with weed cover, but were significantly higher at sewage-exposed sites ($F_{1,10}$=5.9; p=0.036). Equations describing the relationships between fish biomass density and weed cover are given in Table 1.

Secondary production. Patterns of estimated secondary production similar to those for biomass density were obtained using both estimation methods (Fig. 4; correlation between P_{GIS} and P_{IGR}: r^2=0.89; $F_{1,159}$=1332; p<0.00001). Both methods indicated a positive correlation of piscivore production with weed cover (log P_{GIS}: $F_{1,8}$=16.6; p=0.0036; log P_{IGR}: $F_{1,8}$=9.0; p=0.017), and a strong increase in production with sewage subsidy (log P_{GIS}: $F_{1,8}$=6.1; p=0.039; log P_{IGR}: $F_{1,8}$=8.5; p=0.019). There was no significant main effect of weed cover on benthivore production estimated using either method, but ANCOVA did indicate a main effect of sewage exposure for the daily (IGR) estimate (F=9.9; p=0.010). In no case was there a significant interaction between the independent variables. Equations describing the relationships between fish production and weed cover are given in Table 1.

ANCOVA revealed no effect of sewage exposure or weed cover on the log P vs log B relationship. For all species, log P was strongly correlated with log B among sites ($F_{1,303}$=3670; p<0.00001; Fig. 6), although this relationship differed between methods (GIS and IGR) in both slope ($F_{1,303}$=31.7; p<0.00001) and intercept ($F_{1,303}$=117; p<0.00001). There was also a main effect of species ($F_{15,303}$=5.0; p<0.00001), but post-hoc multiple comparisons revealed that this was restricted to a difference between the three species with highest intercepts (alewife, rock bass, walleye) and the two with lowest intercepts (emerald and

Figure 4. Fish biomass (B) and production (P) at sewage-exposed (closed circles), reference and downstream (open circles) sites on the St. Lawrence River, as a function of the fraction of substrate covered by submerged macrophytes. Production was estimated by growth increment summation (GIS) and instantaneous growth rate (IGR) methods.

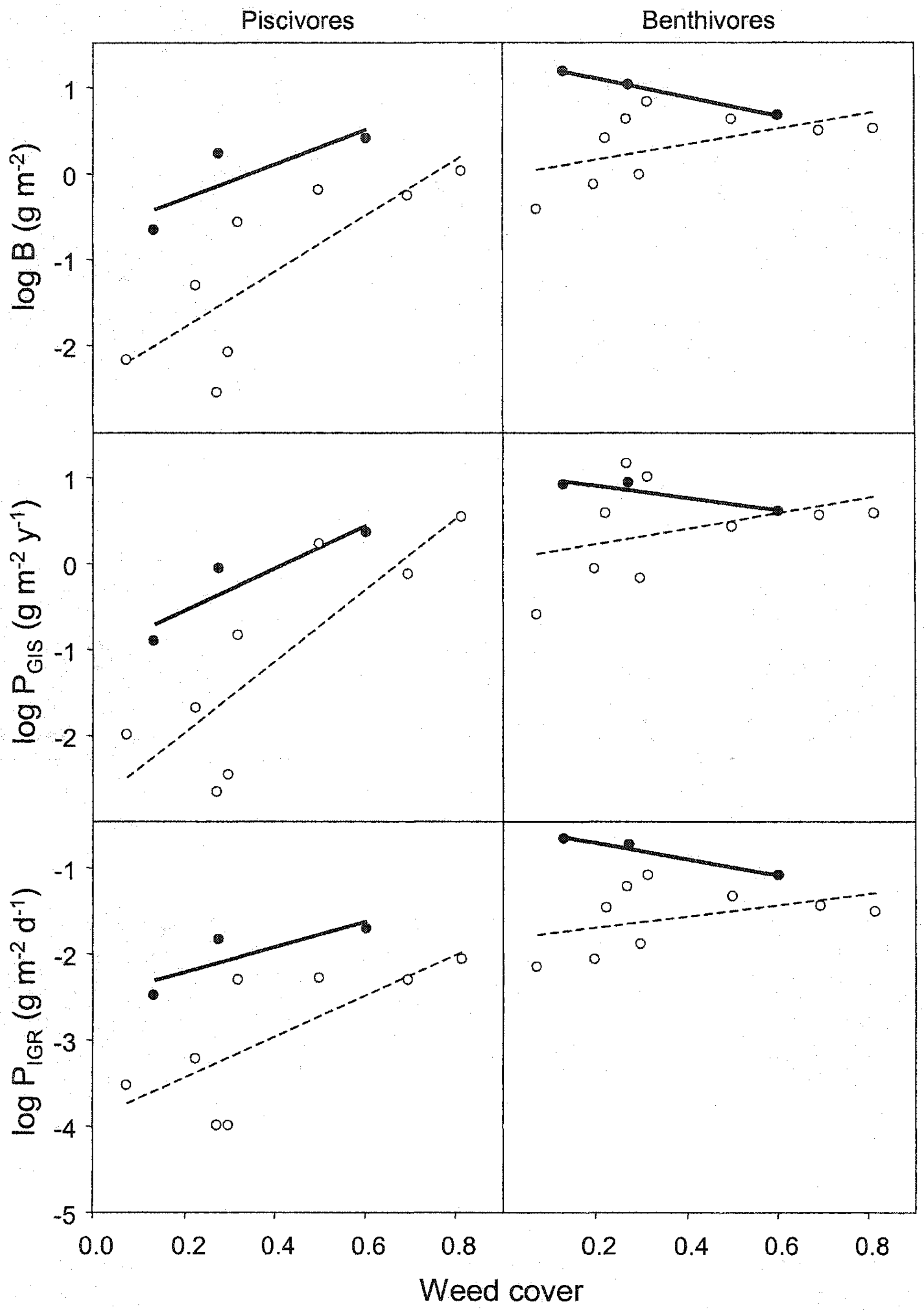

Piscivores
Benthivores
log B (g m^{-2})
log P_{GIS} (g m^{-2} y^{-1})
log P_{IGR} (g m^{-2} d^{-1})
1
0
-1
-2
1
0
-1
-2
-1
-2
-3
-4
-5
0.0
0.2
0.4
0.6
0.8
0.2
0.4
0.6
0.8
Weed cover

Table 1. Regression equations describing biomass (B, g/m^2) and production estimated by growth increment summation (P_{GIS}, g m^{-2} y^{-1}) and instantaneous growth rate (P_{IGR}, g m^{-2} d^{-1}) methods. WC is the fraction of site area covered by macrophytes at reference (Ref, n=9) and sewage-exposed (Sew, n=3) sites in the St. Lawrence River.

Trophic level	Sites	Equation	r^2	SEE
Piscivores	Ref	$\log B = -2.45 + 3.25 \bullet WC$	0.64	0.665
		$\log P_{GIS} = -2.79 + 4.12 \bullet WC$	0.68	0.757
		$\log P_{IGR} = -3.92 + 2.39 \bullet WC$	0.53	0.602
	Sew	$\log B = -0.68 + 1.95 \bullet WC$	0.68	0.455
		$\log P_{GIS} = -1.05 + 2.47 \bullet WC$	0.85	0.352
		$\log P_{IGR} = -2.52 + 1.45 \bullet WC$	0.71	0.320
Benthivores	Ref	$\log B = -0.04 + 0.91 \bullet WC$	0.29	0.370
		$\log P_{GIS} = 0.03 + 0.88 \bullet WC$	0.14	0.560
		$\log P_{IGR} = -1.85 + 0.65 \bullet WC$	0.18	0.360
	Sew	$\log B = 1.29 - 1.09 \bullet WC$	0.99	0.007
		$\log P_{GIS} = 1.03 - 0.71 \bullet WC$	0.86	0.096
		$\log P_{IGR} = -0.55 - 0.95 \bullet WC$	0.98	0.044

blacknose shiners). None of the species-specific log P vs log B relationships had slopes significantly different from one (Table 2). Annual P/B (GIS) ranged from 0.26 to 1.4 (mean 0.81) and daily P/B (IGR) from 0.001 to 0.056 (mean 0.019).

Pathways of enhanced production. Estimates of total annual invertebrate production at the sewage-exposed sites were between 14 and 160 g m^{-2} y^{-1} (Table 3). The highest value was calculated from piscivore production at high weed cover, where the $\delta^{15}N$ estimate of dietary sewage fraction was lowest. Therefore, annual invertebrate production based on assimilation of SDPOM varied less, from 11 to 65 g m^{-2} y^{-1}. Daily invertebrate production estimates at the sewage-exposed sites were between 0.34 and 2.0 g m^{-2} d^{-1}, and daily production based on SDPOM between 0.26 and 0.73 g m^{-2} d^{-1}.

Total excess production (all invertebrate production at sewage-exposed sites in excess of that at reference sites of similar weed cover) was between 5 and 130 g m^{-2} y^{-1}, and between 0.32 and 1.9 g m^{-2} d^{-1} (Table 3), representing up to 30-fold increases with sewage enrichment. On average, about 70% of excess invertebrate production in the study reach was based on assimilation of SDPOM (Table 4; Fig. 6).

Fluxes of sewage nutrients. Estimates of the areal flux of SDPOM into the benthic foodweb ranged from 550 to 3300 g m^{-2} y^{-1}, and from 13 to 79 g m^{-2} d^{-1}, depending on the level of weed cover and on the trophic level used to make the estimate. Averaged across trophic levels and scaled up to 1.23 km^2 of littoral zone in the 10 km reach downstream of the wastewater outfall, this represents 2100 tonnes of SDPOM per year being consumed by invertebrates, or 43 tonnes per day. This flux accounts for only 2% of the total annual discharge of SDPOM into the St. Lawrence, but 77% of the daily discharge in summer.

Estimates of excess primary production at sewage-exposed sites (that fraction of excess production not attributable to SDPOM) ranged from 0 to 3700

Table 2. Intercepts (a) and slopes (b) of taxon-specific relationships between log production and log biomass among littoral sites in the St. Lawrence River. Annual production (P) was estimated by growth increment summation (GIS) and daily production by instantaneous growth rate (IGR) methods.

		log P_{GIS} (annual)			log P_{IGR} (daily)		
Species	n	a	b	P/B	a	b	P/B
alewife	8	-0.341	1.06	0.52	-1.306	1.06	0.056
basses[a]	12	-0.480	1.15	0.59	-1.962	1.22	0.025
blacknose shiner	10	-0.578	1.05	0.26	-1.893	1.09	0.014
johnny darter	12	-0.015	1.13	1.30	-1.901	1.00	0.012
emerald shiner	12	-0.450	1.04	0.41	-1.829	0.98	0.014
golden shiner	8	-0.388	1.19	0.82	-1.756	1.00	0.018
banded killifish	8	-0.214	0.98	0.59	-2.053	0.97	0.008
logperch	11	-0.161	1.16	1.11	-1.651	0.91	0.017
yellow perch	12	-0.531	1.20	1.02	-2.019	0.95	0.007
pikes[a]	10	-0.259	1.11	0.95	-1.514	0.81	0.012
pumpkinseed	8	-0.615	1.24	0.57	-1.789	1.00	0.016
rockbass	11	-0.140	1.24	1.42	-1.584	0.89	0.019
spottail shiner	12	-0.320	1.07	0.60	-1.800	1.04	0.018
suckers[a]	12	0.229	0.94	1.15	-1.923	1.00	0.012
troutperch	9	-0.286	1.18	0.74	-1.842	1.03	0.015
yellow walleye	6	0.197	0.82	0.93	-1.060	0.72	0.038
mean P/B				0.81			0.019

[a] Species observed at fewer than 6 sites were combined with similar species: basses are largemouth and smallmouth bass; pikes are northern pike, muskellunge and chain pickerel; suckers are white sucker and silver redhorse.

Table 3. Production of benthic invertebrates (P) and the amount of sewage-derived particulate organic matter (SDPOM) consumed to support this production at three sewage-exposed sites in the St. Lawrence River. D_{SDPOM} is the dietary fraction of SDPOM estimated from $\delta^{15}N$ and A is the area (km^2) of sewage-exposed littoral zone within the 10 km study reach at each level of weed cover (WC).

			Benthic invertebrate P[a]				SDPOM consumed			
			GIS ($g\ m^{-2}\ y^{-1}$)		IGR ($g\ m^{-2}\ d^{-1}$)		GIS ($t\ y^{-1}$)		IGR ($t\ d^{-1}$)	
WC	D_{SDPOM}	A	pisc	benth	pisc	benth	pisc	benth	pisc	benth
0.15	0.78	0.61	14	84	0.34	2.0	340	2000	8.1	48
0.30	0.50	0.42	32	66	0.55	1.5	340	700	5.8	16
0.60	0.36	0.20	160	41	1.4	0.79	600	150	5.2	2.9
Total[b]		1.23					1300	2800	19	67

[a] Invertebrate P was back-calculated from fish production estimated by growth increment summation (GIS, $g\ m^{-2}\ y^{-1}$) and instantaneous growth rate (IGR, $g\ m^{-2}\ d^{-1}$) methods for piscivores (pisc) and benthivores (benth).

[b] Total littoral zone area in the plume and total SDPOM consumption over the 10 km study reach.

Table 4. Production of benthic invertebrates (P) in excess of that expected for reference sites of similar weed cover (WC) and the fraction of excess invertebrate production at these sites which is based on consumption of sewage-derived particulate organic matter (SDPOM).

	Excess benthic invertebrate P[a]				Fraction of excess P based on SDPOM				
	GIS ($\text{g m}^{-2}\text{ y}^{-1}$)		IGR ($\text{g m}^{-2}\text{ d}^{-1}$)		GIS		IGR		
WC	pisc	benth	pisc	benth	pisc	benth	pisc	benth	mean
0.15	14	70	0.32	1.9	0.81	0.94	0.82	0.86	0.86
0.30	30	47	0.51	1.3	0.53	0.71	0.54	0.59	0.59
0.60	130	5	1.2	0.44	0.45	0.00	0.42	0.65	0.38
Mean[b]					0.65	0.71	0.66	0.73	0.69

[a] Invertebrate P was back-calculated from fish production estimated by growth increment summation (GIS, $\text{g m}^{-2}\text{ y}^{-1}$) and instantaneous growth rate (IGR, $\text{g m}^{-2}\text{ d}^{-1}$) methods for piscivores (pisc) and benthivores (benth).

[b] Mean values, weighted by the area of littoral zone in the 10 km study reach at each level of weed cover (see Table 3 for areas).

g m^{-2} y^{-1}, and from 2.8 to 35 g m^{-2} d^{-1}, depending on the level of weed cover and on the trophic level used to make the estimate. Assuming that these primary producers contain 2% phosphorus, this represents an uptake in the study reach of 15 tonnes of P per year, or 0.34 tonnes of P per day. This flux accounts for only 6% of the total annual discharge of dissolved P, but 40% of the daily discharge in summer.

Discussion

Studies of eutrophication in freshwater systems have focused almost exclusively on nuisance algal blooms stimulated by inorganic nutrients. Previous work on organic enrichment has usually been in systems so heavily eutrophied that sediment or water column anoxia was a dominant environmental factor. What work has been done on modest levels of organic enrichment has largely been in marine systems, and most has considered only the response of benthic macroinvertebrate community structure. The present study provides the opportunity to develop general ideas about higher-level ecological consequences of enrichment, and relates these consequences to characteristics of the receiving system.

Exploitation of sewage resources: Stable isotope analysis enabled us to identify three sites which were consistently exposed to Montreal's sewage plume, where previous studies have had to rely on instantaneous measurements of exposure. $\delta^{13}C$ is the isotopic ratio most commonly employed in dietary studies, but we found stronger (almost 8‰) and more consistent separation between endmembers in $\delta^{15}N$ (see also deBruyn and Rasmussen *in press*). Also, $\delta^{13}C$ showed wide variation among reference sites whereas $\delta^{15}N$ did not. This was partly due to differences in water chemistry among sites (the DIC pool of Great Lakes water is about 10‰ enriched in ^{13}C over other large rivers like the Ottawa; Leggett et al. 1999; Yang et al. 1996) but may also reflect local flow regimes: low current can reduce photosynthetic discrimination against ^{13}C by enhancing the formation of a CO_2-depleted boundary layer at the surface of algal cells (Finlay et al. 1999). Algal $\delta^{15}N$ is influenced by human population density (Cabana and Rasmussen 1996) but varies little with local flow regime (MacLeod and Barton 1998).

The range of invertebrate production estimated at our reference sites was similar to values reported from other systems and consistent with invertebrate biomass in the St. Lawrence. Solving the benthivore equations in Table 1 for production at zero and 100% weed cover (assuming 10% conversion of invertebrate into fish biomass) produces annual invertebrate P estimates of 11 and 81 g m^{-2} y^{-1}, respectively. Benke et al. (1984) found a similar range of areal production rates for a subtropical blackwater river (10 g m^{-2} y^{-1} on sand or mud, 60-70 g m^{-2} y^{-1} on snags). Densities of invertebrates >0.5 mm at our sites range from about 2 g m^{-2} on bare sediment to about 4 g m^{-2} in dense weedbeds (deBruyn and Rasmussen, unpublished data). Annual P/B estimates were therefore on the order of 5 to 20, similar to the 5-10 range reported by Benke et al. (1984) for univoltine insects and the mean annual P/B of 5.3 for 164 populations of lake invertebrates (Plante and Downing 1989). It is important to note also that our invertebrate production estimates represent a minimum value, as they do not include the production of emerging adults or resting stages.

Invertebrate production at the sewage-exposed sites (up to 180 g m^{-2} y^{-1}) was very high relative to our reference sites and values reported for other systems, but not unreasonable given the extent of enrichment. Benthic invertebrate densities were 2- to 4-fold higher in a sewage-exposed reach of a Michigan stream (Ellis and Gowing 1957) and experimental additions of grain or soybean have produced 1.5- to 2.9-fold increases in total invertebrate biomass in mid-sized rivers (Mundie et al. 1983; Johnston et al. 1990). These studies only reported increases in standing stock of invertebrates; if growth rates also increase, the enhancement of secondary production may be much higher. King and Ball (1967) reported faster growth and higher densities of primary consumers downstream of a sewage outfall, and could attribute less than 10% of secondary production to autochthonous production.

Response of higher trophic levels: Our estimates of total fish production at low weed cover (1.4 g m^{-2} y^{-1} at 15% WC) are similar to those measured in lakes of similar nutrient concentrations (Downing et al. 1990). At higher levels of weed cover, however, total fish production was nearly triple this (4.0 g m^{-2} y^{-1} at 60% WC). Epiphytic primary production is readily transferred to higher consumers, and densely vegetated sites support a disproportionately large fraction of secondary production in rivers (Thorp and Delong 1994).

The absolute increase in piscivorous fish biomass at sewage-exposed sites was greatest at high weed cover. This is because the most abundant piscivores in this system are esocid fishes (pikes), which are ambush predators typically associated with macrophyte beds and woody debris. We observed a good relationship between piscivore density and macrophyte cover among our reference sites (Fig. 4). Relatively bare sites provide poor habitat for this type of predator, irrespective of the density of prey fish. The true degree of enhancement at bare sites is probably better reflected in the increase in density of benthivorous fishes, many of which do not share this habitat requirement.

Benthivorous fishes were most strongly enhanced at the relatively bare site, although the nonlinear relationship between biomass and weed cover at reference sites prevented ANCOVA from detecting this interaction. Benthivore biomass at the reference sites increased up to about 30% weed cover, then remained approximately constant at more vegetated sites. Interestingly, this is about the level of weed cover beyond which piscivore densities started to increase. It may be that at bare sites piscivores are ineffective and benthivore biomass is controlled by resources (bottom up), whereas at weedy sites piscivores are able to respond to increases in prey density and benthivore biomass is controlled by exploitation (top down).

Patterns of fish production among sites were similar to patterns of biomass because we were able to detect effects of weed cover and sewage exposure on fish density, but not on fish growth. Previous work has reported increases in gut fullness (Ellis and Gowing 1957), condition (Ellis and Gowing 1957) and growth rate (Katz and Howard 1955; Eggers et al. 1978; Johnston et al. 1990) of fishes in sewage-enriched streams. The methods we used to estimate production were not well suited to detecting differences in growth rates, however. We had to pool all twelve sites to estimate instantaneous growth rates (IGR), and this had the effect of averaging growth across sites. Thus, IGR only reflected differences among sites in total biomass and the distribution of that biomass among age classes. Growth increment summation (GIS) would only reveal differences in growth rate among sites if individuals returned to the same site each year. Otherwise, GIS would tend to underestimate any site-specific increase in growth rate, as overall faster growth would tend to reduce the observed increment between older (slower growing) and younger (faster growing) age classes. We found no effect of weed cover or sewage exposure on the P/B relationship for any species using either production estimate. Either fish growth rates are independent of basal productivity or these species do not display interannual site fidelity.

The enhancement of secondary production at sewage-exposed sites could not be attributed to one or a few species that were disproportionately productive, because P/B varied little among species (Table 2). Post-hoc multiple comparisons identified a difference between the three fastest growing species and the two slowest, but this difference was not consistent between production estimation methods (Fig. 5). Downing et al. (1990) report a mean annual fish community P/B of 0.76, similar to our mean P_{GIS}/B of 0.81.

Pathways of enhanced production: Stable isotope ratios of primary consumers at the reference sites indicated that the taxa we sampled were feeding primarily on local benthic production throughout this reach (consistent with the

Figure 5. Production vs. biomass among 12 littoral sites in the St. Lawrence River. Labelled species are those with significant differences in elevation indicated by ANCOVA and post-hoc multiple comparisons. Production was estimated by growth increment summation (GIS) and instantaneous growth rate (IGR) methods.

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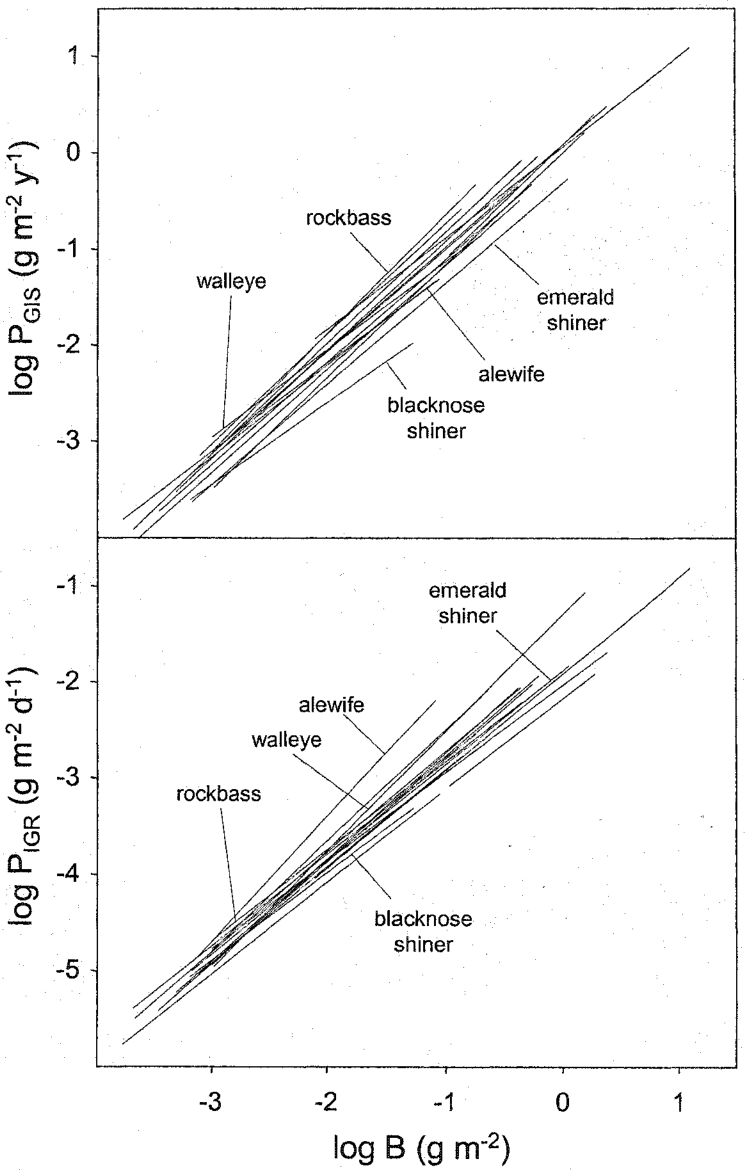


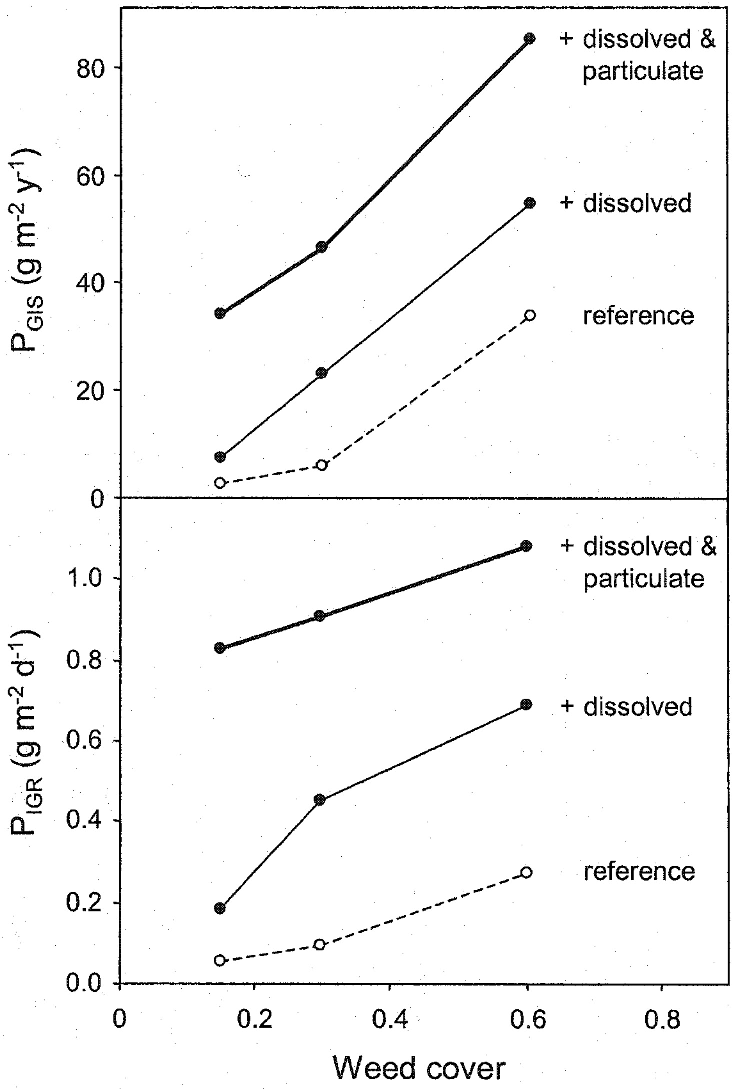
1
0
-1
-2
-3
log P_{GIS} (g m^{-2} y^{-1})
rockbass
walleye
emerald shiner
alewife
blacknose shiner
-1
-2
-3
-4
-5
log P_{IGR} (g m^{-2} d^{-1})
emerald shiner
alewife
walleye
rockbass
blacknose shiner
-3
-2
-1
0
1
log B (g m^{-2})

prediction of Thorp and Delong 1994). The inferred diet of these consumers had $\delta^{13}C$ ranging from –24 to –11‰ and $\delta^{15}N$ of about +6 to +8‰, too heavy in both isotopes to include much POM from either water mass (Fig. 2). Benthic production, however, is typically enriched about 7‰ in ^{13}C over pelagic production because boundary-layer CO_2 limitation reduces photosynthetic fractionation (France 1995; Hecky and Hesslein 1995; Vander Zanden and Rasmussen 1999).

At the three sewage-exposed sites, $\delta^{15}N$ provided an estimate of the dietary fraction of SDPOM (D_{SDPOM}) in primary consumers. Using $\delta^{15}N$ to identify diet requires information on trophic fractionation for both diet endmembers or the assumption that these are equal. We were able to infer the trophic fractionation shift by extrapolating our dietary mixing model. This sort of estimate is unavoidably imprecise, but the mean value (+1.8‰) matches well with what other authors have found for primary consumers fed N-rich diets (Adams and Sterner 2000). We also found that D_{SDPOM} varied inversely with weed cover (Fig. 3), reflecting a relatively greater contribution of autochthonous production at densely vegetated sites (Table 4; Fig. 6).

We observed an overall 12.5-fold increase in secondary production in the 10 km reach downstream of Montreal's sewage outfall, supported by a combination of particulate and dissolved nutrient enrichment. The absolute contribution of particulate nutrients was approximately equal across a range of weed cover on an annual basis, comprising an annual flux of about 1.7 kg/m^2 of SDPOM into the foodweb in our study reach. This represented only a small fraction of the total annual discharge of SDPOM into the St. Lawrence (2%), but amounted to 77% of the daily discharge in summer. The biota of the littoral St. Lawrence very efficiently captures and assimilates SDPOM, but only for a few months in summer. This is consistent with a view of large rivers as heterotrophic systems, well suited to exploiting allochthonous inputs of labile organic matter.

Figure 6. Macroinvertebrate production at three sewage-exposed sites on the St. Lawrence River, estimated from annual (P_{GIS}) and daily (P_{IGR}) fish production (from equations in Table 1; see text for details). Bold line (closed circles) is total production at sewage-enriched sites, fine line (closed circles) is the portion of that production based on stimulation of local production by dissolved nutrients (estimated from $\delta^{15}N$). Dashed line (open circles) is baseline production expected at a reference site of similar weed cover.


+ dissolved &
particulate
+ dissolved
reference
P_{GIS} (g m^{-2} y^{-1})
0
20
40
60
80
+ dissolved &
particulate
+ dissolved
reference
P_{IGR} (g m^{-2} d^{-1})
0.0
0.2
0.4
0.6
0.8
1.0
0
0.2
0.4
0.6
0.8
Weed cover

The relative importance of dissolved nutrients, on the other hand, depended strongly on weed cover, ranging from 16% at a relatively bare site to 52% at the most densely vegetated site. The absolute flux of dissolved P into the foodweb in our study reach ranged from 3.4 to 37 g m^{-2} y^{-1}. This is also only a small fraction of the total annual discharge of P (6%), but it amounts to about 40% of the daily discharge in summer. As for particulate nutrients, the biota of the St. Lawrence very efficiently captures and assimilates dissolved nutrients, although this is greatest at sites with abundant macrophytes.

Thus, the overall increase in secondary production from sewage was enhanced by submerged macrophytes. The physical structure of the macrophytes greatly increased the surface area on which macroinvertebrates could access suspended particulates, but simultaneously acted as a barrier to water flow, diverting discharge around the site. As a consequence, weedy sites trapped and assimilated no more POM than relatively bare sites. A more important effect of macrophyte structure was to increase the illuminated surface area on which epiphytic biofilm could develop. This permitted a much greater capacity to trap dissolved phosphorus and stimulated the production of higher trophic levels nearly as much as did assimilation of POM.

The foodweb of the St. Lawrence was able to accommodate this large subsidy of particulate and dissolved nutrients because it is protected from the negative effects of nutrient enrichment by hydrodynamic forces. Net sediment accumulation is prevented by high current speeds, strong wave action, and a prodigious spring freshet (Carignan and Lorrain 2000). Water column oxygen depletion is prevented by strong vertical mixing (St. Lawrence Centre 1996). However, these protective forces may be weakened under the conditions of low discharge projected for the St. Lawrence in the next few decades. Global warming models predict a mean 40% reduction in flow, with minimum flow 60% below present mean levels (IJC 1993). Proposed diversions of water to the U.S. would also reduce flow. In addition, water level records since 1860 indicate that the last

25 years have been a period of extremely high flow for the St. Lawrence, and that this period is ending. Lower discharge favors an increase in the area colonized by macrophytes (Hudon 1997). According to the model we have outlined above, these changes should enhance the retention of both particulate and dissolved nutrients, focus enrichment effects in a smaller area, and increase the likelihood of negative effects such as sediment oxygen depletion. How this scenario plays out will provide an interesting test of our ideas.

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Connecting Statement

In the preceding chapter, I quantified the degree to which consumer production in the St. Lawrence River is enhanced by sewage nutrients and organic matter. I demonstrated that sewage represents a substantial subsidy of basal resources to the littoral foodweb, producing a greater than tenfold increase in secondary production over reference sites. In the next chapters, I explore some of the consequences of this enrichment for the structure and function of the receiving water community. First, I use body size distributions to show that sewage enrichment does not increase densities of all organisms equally. Large organisms become disproportionately abundant, reflecting the importance of consumer (top-down) control in the size structure of communities.

CHAPTER 3: ALTERED BODY SIZE DISTRIBUTIONS IN A LARGE RIVER FISH COMMUNITY ENRICHED BY SEWAGE

deBruyn, A.M.H., D.J. Marcogliese, and J.B. Rasmussen. Altered body size distributions in a large river fish community enriched by sewage. submitted to Canadian Journal of Fisheries and Aquatic Science

Abstract

The productivity of a habitat sets the upper bound of potential energy usage, and thus the maximum density of organisms at a given body size. Larger organisms have higher per capita energy requirements, and therefore achieve lower maximum densities. However, the effect of productivity on the density-body size relationship seems to depend on the approach taken to study this relationship. Furthermore, foodweb theory suggests more complex responses than the simple bottom-up control considered by previous work. We used two common approaches to study size distributions in a littoral fish community across a natural gradient of epiphytic primary production, and at sites enriched by primary-treated sewage. The two approaches provided complementary information on the ecological implications of body size. The upper bound of the interspecific density-body size relationship supported universal energetic constraints on the regional assemblage, but revealed substantial variation in size distributions at a local scale. Multivariate analysis of the modes composing the normalized biomass spectrum provided insight into the factors responsible for this local variation in size distributions. Only the largest organisms had higher densities at higher levels of productivity. Densities of smaller organisms were controlled by a combination of habitat characteristics and feeding interactions.

Introduction

Body size is arguably the most fundamental aspect of ecology, spanning more than 21 orders of magnitude. Size determines how an organism perceives its physical environment, and size scales with biological characteristics ranging from individual metabolic rate to species richness (Peters 1983). For more than 60 years, ecologists have identified statistical patterns in the size structure of communities that seemingly reflect the operation of general principles or natural laws. These empirical investigations have followed two parallel but rarely intersecting paths. Community ecologists have focused on the negative allometric scaling of population density among species, invoking energetic constraints to explain the upper limit of density possible for a species of a given body size. Contemporary work by a number of (aquatic) ecosystem ecologists has largely foregone taxonomic distinctions, considering how the total density of organisms is distributed along a spectrum of logarithmic size classes. These two parallel lines of investigation offer complementary insights into the factors that influence community size structure.

The interspecific relationship between population density and body size has been examined in a wide variety of taxonomic groups and in a few entire natural communities. However, there is little consensus regarding the form of the relationship or the mechanisms that generate it. Data are usually plotted on double log axes, where a linear relationship reflects an underlying power function. When a linear relation is observed, it often has an OLS (ordinary least squares regression) slope near -0.75. This is the inverse of the allometric scaling coefficient for per capita energy requirements (+0.75), and it has been suggested that energy consumption per population is therefore independent of body size, reflecting an underlying energetic constraint on population density (the "energetic equivalence rule"; Damuth 1987). Under the hypothesis that energetic constraints are most important to the most abundant species (those adjacent to the upper bound of the density-body size relationship), some authors have calculated the maximum density across log size classes, and expressed the allometric scaling of this value, the "upper-bound slope" (Brown and Maurer 1987; Lawton 1989; Blackburn et al. 1992, 1993; Blackburn and Lawton 1994; Marquet et al. 1995). Often, the relation between density and body size is approximately triangular (Brown and Maurer 1987; Gaston and Lawton 1988). Even if energy requirements set the upper bound of density, the effect of body size on energy acquisition and conversion processes favours medium-size species within major taxonomic groups at both ecological and evolutionary scales (Brown et al. 1993).

Marquet et al. (1995) noted that the energy available to a species is determined both by the basal productivity of its habitat and by the assemblage with which it must share this productivity. This suggests that perhaps energetic hypotheses are better addressed by the allometric scaling of total density, rather than density per species (Griffiths 1992). This has been the approach taken in aquatic ecology. The total density-body size relationship is commonly expressed as the normalized biomass spectrum (NBS), obtained by summing all biomass within $\log_2$ size classes, then normalizing these sums to the lower bound (= width) of the size interval. This calculation estimates the total density of individuals within each size class, irrespective of taxonomic identity. NBS slopes are commonly near -1.0, which reflects a roughly uniform distribution of biomass over logarithmically increasing size classes (Vidondo et al. 1997). This pattern has been interpreted to mean that size structure reflects the flow of energy and matter from small to large organisms in the pelagia (Borgmann 1997), although similar slopes are observed in the benthos, where most large organisms are microphagous (Rasmussen 1993).

Both approaches to the density-body size relationship rely heavily on energetic arguments, but the effect of varying productivity on this relationship is far from clear (Marquet et al. 1995; Blackburn and Lawton 1994). It is widely recognized that species' densities are influenced by a combination of resource availability and exploitation by predators (Power 1992; Hunter and Price 1992). Size-structured feeding relationships are common in aquatic systems (Mittelbach and Persson 1998), and this favours top-down influences on body size distributions in pelagic (Carpenter et al. 1996) and benthic (Blumenshine et al. 2000) communities. Changes in body size distributions with increasing productivity could in fact reflect cascading trophic interactions, with higher (large) predator densities in more productive systems controlling the density of smaller size classes. If body size corresponds roughly to trophic level, foodweb models with consumer control (e.g., Hairston et al. 1960; Oksanen et al. 1981) predict that increasing productivity will produce uneven increases in density across the size spectrum (Sprules 1988; Fig. 1).

Here we address the effect of productivity directly, and we compare the results obtained using the two alternative approaches outlined above. We studied size distributions in a littoral fish community across a natural gradient of epiphytic primary production, and by exploiting a large-scale natural experiment. The municipal wastewater treatment plant of Montreal, Quebec, has been discharging >450 tonnes of phosphorus and >90,000 tonnes of particulate organic matter annually into the St. Lawrence River since 1988 (Purenne 1998). High current speeds and strong vertical mixing prevent deoxygenation and net sedimentation in this reach of the river, so the primary effect of this discharge is sustained enrichment. This type of enrichment has been linked to enhanced production of benthic macroinvertebrates (Ellis and Gowing 1957; King and Ball 1967) and fish (Katz and Howard 1955; Eggers et al. 1978).

Methods

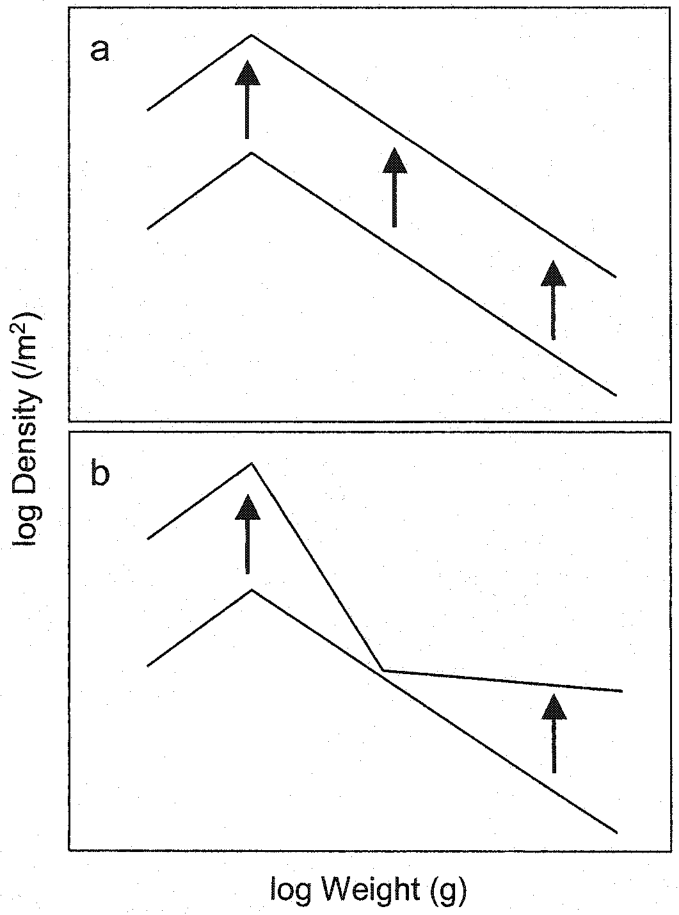
Study system. The St. Lawrence is a large, fast-flowing, temperate river. Nutrient levels are moderate (dissolved $P < 30$ μg/L; dissolved $N < 0.5$ mg/l) and pelagic productivity is low (median summer chlorophyll-*a* < 2.5 μg/L; Hudon and Sylvestre 1998). Flow rates are typically 2-3 m/s in the main channel, and net sedimentation of suspended material is restricted to the deepest areas outside the main channel. Permanent deposition is a small component of the suspended solids budget of this river (Carignan and Lorrain 2000).

The Montreal Urban Community (MUC) wastewater treatment plant is a primary treatment facility serving 1.8 million people on the Island of Montreal (Purenne 1998). This wastewater is treated to promote coagulation, passed through settling ponds, and discharged directly to the St. Lawrence River via an underwater pipe. Effluent is discharged at an average rate of $2\text{x}10^6$ m^3/d, with an average of approximately 100 mg/l (wet wt.) of suspended particulate matter, 0.5 mg/l total phosphorus, and 9 mg/l total nitrogen (Deschamps et al. 1998; Purenne 1998). On an annual basis, this discharge contributes 650 tonnes of phosphorus and $9\text{x}10^4$ tonnes of particulate matter to the weakly productive waters of the St. Lawrence River (Purenne 1998).

We sampled littoral fish from twelve sites downstream of the island of Montreal, Canada, chosen to reflect a gradient of macrophyte cover, and therefore a gradient of epiphytic primary productivity. Three of these were in the discharge plume of the municipal wastewater treatment plant, within 10 km of the outfall. The remainder were reference sites, hydrodynamically isolated from the plume. Entry of sewage-derived organic matter into the littoral foodweb was confirmed by stable isotope analysis of benthic invertebrates and benthivorous fish (deBruyn et al., unpublished data).

Sampling and analysis. Fish were collected on two visits to each site between July 17 and September 7, 2000, using a 40 m x 2 m seine (0.5 cm mesh). At least three seine hauls were taken on each visit, 50 to 100 m apart and successively upstream. One or two additional hauls were taken if low numbers of fish were obtained. Five to ten individuals of each species per visit (or as many as were available) were sacrificed and frozen for other studies. All other fish were measured before release, and their wet weights were calculated using length-weight relationships derived from sacrificed fish.

Figure 1. Schematic representation of how the size distribution of a three-level food chain is predicted to respond to basal enrichment, considering a) only resource control, and b) resource and consumer control.


a
b
log Density (/m^2)
log Weight (g)

Size distributions. We estimated the upper bound of the interspecific density -body size relationship according to the method of Blackburn et al. (1992), with the following modification. This method effectively assumes that only the mean (or mean adult) size of a species is important in its ecological and evolutionary interactions. This may be a reasonable assumption for species that rapidly attain adult size (e.g., birds). It is probably not a good assumption for species that grow slowly, occupy a wide range of body sizes throughout their lifespan (e.g., oviparous species), have indeterminate growth form (e.g., fish), or show plasticity of form within a population (again, fish are a good example). We therefore treated each age class of each species as an independent datum--effectively, each age class was considered to be ecologically equivalent to a species. If the unit of study was the complete community of a closed system, this would superimpose species survivorship curves (many small young versus few large adults) on the density-body size pattern. However, our study system is not closed. The littoral zone of temperate rivers like the St. Lawrence is recolonized each spring by 1+ and older fish. Young of the year are produced in situ by spawning adults, presumably according to the site's suitability for rearing young. Each age class of a species independently selects its summer habitat, and should thus be considered independently of other age classes. Treating age classes separately also at least partially accommodates the strongly size-structured nature of fish ecology (e.g., ontogenetic diet and habitat shifts, predator-prey size ratios, etc.; Mittelbach and Persson 1998). Best-fit lines were calculated for the positively and negatively sloped portions of the upper bound by OLS regression. Maximum energy use per size class was calculated by multiplying these upper-bound densities by individual total metabolism, using an allometric scaling coefficient of 0.81 (Peters 1983).

Normalized biomass spectra were constructed by summing biomass densities of fish (g wet wt./m^2) within the same $\log_2$ size classes as above, regardless of taxon, and plotting $\log_{10}$(sum of biomass in each size class/range of the size class) against $\log_{10}$ of the maximum body size in each class (Sprules and

Munawar 1986). Best-fit lines were calculated for the positively (< 1 g) and negatively sloped (> 1 g) portions of each distribution by OLS regression. Total energy use per size class was calculated as above.

Effect of productivity. We performed two analyses to test for effects of productivity on size distributions. First, we used ANCOVA to compare slopes and intercepts between sewage-enriched and reference size distributions. Mean NBS and upper bound lines were constructed by taking the mean value within each size class, among either reference or sewage sites. This analysis tested for a categorical effect of sewage enrichment on the parameters of the size distribution.

Next, we used OLS regression to test for a continuous effect of productivity (among all sites) on the slopes, elevations, and variance explained (r^2) of upper bound and NBS best-fit lines. Secondary production was estimated for each fish species at each site using the instantaneous growth rate method (Rigler and Downing 1984). Total production of benthic invertebrate primary consumers was then back-calculated from fish production (Johnson et al. 1998) to provide an overall measure of productivity for each site. We assumed conversion efficiencies of 10% for benthivorous fish and 15% for piscivorous fish, reflecting differences in assimilation efficiency (1 - fecal and urinary losses) and growth efficiency (growth/consumption) between trophic levels (Sherwood et al. 2000; Trudel et al. 2001; Pazzia 2001).

Effect of site characteristics. We used Principal Components Analysis (PCA) to examine the relationships among size classes, and between size classes and site characteristics. Variables included in the PCA were log-transformed total densities in each size class (log g wet wt./m^2), weed cover (percent), current velocity (nominal scale), sediment slope (percent), and sewage contribution to the diets of primary consumers (percent, deBruyn et al., unpublished data). Most sites had too many empty size classes in the interspecific density-body size upper bound, so only total densities (i.e., NBS) could be analyzed by PCA. All variables were standardized to Z-scores before PCA, in order that each contribute equal variance to the analysis.

Groups of NBS size classes that covaried strongly were combined into "peaks" (Rasmussen 1993). We hypothesized that the relationships between total peak densities and site characteristics were mediated by foodweb interactions. We therefore subdivided each peak into three groups of species with similar prey and similar predators ("trophic species"). Most species (primarily Cyprinidae, Centrarchidae, and Percidae) were considered to be generalist benthivores, feeding on sediment- and macrophyte-dwelling invertebrates. These species are vulnerable to predation by piscivorous fish (primarily Esocidae). Suckers (Catastomidae) were considered separately, as these fishes have mouthparts specialized to feeding only on sediment and sediment-dwelling organisms. Additionally, suckers reach large sizes and tend to avoid macrophyte beds; they are therefore less vulnerable than other benthivorous species to the piscivores in these habitats. We then performed a PCA of total peak density (3 peaks X 3 trophic species) and site characteristics.

Results and Discussion

A total of 19,404 fish were captured, >95% of which were age 0+ to 1+. Generalist benthivores included johnny darter (*Etheostoma nigrum)*, logperch (*Percina caprodes),* pumpkinseed (*Lepomis gibbosus)*, rock bass (*Ambloplites rupestris)*, troutperch (*Percopsis omiscomaycus)*, banded killifish (*Fundulus diaphanus),* yellow perch (*Perca flavescens)*, smallmouth bass (*Micropterus dolomieui)*, largemouth bass (*Micropterus salmoides*), spottail shiner (*Notropis hudsonius)*, emerald shiner (*Notropis atherinoides)*, golden shiner (*Notemigonus crysoleucas),* blacknose shiner (*Notropis heterolepis*) , and brown bullhead (*Ictalurus nebulosus*) . Suckers were white sucker (*Catastomus commersoni)*, and silver redhorse (*Moxostoma anisurum).* Piscivores were northern pike (*Esox lucius)*, chain pickerel (*Esox niger*), muskellunge (*Esox masquinongy*), and yellow walleye (*Stizostedeon vitreum vitreum).*

Productivity and maximum density: It is generally recognized that the basal energy flux (productivity) of a habitat sets the upper bound of potential energy usage, and thus the maximum possible density of species at a given body size (Lawton 1990; Cyr et al. 1997; Maurer and Brown 1988; Currie and Fritz 1993), but the effect of basal productivity on the interspecific density-body size relationship has rarely been directly tested. Leaper and Raffaelli (1999) reported that the upper bound of the density-body size relationship was insensitive to gross changes in productivity for a well-documented estuarine foodweb. Blackburn et al. (1994), on the other hand, found that the slope of this relationship was shallower for breeding birds than for wintering birds in Britain, and attributed this to immigration of large, abundant species such as waterfowl and waders. Because migration is usually motivated by feeding opportunities, this could be interpreted as an effect of greater productivity in summer than winter.

Our results for the littoral fish community of the St. Lawrence River support those of Blackburn et al. (1994). More productive sites had a relative predominance of larger individuals (Fig. 3a) and this resulted in a shallower negative (>1 g) upper-bound slope for sewage-enriched sites combined ($b=-0.59$; $r^2=0.63$) than for reference sites combined ($b=-0.94$; $r^2=0.86$) (Table 1; Fig. 4). The density-body size relationship was approximately triangular, with a peak near 1 g (Fig. 2a). ANCOVA revealed a significant effect of sewage enrichment on the negative upper bound slope of this relationship ($F_{1,20}=4.94$; $p=0.037$), but no effect on the elevation ($F_{1,20}=0.91$; $p=0.37$; Fig. 3a). OLS regression also detected a continuous effect of productivity on the negative upper-bound slope of the interspecific density-body size relationship ($F_{1,10}=7.36$; $p=0.022$), but this was weak ($r^2=0.42$; Fig. 4). ANCOVA could detect no effect of sewage enrichment on the slope ($F_{1,2}=5.81$; $p=0.073$) or elevation ($F_{1,2}=3.40$; $p=0.14$) of the positively-sloped portion of the upper bound. Our results also parallel those for British birds in the underlying mechanism: in both cases, the shallower slope resulted from

Figure 2. Size structure of the St. Lawrence River littoral fish community at reference (open circles) and sewage-enriched sites (closed circles): a) density vs. body size among species-year classes (see text for details); and b) total biomass of all individuals in $\log_2$ size classes.

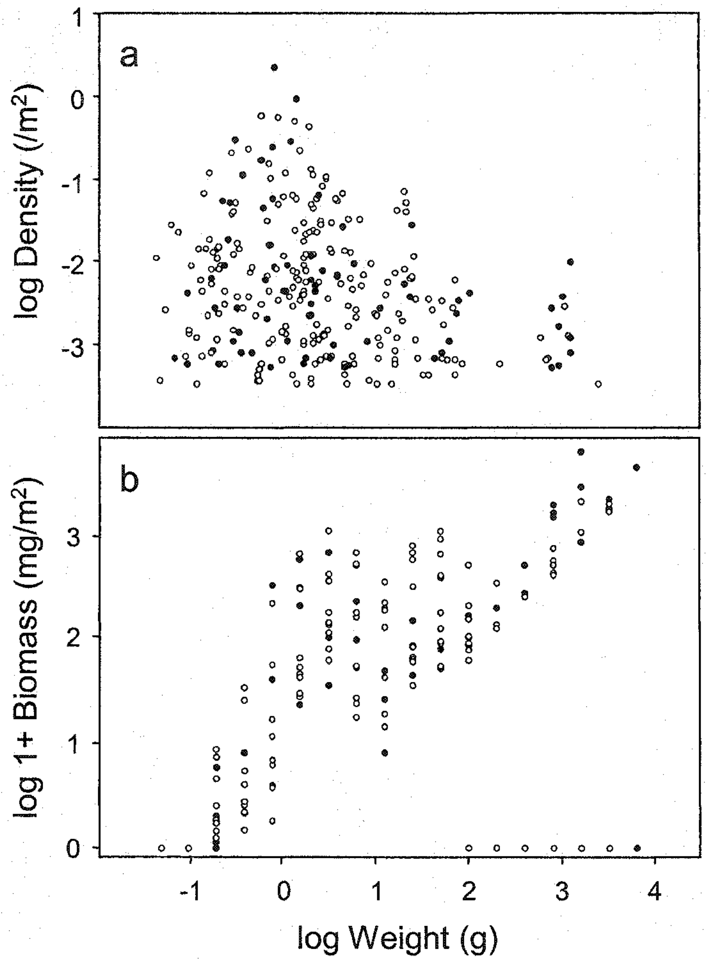
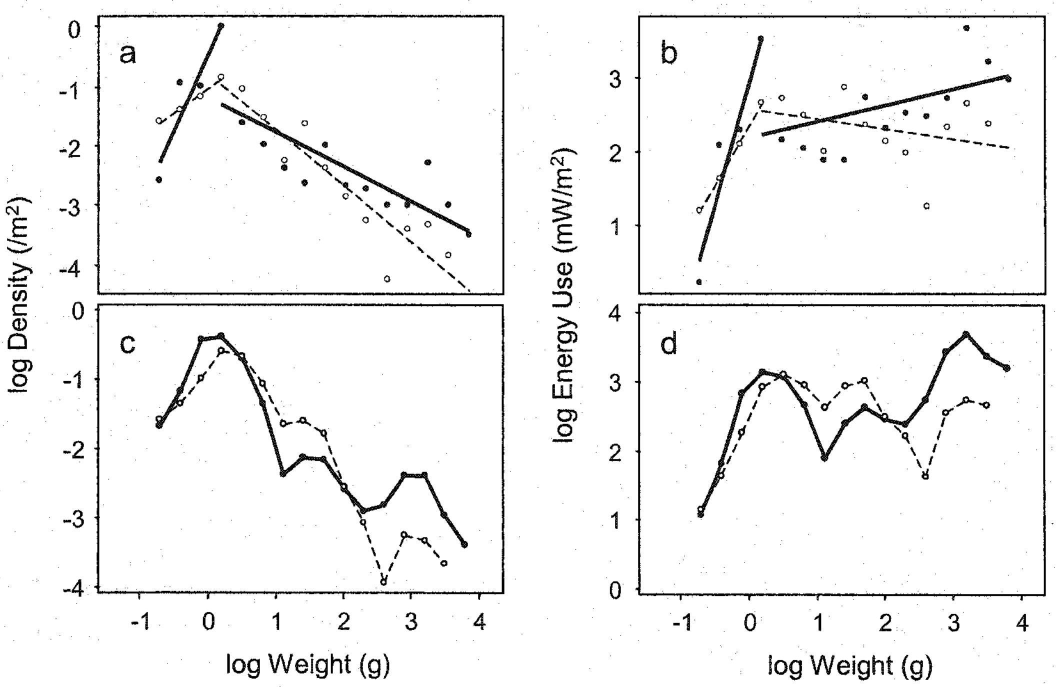

a
b
log Density (/m²)
log 1+ Biomass (mg/m²)
log Weight (g)
1
0
-1
-2
-3
3
2
1
0
-1
0
1
2
3
4

Figure 3. Size dependence of a) maximum density, b) maximum energy use, c) total density, and d) total energy use of size classes in the St. Lawrence River littoral fish community. Points are mean values per size class for reference (open circles) and sewage-enriched sites (closed circles).


a
b
c
d
log Density (/m2)
log Energy Use (mW/m2)
log Weight (g)
log Weight (g)
0
-1
-2
-3
-4
3
2
1
4
-1
0
1
2
3
4

larger individuals moving into highly productive patches in space (our results) or time (Blackburn et al. 1994).

The mean negative slope for all reference sites combined was –0.94, comparable to those reported in the literature (Blackburn and Lawton 1994), and consistent with an approximately constant maximum population energy use across size classes. Maximum population energy use at reference sites (Fig. 3b) increased slightly up to 1 g, but remained approximately constant thereafter (slope not significantly different from zero; b=-0.13; $t_{1,11}$=1.22; p=0.28). Sewage enrichment did not increase the mean value of this maximum energy use, but the slope of the upper bound was significantly steeper, indicating a relatively higher maximum energy use for large species and a relatively lower maximum energy use for medium-sized species. At sewage-enriched sites, maximum population energy use continued to increase above 1 g (b=0.42; $t_{1,11}$=4.56; p=0.00081). This is in direct contradiction to the energetic equivalence rule (Damuth 1987). Universal energetic constraints may be supported at large spatial and temporal scales, but other factors seem to be more important at a local scale.

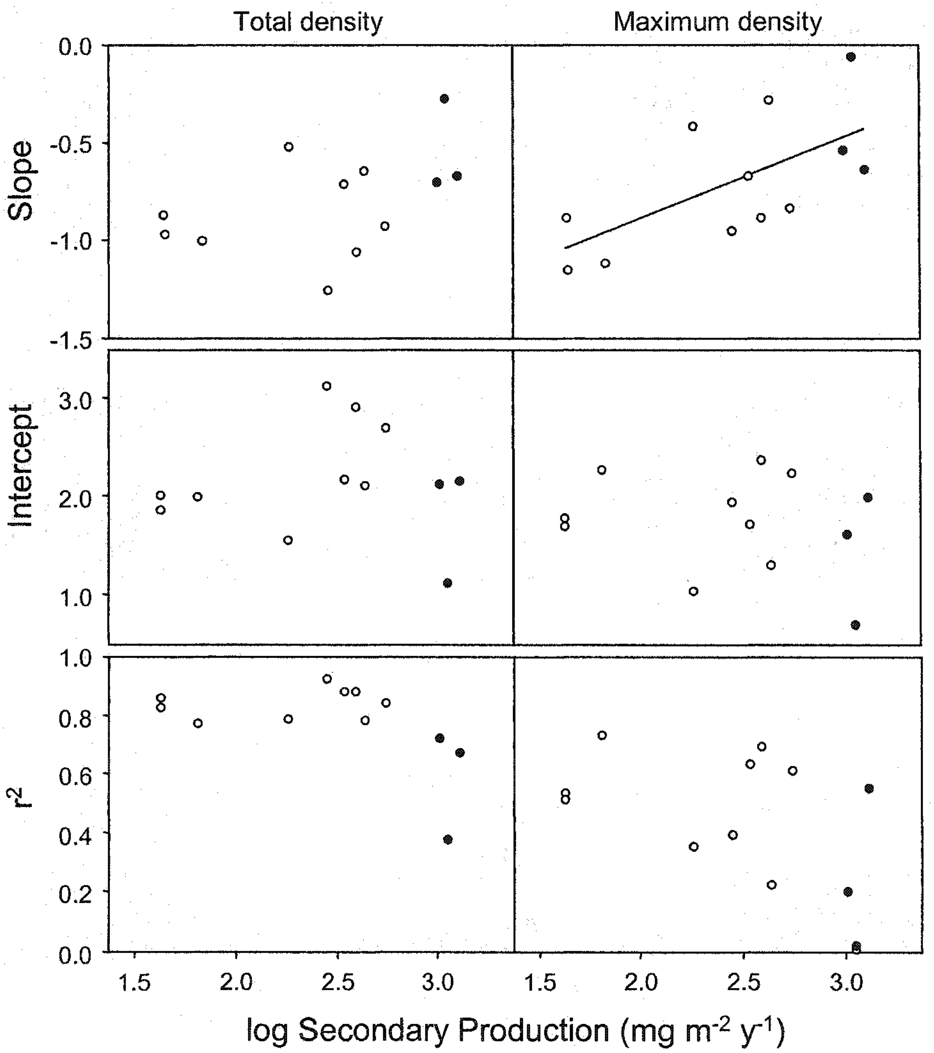
Productivity and total density: Productivity has been directly addressed more often in studies of the NBS. These studies typically report that more productive systems exhibit a shallower NBS slope (Peters 1983, 1985; Sprules and Munawar 1986; Ahrens and Peters 1991; Bourassa and Morin 1995; but see Morin and Nadon 1991 for no trend, Rasmussen 1993 and Cyr et al. 1997 for the opposite trend). In at least two of these studies, the shallower slope resulted from an increase in density of larger size fractions (Bourassa and Morin 1995; Sprules and Munawar 1986). We found similar trends for the NBS of the St. Lawrence littoral fish community. More productive sites had a relative predominance of larger individuals (Fig. 3) and this resulted in a shallower NBS slope (Table 1; Fig. 4).

Table 1. Summary statistics for the normalized biomass spectrum (NBS) and the negative upper-bound slope of the interspecific density-body size relationship for littoral fish communities at reference and sewage-enriched sites in the St. Lawrence River.

Parameter	Reference (n=9)		Sewage-enriched (n=3)	
NBS				
slope	-0.88±0.22	(-1.25 to -0.52)	-0.55±0.24	(-0.70 to -0.27)
elevation	2.28±0.52	(1.57 to 3.13)	1.82±0.58	(1.14 to 2.17)
r^2	0.84±0.05	(0.77 to 0.93)	0.60±0.19	(0.38 to 0.73)
upper-bound				
slope	-0.80±0.29	(-1.15 to -0.28)	-0.41±0.31	(-0.63 to -0.06)
elevation	1.83±0.45	(1.06 to 2.38)	1.45±0.67	(0.71 to 2.01)
r^2	0.53±0.17	(0.23 to 0.74)	0.26±0.28	(0.01 to 0.56)

mean ±s.d. (range)

Figure 4. Effect of site productivity on parameters of the normalized biomass spectrum (left panels) and the interspecific density-body size relationship (right panels) for the St. Lawrence River littoral fish community at reference (open circles) and sewage-enriched sites (closed circles).


Total density
Maximum density
Slope
0.0
-0.5
-1.0
-1.5
Intercept
3.0
2.0
1.0
r^2
1.0
0.8
0.6
0.4
0.2
0.0
1.5
2.0
2.5
3.0
1.5
2.0
2.5
3.0
log Secondary Production (mg m^{-2} y^{-1})

ANCOVA revealed a significant effect of sewage enrichment on the negative slope of the NBS ($F_{1,20}$=6.17; p=0.021), but no effect on the elevation ($F_{1,20}$=2.60; p=0.12; Fig. 3c). OLS regression could detect no continuous effect of productivity on the NBS slope, although we did observe a weak trend toward a shallower NBS slope at more productive sites (r^2=0.20; $F_{1,10}$=2.43; p=0.15; Fig. 4). This trend was driven by the three sewage-enriched sites, which had shallower slopes on average than the reference sites (two-sample $t_{1,10}$=2.20; p=0.05). ANCOVA could detect no effect of sewage enrichment on the slope ($F_{1,2}$=0.001; p=0.92) or elevation ($F_{1,2}$=0.91; p=0.13) of the positively-sloped portion of the NBS. The negative slope was shallower for the combined sewage-enriched sites (b=-0.62; r^2=0.74) than for combined reference sites (b=-0.99; r^2=0.91). Consequently, total size-class energy use (Fig. 3d) at reference sites increased slightly up to 1 g, but remained approximately constant thereafter (b=-0.18; slope not significantly different from zero; $t_{1,11}$=1.87; p=0.88). At sewage-enriched sites, maximum population energy use continued to increase above 1 g (b=0.28; $t_{1,11}$=2.47; p=0.031).

The poor linear fit of NBS at sewage-enriched sites reflected an uneven distribution of biomass across the size spectrum (Fig. 2b). Total density of organisms per size class showed a peaked shape similar to that observed for maximum (upper-bound) density, increasing up to 1 g and declining at higher body sizes. The negative portion of the size spectrum at reference sites had a mean slope near –1 and was reasonably well described by linear regression (Table 1; Fig. 3c). Spectra from sewage-enriched sites were more strongly trimodal, and were not well described by linear regression (Table 1; Fig. 3c). Mean r^2 was significantly lower at sewage-enriched sites for the negative slope of the NBS ($t_{1,10}$=3.88; p=0.003).

Nonlinear size spectra are commonly observed in aquatic systems and it has been suggested that the NBS is in fact composed of several to many small unimodal distributions (Ahrens and Peters 1991; Sprules and Goyke 1994). These component modes vary independently, respond to different environmental characteristics, and may represent major functional groups of organisms (Tessier and Horowitz 1990; Strayer 1991; Rasmussen 1993). PCA of size classes and site characteristics identified three orthogonal components which together expressed 54.3% of the total variance (Table 2). Each component expressed covariance in several adjacent $\log_2$ size classes, corresponding to the peaks apparent in Fig. 3: the "small" peak comprised fish 0.2-12.8 g, the "middle" peak 12.8-205.2 g, and the "large" peak 205.2-6553.6 g. All twelve sites had biomass peaks in the lower and middle parts of the spectrum. The six most productive reference sites and all three sewage-enriched sites also had a third peak in the upper part of the size range. These peaks were correlated with different site characteristics, and differences in size distributions among sites seemed to result from variation in the different factors controlling the three peaks.

Other influences on body size distributions: PCA of trophic species' densities in each peak and site characteristics (4 components, expressing 72.7% of total variance; Table 3) offered insight into the mechanisms behind these relationships. Only the largest size classes (the large peak) increased with sewage enrichment. We found better correlations of most small and medium-sized fish with site characteristics than with productivity. Small and medium non-piscivores were primarily associated with low current, irrespective of the level of weed cover or sewage enrichment. Medium benthivores and suckers also covaried with weed cover, but in opposite directions: benthivore densities were highest at weedy sites, whereas suckers were associated with relatively bare sites. The proportion of the variance in weed cover captured by the PCA was large (component loading score 0.89) but only weakly correlated with productivity (component loading score 0.36). Therefore, the influence of weed cover on fish densities seemed to be as a physical structure of the habitat. In addition, we observed an interaction between site characteristics and productivity. The response of the large peak to sewage enrichment depended qualitatively on weed cover: at low weed cover, the large peak comprised predominantly suckers, whereas at high weed cover it was

Table 2. Principal component loading scores for densities of fish in $\log_2$ size classes and characteristics of the littoral habitat among sites in the St. Lawrence River. Only scores >0.5 are shown.

	Component (Variance explained)		
	I	II	III
Variable	(20.1%)	(17.8%)	(16.4%)
Weed cover	-	-	0.80
Sediment slope	-	-	-
Current	-	-	-
Sewage enrichment	-	0.83	-
< 0.1 g wet wt.	-	-	-
0.1 - 0.2	-	-	-
0.2 - 0.4	0.78	-	-
0.4 - 0.8	0.84	-	-
0.8 - 1.6	0.88	-	-
1.6 - 3.2	0.76	-	-
3.2 - 6.4	0.74	-	-
6.4 - 12.8	0.56	-	-
12.8 - 25.6	-	-	0.75
25.6 - 51.2	-	-	0.81
51.2 - 102.4	-	-	0.51
102.4 - 204.8	-	-	0.71
204.8 - 409.6	-	0.53	-
409.6 - 819.2	-	0.76	-
819.2 - 1638.4	-	0.88	-
1638.4 - 3276.8	-	0.61	-
3276.8 - 6553.6	-	0.50	-

Table 3. Principal component loading scores for densities of fish in three peaks of the normalized biomass spectrum and characteristics of the littoral habitat among sites in the St. Lawrence River. Only scores >0.5 are shown, with a few exceptions (see text for details).

		Component (Variance explained)			
		I	II	III	IV
Variable		(24.0%)	(18.5%)	(15.0%)	(15.8%)
Weed cover		-	0.89	-	-
Slope		-	-	0.84	-
Current		-	-	0.69	-0.51
Sewage enrichment		0.90	-	-	-
Secondary production		0.76	0.36	-	-
Small	Benthivores	-	-	-	0.91
	Suckers	-	-	-	0.53
	Piscivores	0.56	-	-	-
Middle	Benthivores	-	0.60	-	0.61
	Suckers	-	-0.67	-	0.44
	Piscivores	-	-	0.80	-
Large	Benthivores	0.80	-	-	-
	Suckers	0.82	-	-	-
	Piscivores	0.42	0.79	-	-

predominantly piscivores. This is because the most abundant piscivores in this system are esocid fishes (pikes), which are ambush predators typically associated with macrophyte beds and woody debris. Relatively bare sites provide poor habitat for this type of predator, irrespective of the density of prey fish.

The pattern of trophic species' responses to sewage enrichment in the St. Lawrence supports the view that the NBS reflects a size-structured foodweb (Sprules 1988; Borgmann 1997). Large benthivores responded strongly to enrichment at all levels of weed cover, revealing a higher rate of production of benthic invertebrate prey. Despite this, densities of medium and small benthivores did not respond to enrichment (Table 3). Overall, the middle peak became smaller with sewage enrichment (Fig. 3), as predicted by models of consumer control (Fig. 1). Higher densities of large piscivores at sewage-enriched sites support the hypothesis that exploitation (top-down control) is a more important determinant of benthivore densities than resource abundance. This hypothesis is consistent with recent work on the effects of enrichment on foodwebs with heterogeneous trophic levels: vulnerable prey are strongly controlled by exploitation, whereas protected prey are free to respond to an increase in resources (Leibold 1989; Hulot et al. 2000; Persson et al. 2001). In aquatic systems, vulnerability is largely a matter of predator-prey size ratios (Mittelbach and Persson 1998).

Reconciling the two approaches: The interspecific upper bound and the NBS address the relationship between density and body size in fundamentally different ways. These approaches converge when there is only one species per size class, and one size class per species. However, real assemblages always contain more species than size classes, and richness is usually highest at intermediate body sizes (Hutchinson and MacArthur 1959; Maurer and Brown 1988). This sort of assemblage produces a relatively dense cluster of points in the center of an interspecific relationship, and a peak in the NBS. It is therefore inappropriate to directly compare interspecific slopes and NBS slopes (but see

Griffiths 1992; Cyr et al. 1997). The two approaches may only be reconciled with careful attention to the types of hypotheses which may be addressed with each.

The form of the interspecific density-body size relationship is usually attributed to ecological constraints acting over evolutionary time. By treating each species as an independent datum, this approach implicitly assumes that each species is responding to a common, external driver in a size-dependent way. It has been suggested that this driver is energetic, and that it may be manifested through competition with other members of the community (Damuth 1987; Blackburn et al. 1994), but the underlying constraint is still external to the biota. Thus, the slope of this relationship, or at least the slope of its upper bound, should be invariant. At a coarse scale, this view is supported in the St. Lawrence. The mean upper-bound slope for all sites combined (reference and sewage-enriched) is -0.82 (SE=0.098; r^2=0.87; $F_{1,11}$=71; p=0.0000039), statistically indistinguishable from that predicted by the energetic equivalence rule. At a local scale, however, there is considerable variation in the upper-bound slope. The trend toward shallower slopes at more productive sites, in particular, indicates that the energetic equivalence rule is not supported at small spatial scales.

The NBS, on the other hand, considers the size spectrum to represent a functionally integrated community. While the area under the NBS (total community biomass) may be energetically constrained, the shape of the NBS is taken to reflect ecological processes which govern the transfer of energy among trophic groups (Sprules 1988; Borgmann 1997). Our results support a growing body of evidence against a simple linear relationship between total density and body size. Modality in the NBS was pronounced, and the response of the NBS to varying productivity was not well reflected by a linear best-fit. However, we were able to explain much of the variance in the shape of the NBS with a very simplified consideration of habitat requirements and feeding relationships.

Thus, these two approaches offer complementary information on the ecological implications of body size. The interspecific density-body size relationship speaks to processes governing the size structure of assemblages on large spatial and temporal scales, whereas the NBS reflects local processes acting on short time scales. We suggest that there is a hierarchy of explanations for the density-body size relationship. Our data support previous evidence for universal energetic constraints on the size structure of regional assemblages, but they also highlight the importance of factors that influence the local abundance of various components of the size spectrum. We hope that these observations will help to reconcile these two largely independent approaches, and to better integrate both with other aspects of ecology.

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Connecting Statement

In the preceding chapter, I showed that sewage-enriched sites have a relatively higher proportion of large organisms than reference sites. This is in direct contradiction to energetic explanations for body size distributions., but is consistent with hypotheses of top-down (consumer) control of prey density. In the following chapter, I explore these ideas in more depth. I show that all three consumer trophic levels increase in response to sewage enrichment, but the membership of each shifts toward larger forms that are less vulnerable to predation.

CHAPTER 4: VARIABLE TROPHIC CONTROL IN A SEWAGE-ENRICHED RIVER FOOD WEB

deBruyn, A.M.H. and J.B. Rasmussen. Variable trophic control in a sewage-enriched river food web. prepared for American Naturalist

Abstract

The classic dialectic of top-down vs. bottom-up control in food webs is slowly being replaced by a recognition that consumer and resource effects jointly determine trophic level biomass. A central feature of this synthesis has been the observation that food chains are rare in nature: trophic linkages are complex because prey are not uniform in their vulnerability to predation. We studied the effect of prey heterogeneity on trophic control in the littoral food web of the St. Lawrence River by exploiting a natural sewage enrichment experiment across a gradient of habitat structure. At sewage-enriched sites, we observed a dramatic increase in abundance of piscivores (top predators) and large suckers (invulnerable intermediate consumers), but no change in smaller benthivorous fishes (vulnerable intermediate consumers). These effects cascaded to the level of benthic invertebrates (primary consumers), permitting an increase in the prey of benthivores, but no increase in the prey of suckers. Furthermore, the relative magnitudes of these increases in abundance were related to habitat structure. Our results are consistent with the predictions of a simple food web model that recognizes heterogeneity within each trophic level.

Introduction

The potential biomass of all organisms in a food web is ultimately controlled by the supply of basal resources, but the distribution of biomass among types of organisms may be strongly influenced by consumer exploitation (Fretwell 1977; Oksanen et al. 1981; Hunter and Price 1992; Power 1992; Strong 1992). Consumer control of prey biomass is favoured when predators are efficient (noninterfering, limited only by food) and prey are vulnerable (undefended, accessible); in extreme cases, these conditions permit a community trophic cascade (e.g., Kerfoot and Sih 1987; Power 1990b; Carpenter and Kitchell 1993). It is likely, however, that community cascades represent exceptional cases (Hunter and Price 1992; Power 1992; Strong 1992; Polis and Strong 1996; Polis et al. 2000). Most food webs have more complex dynamics and the importance of consumer control depends on many factors which are poorly understood.

Linear food chain models with consumer control predict that enrichment will increase the biomass of the top predator and every second trophic level below (Rosenzweig 1971; Fretwell 1977; Oksanen et al. 1981; Oksanen 1991). Often, however, adjacent trophic levels covary (McQueen et al. 1986; Leibold 1989; Hansson 1992; Mazumder 1994; Brett and Goldman 1997) or the top trophic level does not respond to enrichment (Schmitz 1994; Balcianus and Lawler 1995; Mikola and Setala 1998). Mechanisms that have been proposed to account for this discrepancy include predator interference (Arditi and Ginzburg 1989), omnivory (Polis; McCann and Hastings 1997), spatial heterogeneity (Jansen 1995; Scheffer and de Boer 1995; Abrams and Walter 1996), and heterogeneity within trophic levels (Yodzis and Innes 1992; Abrams 1993).

Prey heterogeneity, in particular, has received much theoretical attention. Abrams (1993) used Lotka-Volterra-type models to show that heterogeneity within trophic levels permits every possible combination of increasing, decreasing, or unchanging trophic level biomass in response to basal enrichment. Consumer control in these models was strong, but the outcome for each trophic level depended on the pattern of feeding linkages and the relative vulnerability of prey types. When prey vary in their susceptibility to predation, consumer-induced changes in the density of one prey type can be compensated by changes in other, less vulnerable types (Leibold 1989; Hunter and Price 1992; Schmitz 1994; Rosemond 1996; Leibold et al. 1997; Chase 1998, 1999; Mikola and Setala 1998; Pace et al. 1998). If this compensation is incomplete (e.g., if there is a trade-off between prey vulnerability and competitive ability), the food web may still exhibit a community cascade (Rosemond 1996). These subtleties are completely obscured by lumping organisms into trophic levels.

Despite the impressive body of theoretical work, empirical tests of this mechanism are still quite rare. The strongest support comes from enrichment experiments using microbial food webs in laboratory microcosms (Balciunas and Lawler 1995; Bohannan and Lenski 1999) and model pelagic food webs (Hulot et al. 2000; Persson et al. 2001). Evidence from the field is less clear. Comparative studies have reported a progression toward less edible algae (Cattaneo 1987; Trimbee and Prepas 1987; McCauley et al. 1988; Watson et al. 1992; but see Sarnelle 1994) and zooplankton (Bays and Crosman 1983; Mills and Schiavone 1982; but see Pace 1986) across productivity gradients. Similarly, experimental and comparative studies have reported a shift toward relatively invulnerable prey fishes with increasing piscivory (Tonn and Magnuson 1982; He and Wright 1992). However, none of this previous work directly addressed how prey vulnerability affected the strength of consumer control. In addition, none were concerned with whether these effects extended beyond the two adjacent trophic levels under study.

We tested the effect of prey heterogeneity on consumer control among three trophic levels. We compared model predictions with the results of a field study of a speciose, moderately complex food web. Our study combines a comparative approach (a gradient of habitat structure) with a natural experiment (anthropogenic enrichment). Here we report that biomass densities of consumers at adjacent trophic levels increase with sewage enrichment, but for intermediate consumers this is entirely due to increases in species that are relatively invulnerable to predation. At the level of primary consumers, only species whose predators are under top-down control increase with sewage enrichment. Furthermore, we report that the effect of prey heterogeneity on trophic control is mediated by habitat structure, consistent with the predictions of our simple food web model.

Methods

Study System

The St. Lawrence is a large, fast-flowing, temperate river. Nutrient levels are moderate (dissolved P < 30 μg/L; dissolved N < 0.5 mg/l) and pelagic productivity is low (median summer chlorophyll-*a* < 2.5 μg/L) (Hudon and Sylvestre 1998). Flow rates are typically 2-3 m/s in the main channel, and net sedimentation of suspended material is restricted to the deepest areas outside the main channel (Carignan and Lorrain 2000). The city of Montreal, Quebec (population 1.8 million) discharges primary-treated sewage at a rate of 30 m^3/s, contributing 90,000 t/y particulate organic matter (POM) and 450 t/y phosphorus to the St. Lawrence River (Purenne 1998). Despite the absence of sediment accumulation downstream of Montreal (Carignan and Lorrain 2000), sewage-derived POM constitutes up to 90% of the diet of benthic primary consumers within 10 km of the outfall (deBruyn and Rasmussen, in press). Sewage enrichment stimulates a greater than 10-fold increase in secondary production within this reach, most of which can be attributed to consumption of sewage-derived POM by benthic primary consumers (deBruyn et al., unpublished manuscript).

Littoral zones in this reach of the St. Lawrence support a four-level food web based mainly on attached algal/bacterial biofilm and advected detritus (Fig. 1a; Table 1). At enriched sites, sewage organic matter is also an important component of the diets of invertebrate primary consumers (36-78%: deBruyn et

Figure 1. Schematic representation of the food web of the littoral St. Lawrence River, a) showing all known trophic linkages, and b) further simplified for mathematical modeling, showing only the most energetically important linkages. Trophic species are: 1. piscivores; 2. minnows; 3. invertivores; 4. suckers; 5. weedbed invertebrates; 6. sediment invertebrates; 7. filamentous algae; 8. weedbed algal/bacterial biofilm; 9. advected detritus and sewage organic matter; 10. sediment algal/bacterial biofilm. See text and Table 1 for taxonomic composition of trophic species. Dashed box encloses trophic species associated primarily with weedbeds.

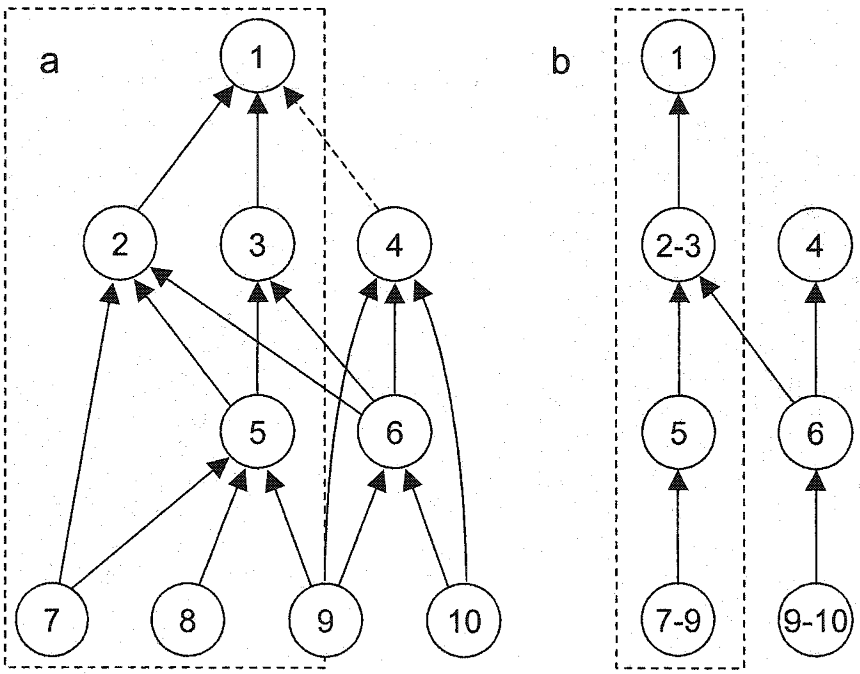

a
1
2
3
4
5
6
7
8
9
10
b
1
2-3
4
5
6
7-9
9-10

Table 1. Taxonomic composition and diet composition of trophic species used to model the littoral food web of the St. Lawrence River. Diet components are algae (A), invertebrates (I) and fish (F). Values (based on the contents of *n* guts) are fraction of total identifiable volume, weighted by population age structure.

Trophic species Species included	Diet *n*	 A	 I	 *F*
Piscivores				
Northern pike (*Esox lucius*)	4			1.0
Muskellunge (*Esox masquinongy*)	5			1.0
Chain pickerel (*Esox niger*)	5			1.0
Smallmouth bass (*Micropterus dolomieui*)	12		0.03	0.97
Largemouth bass (*Micropterus salmoides*)	5			1.0
Yellow walleye (*Stizostedeon vitreum*)	59			1.0
Benthivores				
Yellow perch (*Perca flavescens*)	75	0.02	0.87	0.11
Logperch (*Percina caprodes*)	65		1.0	
Brown bullhead (*Ameiurus nebulosus*)	10		1.0	
Pumpkinseed (*Lepomis gibbosus*)	11		1.0	
Troutperch (*Percopsis omiscomaycus*)	30		1.0	
Johnny darter (*Etheostoma nigrum*)	57		1.0	
Rock Bass (*Ambloplites rupestris*)	44		1.0	
Banded killifish (*Fundulus diaphanus*)	9		1.0	
Alewife (*Alosa pseudoharengus*)	23		0.95	0.05
Emerald shiner (*Notropis atherinoides*)	40	0.40	0.60	
Spottail shiner (*Notropis hudsonius*)	35	0.16	0.84	
Golden shiner (*Notemigonus crysoleucas*)	23	0.11	0.89	
Blacknose shiner (*Notropis heterolepis*)	37	0.59	0.41	
Suckers				
White sucker (*Catastomus commersoni*)	48	0.04	0.96	
Silver redhorse (*Moxostoma anisurum*)	23		1.0	

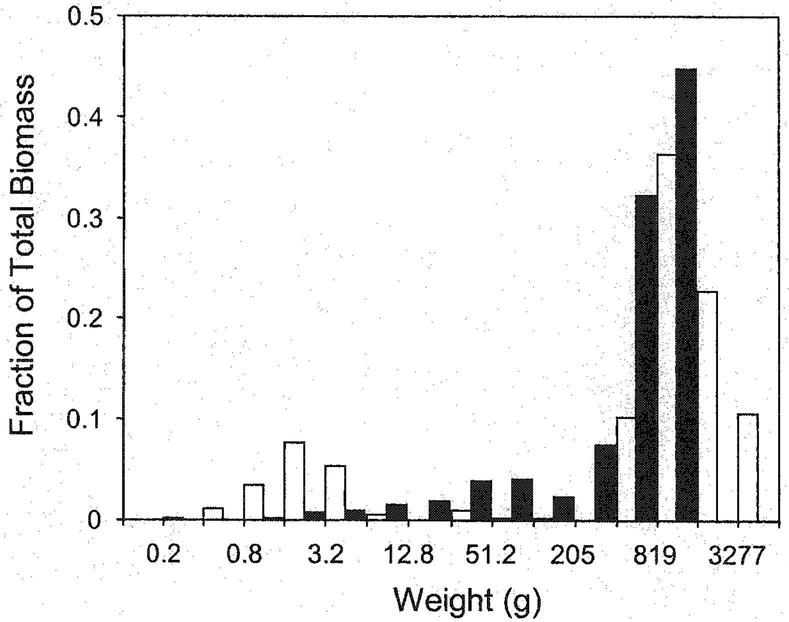
al., unpublished manuscript). In densely vegetated areas (weedbeds), the dominant primary consumers are chironomid larvae that build tubes attached to rooted plants; on bare sediment and low understory vegetation, the dominant primary consumers are amphipods and chironomid larvae. Generalist benthivores (mainly Percidae and Centrarchidae) feed on invertebrates both inside and outside weedbeds. Minnows (Cyprinidae) consume invertebrates and periphytic algae, but the energetic importance of algae to these fish is small (~15%; Table 1) and the grazing rate of cyprinids is certainly small relative to that of herbivorous invertebrates. We therefore aggregated these species with the benthivores. Suckers (Catastomidae) consume sediment-dwelling invertebrates and zooplankton, and have morphology specialized to feeding off bare sediment and low understory vegetation. Suckers therefore tend to stay away from densely vegetated areas, making them less vulnerable to the weedbed-inhabiting piscivores (primarily pikes, Esocidae) prevalent in the St. Lawrence. Suckers also quickly grow too large to be captured by the piscivores which inhabit these shallow waters (Fig. 2). In addition to invertebrate prey, suckers consume detritus and benthic algae directly, but the energetic importance of these food items is small relative to energy-rich and highly digestible invertebrates (Table 1).

The food web thus can be closely approximated as two food chains linked by generalist intermediate consumers (Fig. 1b). In vegetated areas (weedbeds), the top trophic level is piscivores. In relatively bare areas (sediment/understory), the top trophic level is suckers. All species occur across the study reach, so potential community membership is constant among sites.

Sampling and Analysis

We sampled littoral fish from twelve mid-river island sites downstream of Montreal, Canada, chosen to reflect a gradient of macrophyte cover. Three of these were in the discharge plume of the municipal wastewater treatment plant, within 10 km of the outfall. The remainder were reference sites, hydrodynamically isolated from the plume. Stable isotope analysis of benthic

Figure 2. Distribution of sucker (white bars) and piscivore (dark bars) biomass among $\log_2$ size classes in the littoral food web of the St. Lawrence River. The largest piscivores are pikes (Esocidae), which can only capture suckers <25% of their own length (Nilsson and Brönmark 2000), or about 1/32 of their own mass, equivalent to five $\log_2$ size classes. All suckers in the larger peak, comprising 80% of the total biomass, are invulnerable to these piscivores.



0.5
0.4
0.3
0.2
0.1
0
Fraction of Total Biomass
0.2
0.8
3.2
12.8
51.2
205
819
3277
Weight (g)

invertebrates and benthivorous fish confirmed entry of sewage organic matter into the littoral food web (deBruyn et al., unpublished manuscript).

We collected fish on two visits to each site between July 17 and September 7, 2000, using a 40 m x 2 m seine (0.5 cm mesh). At least three seine hauls were taken on each visit, 50 to 100 m apart and successively upstream. One or two additional hauls were taken if low numbers of fish were obtained. Five to ten individuals of each species per visit (or as many as were available) were sacrificed and frozen for gut content and stable isotope analysis. All other fish were measured before release, and their wet weights were calculated using length-weight relationships derived from sacrificed fish. Gut contents were quantified as volume percent.

Benthic invertebrates were collected on the same two visits, using a kicknet (0.5 mm mesh) to take 0.25 m^2 grab samples of surface sediment and overlying vegetation. Replicate samples were taken in dense weedbeds (2 samples, typically ~1 m depth) and in relatively bare areas (2 samples each at 0.5 m and 1 m depth). Invertebrates were removed from each sample under a dissecting microscope, sorted, and weighed. The biomass density of each taxon for an entire site was then calculated as the product of sample biomass density (g/m^2) and the fraction of total site area in weedbed or bare sediment/understory.

We used fish gut contents (*n*=622) and published diet descriptions (Scott and Crossman 1973) to establish energetically important feeding links among species, then aggregated species into trophic groups with similar resources and predators (Fig. 1b). This food web structure was consistent among sites, although the absolute and relative abundances of organisms in each group varied. We used analysis of covariance (ANCOVA) to test for effects of weed cover (continuous), sewage enrichment (categorical), and their interaction on the observed biomass densities of each trophic species.

Mathematical Model

We constructed a bioenergetic model of the simplified food web described above (Fig. 1b), expressed as the following system of coupled equations (after Yodzis and Innes 1992):

$$dB_i/dt = B_i(r_i\,(1-B_i/K_i) - \Sigma_k B_k J_k)$$

for basal resources, and

$$dB_i/dt = B_i(-T_i + J_i\Sigma_j(1-\delta_j)B_j - \Sigma_k B_k J_k)$$

for consumers, where B_i is the biomass density of trophic species i, r and K are the production-to-biomass ratio and carrying capacity of the basal resources, J is the specific ingestion rate of consumers, $(1-\delta)$ is the assimilated proportion of ingested energy and T is the mass-specific metabolic expenditure of consumers. Consumption terms were summed over all the prey (j) and predators (k) of trophic species i. Specific ingestion rate J was assumed to follow a linear functional response because there are no good estimates of the true shape of the functional response for these species in the wild. The qualitative predictions that follow are not sensitive to this assumption.

We considered the predictions made by the equilibrium solution of this model, despite the fact that our study system is unlikely to be at equilibrium: the littoral zone of rivers like the St. Lawrence is reset each winter as the macrophytes die back, then recolonized each spring by fish that have overwintered in deeper water. It is likely, however, that net immigration is higher at sites with abundant food, and lower at sites with abundant predators (Wootton and Power 1993). Migration thus represents a “shortcut” by which the system can approach equilibrium more quickly than via in situ reproduction or growth. All our sample sites are on midchannel islands, and all these islands have large areas of littoral zone that are not exposed to sewage enrichment. The spatial scale of enrichment is thus fine-grained with respect to the mobility of the fish that inhabit these littoral zones, and thus favours behavioural over demographic responses (Power 1992). Wootton and Power (1993) showed that a model that incorporated a mixture of migration and demography predicted the same changes as purely demographic models.

Results

Model Predictions

The equilibrium solution of the bioenergetic model predicts that sewage enrichment will increase biomass densities of piscivores and suckers (trophic species that have no predators) and weedbed-inhabiting invertebrates (as they are released from predation pressure by top-down control of their predators). On a coarse scale, then, the model predicts an increase in all trophic levels, but one which is heterogeneous within each trophic level.

The model also predicts that the relative magnitude of these increases will be influenced by the relative supply rates of the two basal resources. A higher rate of supply of weedbed resources favours weedbed-inhabiting invertebrates and piscivores, whereas a higher rate of supply of sediment/understory resources favours suckers only.

Empirical Observations

Observed patterns of consumer biomass densities in the St. Lawrence River support the model predictions in almost every case (Fig. 3). ANCOVA (Table 2) revealed that sewage-enriched sites had higher densities of piscivores (mean 6.5-fold increase), suckers (mean 7.5-fold increase) and weedbed-inhabiting chironomid larvae (mean 8.5-fold increase) than reference sites of comparable weed cover. ANCOVA detected no difference in biomass densities of benthivores or total sediment/understory invertebrates between sewage-enriched and reference sites. There was a 3.5-fold increase in the mean density of

Figure 3. Patterns of biomass density of trophic species at reference (open symbols) and sewage-enriched (filled symbols) littoral sites in the St. Lawrence River. Invertebrates on sediment/understory were sampled at 0.5 m (triangles) and 1 m (circles) depths.

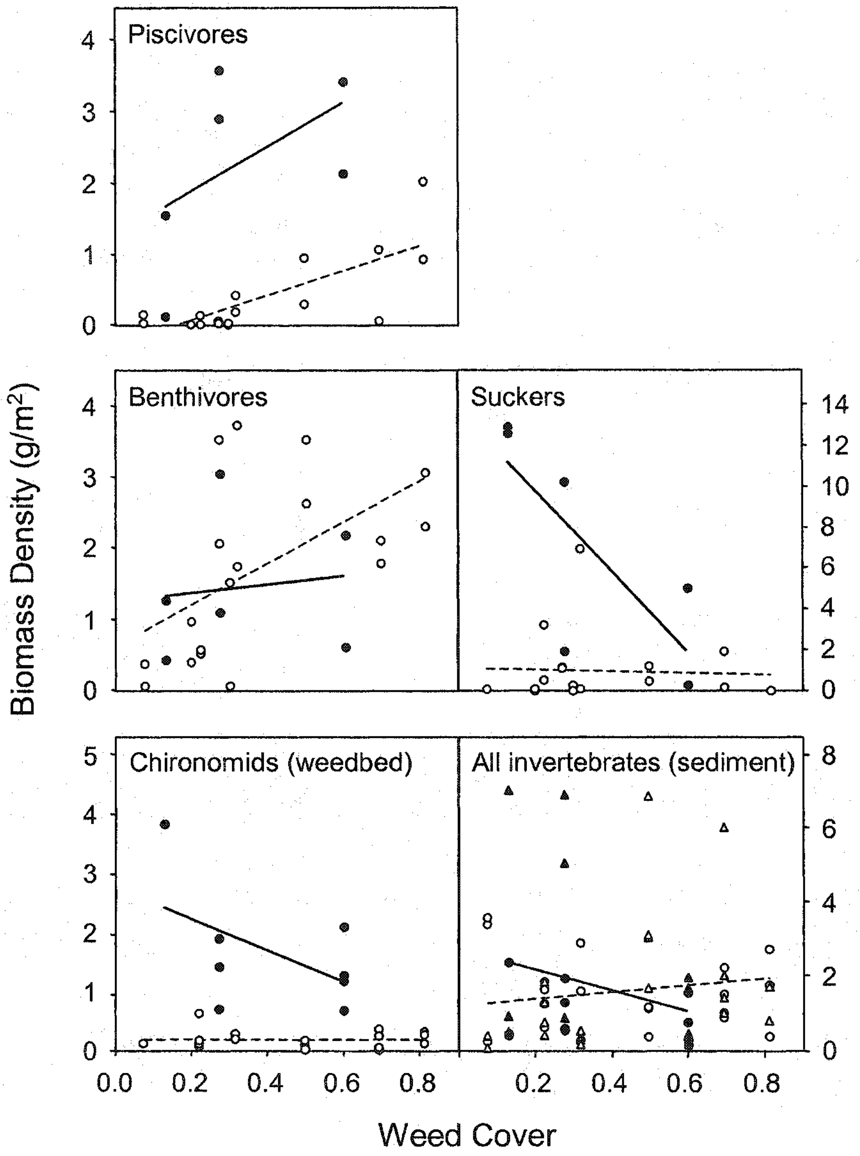

Piscivores
Benthivores
Suckers
Chironomids (weedbed)
All invertebrates (sediment)
Biomass Density (g/m²)
Weed Cover
0
1
2
3
4
5
6
8
10
12
14
0.0
0.2
0.4
0.6
0.8

Table 2. Summary of ANCOVA of the effects of sewage enrichment and weed cover on biomass densities of consumers in the littoral St. Lawrence River.

Source of variation	df	SS	F	P
Piscivores:				
Sewage	1	18.1	43.4	<0.00001
Weed cover	1	4.96	11.9	0.0024
Error	21	8.78		
Benthivores:				
Sewage	1	0.15	0.13	0.72
Weed cover	1	7.08	6.20	0.021
Error	21	24.0		
Suckers:				
Sewage	1	186	33.8	0.00001
Weed cover	1	76.8	13.9	0.0013
Sewage X Weed cover	1	70.0	12.7	0.0020
Error	20	110		
Chironomids (weedbed):				
Sewage	1	10699	23.2	0.00009
Weed cover	1	2832	6.15	0.022
Sewage X Weed cover	1	2768	6.01	0.023
Error	21	9671		
Chironomids (sediment/understory):				
Sewage	1	694	1.08	0.30
Weed cover	1	5704	8.86	0.0043
Error		644		
Total invertebrates (sediment/understory):				
Sewage	1	137	0.03	0.87
Weed cover	1	9	0.002	0.97
Error	1	287415		

chironomid larvae on sediment/understory, but this was not statistically significant and was compensated by a decrease in density of all other taxa.

ANCOVA also indicated a significant interaction between sewage enrichment and weed cover for suckers (Table 2), revealing a dependence of the response to enrichment on the level of weed cover. As predicted by the model, the increase in sucker density with sewage enrichment was greatest at low weed cover. ANCOVA was unable to detect a similar interaction for piscivores, but the apparent trend matched the model prediction of a greater increase at high weed cover (Fig. 3). ANCOVA also reported a significant interaction for weedbed-inhabiting chironomid larvae, but this seems to have been driven by a single point with high leverage and the resulting trend in biomass density for this trophic species was opposite that predicted by the model.

Discussion

Trophic cascades have provided dramatic support for the hypothesis that consumers can control prey biomass. It has been pointed out, however, that systems exhibiting trophic cascades share some unusual characteristics (Hunter and Price 1992; Power 1992; Strong 1992; Polis and Strong 1996; Polis et al. 2000). Most notably, they tend to have very efficient top predators and uniformly vulnerable prey. It is no accident that "runaway consumption" is most often observed in open-water, plankton-based food chains (e.g., Kerfoot and Sih 1987; Carpenter 1988; Carpenter and Kitchell 1993): large piscivores, uniformly slender-bodied planktivores, and a lack of spatial refugia in the homogeneous pelagic environment all contribute to the strength of consumer control.

Systems with heterogeneous prey assemblages do not often show community-wide trophic cascades (Werner et al. 1983; Hambright et al. 1991; Strong 1992; Hambright 1994; Mittelbach et al. 1996; Persson et al. 1996; Polis et al. 2000). Experimental food webs in microcosms (Balciunas and Lawler 1995; Bohannon and Lenski 1999) and mesocosms (Hulot et al. 2000; Persson et al.

2001) support the predictions of mathematical models (Abrams 1993; Chase 1999): relatively invulnerable prey can increase in response to enrichment, producing correlated responses in adjacent trophic levels. Completely invulnerable prey may even prevent any response in the top trophic level by efficiently diverting added nutrients from all pathways that lead to higher consumers. At the same time, consumer control of vulnerable prey can be strong. The importance of consumer control has thus been obscured by the traditional view of food webs as a series of discrete trophic levels.

Prey vulnerability can vary according to a wide range of characteristics, including morphology, physiology, and behaviour. The primary defense of suckers is to quickly grow too large and too tall-bodied for gape-limited piscivores to capture. Adult suckers are a preferred prey item of the larger pikes found in deeper waters, but are invulnerable to the smaller piscivores found in shallow, littoral areas. Size refugia are an important source of variation in prey vulnerability (Paine 1976; Paine et al. 1985; Hambright et al. 1991; Hambright 1994; Balciunas and Lawler 1995; Brönmark and Weisner 1996; Persson et al. 1996; Chase 1998), especially in fish communities where piscivores are gape-limited and must be substantially larger than their prey (Cohen et al. 1993).

In our system, this size refugium is context-dependent. When suckers move to deeper water (e.g., in winter), they become vulnerable to predation by larger individuals of the same piscivore species. By exporting shallow-water resources to areas where adult pikes forage, suckers indirectly enhance the production of the younger pikes which forage in shallow areas. Coupling habitats in this way reinforces the flow of resources to top predators and strengthens top-down control of the more vulnerable prey (Carpenter and Kitchell 1993; Persson et al 1996; Polis and Strong 1996; Polis et al. 1996; Persson and Crowder 1998).

Our main result is that prey heterogeneity strongly mediates top-down control in the littoral food web of the St. Lawrence River. All consumer trophic levels responded to sewage enrichment, but the membership of the two lower levels changed: top predators controlled small, benthivorous fish but were unable to control larger fish, so the intermediate consumer level became dominated by suckers. Consequently, the prey of small fish were free to respond to sewage enrichment, but the prey of suckers were not. The proportion of chironomid larvae on sediment/understory also increased, probably because a fraction of these live on the understory vegetation, where they are less vulnerable to sucker predation. These patterns support the predictions of our mathematical model. Consumer control of vulnerable prey is strong, and these effects cascade to the next lower trophic level.

Furthermore, responses to sewage enrichment were mediated by among-site variation in habitat structure. Pikes are ambush predators, and require coarse debris or dense vegetation to hunt. In addition, the food chain leading to piscivores is based on epiphytic biofilm and intercepted detritus, primarily via midge larvae that scrape this material off vegetation. Suckers feed most effectively on bare sediment or in low understory. Thus, the response of top piscivores was strongest where high weed cover favoured efficient foraging by pikes and the competitive ability of their small, benthivorous prey. The response of suckers was strongest at relatively bare sites, where piscivores are least efficient and suckers can forage most effectively. This is consistent with previous work showing that consumer control can be mediated by the availability of plant cover (e.g., Carpenter and Lodge 1986; Power 1990a). It is also consistent with our mathematical model: a higher rate of supply of weedbed resources favours the chain leading to piscivores, whereas a higher rate of supply of sediment/understory resources favours suckers.

Previous studies have also shown that invulnerable prey can dominate the flow of resources under enriched conditions (Bohannon and Lenski 1999; Persson et al. 2001). Bohannon and Lenski (1999), for example, showed that enrichment of a model microbial food web with uniformly edible *E. coli* produced a response only in their predators (bacteriophage T4), indicating strong consumer control. When a bacteriophage-resistant strain of *E. coli* was also present, however, these invulnerable prey were able to "siphon off" all the added resources, and no response was seen in either the vulnerable prey or the predator. Suckers do not have this degree of control in the St. Lawrence, because the vulnerable benthivorous fishes can feed on weedbed-inhabiting invertebrates, a resource the suckers cannot access. However, the response of piscivores was weakest at relatively bare sites, where this resource is most limited.

In conclusion, our study supports arguments that variation among species within trophic levels can limit the strength of consumer control. Modeling and describing food webs demands some degree of aggregation to overcome the immense complexity in nature, but aggregating all species within trophic levels is a gross oversimplification (Pimm 1982; Polis 1991; Polis and Strong 1996). Important variation in prey vulnerability certainly exists, and recognition of that variation provides more useful and realistic view of food web dynamics.

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Connecting Statement

In the preceding chapters, I described the situation in the St. Lawrence under current water levels. Next, I consider the likely future of this river. Global climate change is altering the global hydrological cycle. The spatial distribution of water is going to change, and as a consequence some rivers will have higher or lower mean discharge than they have in the recent past. Our best models predict that the St. Lawrence is going to have lower discharge, and this may have serious implications for the future of sewage disposal in this river. I present this case study analysis as a model for how we should be thinking about all rivers.

CHAPTER 5: SEWAGE DISPOSAL UNDER FALLING WATER LEVELS IN THE ST. LAWRENCE RIVER

deBruyn, A.M.H. and J.B. Rasmussen. Perspective: Sewage disposal under falling water levels in the St. Lawrence River. submitted to Canadian Journal of Fisheries and Aquatic Science

Abstract

The capacity of a water body to assimilate sewage loading is determined by physical and biological characteristics of the system. Large rivers like the St. Lawrence have a large capacity to dilute and flush waste products, so physical retention and biological processing of that material is primarily restricted to shallow, vegetated areas. Strong physical forces protect the receiving environment from sediment and water-column anoxia, and permit the biota to exploit sewage enrichment. At present, the St. Lawrence effectively flushes Montreal's primary-treated sewage from the local environment. Biological uptake is restricted to the littoral zones of islands near the outfall. Here we argue that these protective forces will be weakened under the conditions of low flow projected for the St. Lawrence in the next few decades. Less dilution, slower current, greater macrophyte cover, and attenuated wave action will all act to enhance retention of sewage nutrients and organic matter. Warmer temperatures and the complex physical structure of macrophyte beds will enhance biological processing of this material, but will also increase the likelihood of anoxic events. We discuss some actions which could be taken to ameliorate likely problems. The analysis outlined here for the St. Lawrence provides a framework for considering the future of other Canadian waters subject to sewage loading.

Introduction

Recent reviews of sewage treatment and disposal in Canada paint an alarming picture (Chambers et al. 1997; Sierra Legal Defence Fund 1994, 1999). Most of the population is served by municipal wastewater treatment facilities, but a large fraction of these provide only preliminary (screening) or primary (settling) treatment (Chambers et al. 1997). Consequently, the 21 cities rated in the National Sewage Report Cards discharge a total of over one trillion litres of primary and untreated sewage each year (Sierra Legal Defence Fund 1994, 1999). These reviews, and most ecological studies, focus attention on the negative effects of sewage disposal. It is important to note, however, that in the majority of cases the rate of sewage loading does not exceed the capacity of the receiving water system to assimilate that waste. Adequate dilution and vertical mixing protect aquatic systems from anoxia and permit the receiving water biota to exploit sewage nutrients and organic matter. It is only when the assimilation capacity is approached or exceeded that receiving systems experience undesirable changes.

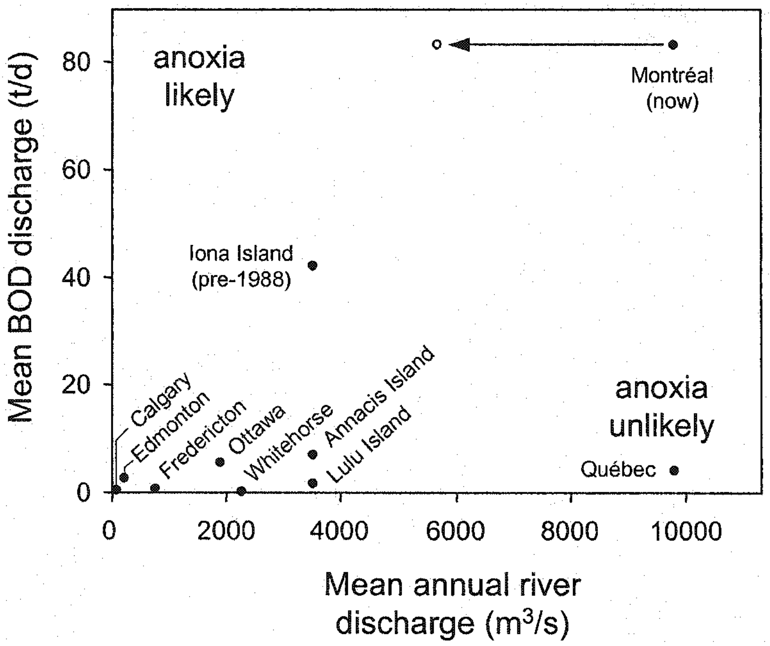
Three Canadian cities earned an 'F' grade on both Report Cards for discharging large volumes of primary or untreated sewage. Two of these, Victoria, BC and St. John's, NF, discharge their waste into oceans. Most large inland cities are forced to provide advanced sewage treatment to protect their waterways. These coastal cities rely on tidal flushing to prevent a local accumulation of waste and the associated negative consequences, although St. John's seems to have outgrown the weak flushing afforded by its constricted harbour mouth. The third, Montreal, QC, has been able to adopt the strategy of a coastal city because of the enormous flushing power of the St. Lawrence River. Montreal's wastewater treatment plant discharges conventional pollutants at a higher rate than any other city in Canada (Fig. 1), but the St. Lawrence seems to be protected by hydrodynamic forces from most adverse impacts.

Here we argue that these protective forces will be weakened under the conditions of low discharge projected for the St. Lawrence in the next few decades. We discuss the likely future of sewage disposal in the St. Lawrence River, primarily with reference to effects on the river ecosystem. We begin by outlining a general conceptual model of how a river's physical and biological characteristics dictate its response to sewage loading. We describe how these characteristics will change as water levels in the St. Lawrence fall, and how these changes will increase the likelihood of adverse impacts. Finally, we make some recommendations for possible management actions.

Assimilative capacity

Rivers have the capacity to assimilate a certain amount of nutrient and organic matter loading before the system is dramatically altered. The first aspect of that

Figure 1. Biochemical oxygen demand (5-day BOD) discharged by some major Canadian cities into their rivers, expressed in relation to the discharge of the receiving water. Vancouver's Iona Island outfall was moved into Georgia Strait in 1988 to ameliorate anoxia problems in the Fraser River. Open circle is Montreal's municipal wastewater under a scenario of 40% lower discharge in the St. Lawrence River


anoxia likely
anoxia unlikely
Montréal (now)
Iona Island (pre-1988)
Calgary
Edmonton
Fredericton
Ottawa
Whitehorse
Annacis Island
Lulu Island
Québec
Mean BOD discharge (t/d)
0
20
40
60
80
0
2000
4000
6000
8000
10000
Mean annual river discharge (m³/s)

capacity is physical, via local dilution and flushing into other parts of the hydrosphere (Officer and Ryther 1977). A given mass of material simply produces a lower final concentration when it is mixed into a larger body of water or more rapidly flushed from the local environment. Conditions that enhance retention (slow current, abundant retention structures, and high surface area of substrate; Minshall et al. 1983) will reduce flushing capacity, but will provide more opportunity for the system to exploit the nutrients.

A second aspect of assimilative capacity is biological uptake, sometimes referred to as the self-purification capacity of a system (e.g., Robach et al. 1993). Inorganic nutrients and dissolved organic matter (DOM) are taken up by algae and bacteria, particulate organic matter (POM) is degraded by bacteria or fungi and consumed by metazoans. The degree to which nutrients can be take up by the biotic community is a function of their retention time within the system, the efficiency with which the local biota can use nutrients in that form, and the degree to which other factors (e.g. light) limit that use. In addition, the system must contain consumers capable of transferring these basal resources to higher trophic levels. Unpalatable or noxious producers are a dead end for nutrient flows, and can produce changes in the physical and chemical environment deleterious to other taxa (e.g., Hötzel and Croome 1994).

A third aspect of assimilative capacity is the interaction between physics and biology. Organic matter and inorganic nutrients in sewage impose a biochemical oxygen demand (BOD), stimulating the consumption of oxygen by heterotrophic bacteria in the sediment and water column. If conditions support efficient physical mixing of oxygen, the respiration of heterotrophic bacteria can rapidly consume DOM, making this energy available to suspension feeders, and mineralize POM, enhancing the rate at which nutrients are flushed from the system. If oxygen is not replenished as quickly as it is consumed by heterotrophs, metazoan consumers will suffer (e.g., Chambers et al. 1997).

The balance between physical retention and flushing determines the degree of exposure of the river system to sewage, and thus the extent of both enrichment and negative effects (Fig. 2). Greater exposure to sewage nutrients produces a greater potential enhancement of community production, but also increases the frequency and severity of sediment and water-column anoxia (Pearson and Rosenberg 1978). At low ratios of sewage loading to flushing, enhancement effects dominate and there is a net increase in community production, without any dramatic changes in the community. This is the situation in the St. Lawrence now. As the ratio of loading to flushing increases, negative effects become more important. The net change in community production is still positive, but the composition of the community becomes biased toward taxa that are tolerant of hypoxia and organic mud. At high ratios of loading to flushing, these negative effects become overwhelming and more and more taxa are excluded, producing a net decrease in community production. Reduced flow in the St. Lawrence will move the river system toward the right of Figure 2.

The assimilative capacity of the St. Lawrence

Montreal's sewage plume. Montreal's sewage treatment plant provides chemically-aided primary treatment, removing about 85% of suspended particulates and phosphorus (Purenne 1998). The outfall is near Île aux Vaches, at the downstream tip of the Island of Montreal. Effluent is discharged at a rate of about 10^9 m^3/yr, contributing 90,000 tonnes of POM (wet wt.), 450 tonnes of phosphorus, and 40,000 tonnes of BOD annually to the waters of the St. Lawrence (Purenne 1998). The general trajectory of the wastewater plume has been described using a Rhodamine dye dispersion study (Boulanger 1984), but the discharge rate of wastewater has since increased 6-fold, from 5 to 30 m^3/s. Also, both the Ottawa River and Great Lakes outflow are regulated, producing seasonal and even daily variation in the width and concentration of the plume. The present extent of the plume is not precisely known, but in general it flows down the small-craft navigation channel (mean depth 5 m) north of the main shipping channel, and intercepts only a few island littoral zones in the reach between Montreal and

Lac St. Pierre. Consequently, retention and biological processing in this reach are currently limited to about the first 10 km from the outfall (deBruyn and Rasmussen, in press; A.M.H. deBruyn, unpublished data).

Channel areas. Large, constrained rivers like the St. Lawrence provide strong dilution and rapid flushing in their channels. Even a high effluent BOD, sufficiently diluted, will therefore cause only a small reduction in downstream dissolved oxygen. However, lateral mixing is very slow in the St. Lawrence downstream of Montreal. The narrow mixing zone between the Ottawa River and Great Lakes water masses persists at least to the mouth of Lac St. Pierre, 60 km downstream of Montreal (Verrette 1990). Sewage is discharged into this mixing zone, and the plume widens only very gradually after initial (mostly vertical) dilution to about 5% effluent. The realized level of dilution is thus substantially less than the potential offered by the entire river, but sufficient to reduce the instream BOD concentration to 1-2 mg/l. The resulting (moderate) oxygen depletion is rapidly replenished from the atmosphere by vertical mixing (Proulx 1998).

Biological processing of sewage in large river channels is typically low. Current speeds in the channels of the St. Lawrence are usually greater than 1 m/s, restricting net sediment accumulation to the deepest areas (Carignan and Lorrain 2000). Low surface area of contact with overlying water limits the access of benthic organisms to suspended and dissolved resources. Deep channel benthos is light-limited, and plankton development is strongly constrained by residence time (Basu and Pick 1996; Pace et al. 1992). Consequently, algal blooms in response to nutrient enrichment are usually only seen in the slack waters behind dams, or in the estuaries of enriched rivers (e.g., Justic et al. 1995; Pinckney et al. 1997).

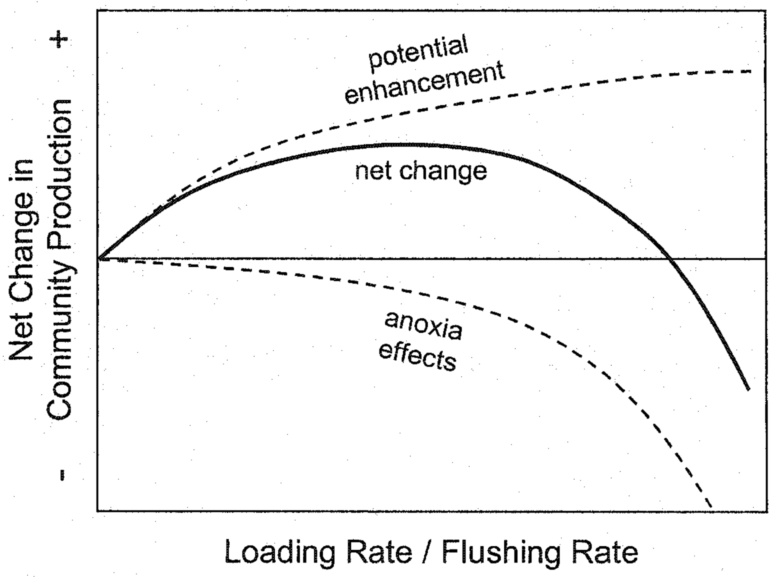
Littoral areas. Shallow, inshore areas of large rivers have much slower current than channels, combined with strong wave action. This enhances both sedimentation and resuspension, ensuring a continual resupply of fresh POM to the sediment (Rasmussen 1993). Macrophytes further enhance particle trapping (Sand-Jensen and Mebus 1996; Vermaat et al. 2000), increasing nutrient concentrations in the sediment (Chambers and Prepas 1994). These forces increase access of the benthic biota to sewage POM.

Temporary physical retention of POM permits rapid biological processing in littoral areas (Thorp and Delong 1994). We estimate that 70% of Montreal's sewage POM is consumed by benthic macroinvertebrates within 10 km of the outfall in midsummer (A.M.H. deBruyn, unpublished data). Large river littoral zones are also more or less well-lit, depending on the nature of riparian vegetation and the slope of the substrate. Macrophytes provide abundant surface area for attached algae and heterotrophic bacteria, and increase the residence time of inorganic nutrients and DOM. In the St. Lawrence, uptake of sewage phosphorus is strongly correlated with macrophyte cover (A.M.H. deBruyn, unpublished data). Macrophytes also provide a physically complex substrate that supports higher densities of macroinvertebrates than bare areas (St. Lawrence Centre 1996). Invertebrate production is further enhanced because shallower, slower-moving water warms up more quickly in spring, reaches higher temperatures in summer, and stays warm longer in fall. Any changes that increase the extent of littoral zone in the St. Lawrence will increase retention and biological processing (Robach et al. 1993).

The future of the St. Lawrence

The St. Lawrence of the next few decades will be very different from that of the recent past. Global climate models linked to a hydrologic model of the Great Lakes Basin predict a mean 40% reduction in flow, with minimum flow 60% below present mean levels (International Joint Commission 1993; Mortsch and Quinn 1996). Proposed diversions of water to the U.S. would also reduce flow. In addition, level records since 1860 indicate that the last 25 years have been a period of extremely high flow for the St. Lawrence, and that this period is ending (Hudon 1997). The physical and biological changes precipitated by this

Figure 2. The balance between positive and negative effects on community production with increasing exposure to sewage organic matter and nutrients. Enhancement effects increase until other factors become limiting (e.g., light, space). Negative effects such as anoxia increase when exposure exceeds the capacity of the biota to process enriching materials.



+
potential enhancement
net change
anoxia effects
-
Net Change in Community Production
Loading Rate / Flushing Rate

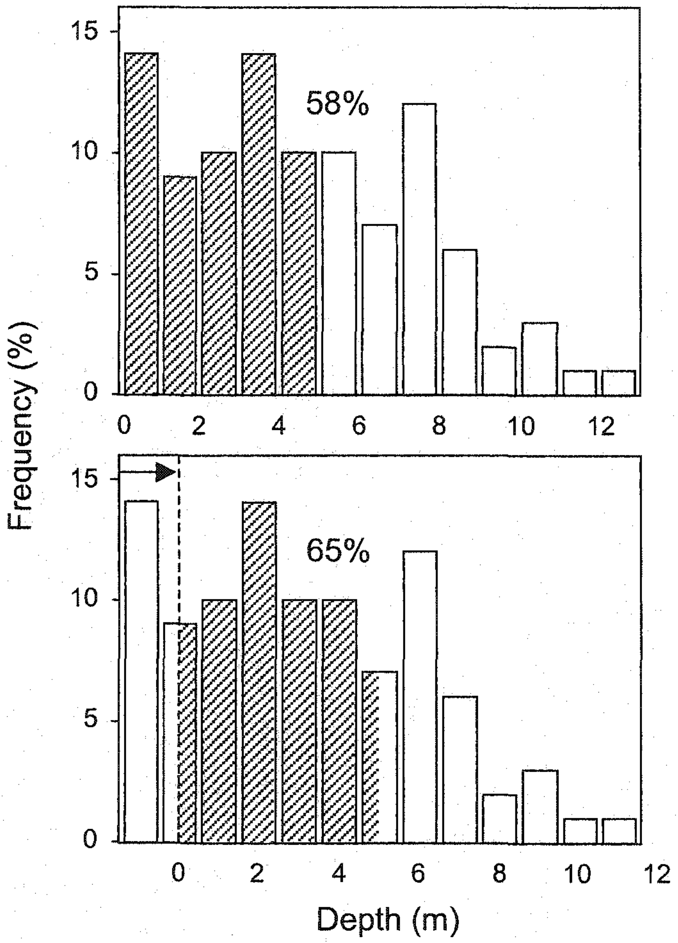
reduction in flow will be complex and difficult to predict with certainty. However, there are a few predictions we can make with reasonable confidence.

A 40% reduction in flow corresponds to a 1.3 m drop in water level, and a consequent shift in the distribution of depths (Fig. 3). Many areas that have been shallow wetlands (e.g., much of Lac St-Pierre) will become wet meadow, and many areas of open water will become macrophyte-dominated marshes. A greater proportion of the bottom will be illuminated, increasing the extent of potential macrophyte colonization (Hudon 1997). Submerged macrophytes further reduce current speed, enhance settling and stabilize sediment. Thus, while lower water levels will decrease the area of the St. Lawrence, a higher proportion of macrophyte cover will increase the mean areal secondary production.

The small-craft navigation channel which carries Montreal's sewage plume will experience some of the most dramatic changes. First, a shift in the depth distribution will increase the fraction of sediment which can support macrophytes (Fig. 3). All of the islands in this reach will become larger, and all of their littoral zones will extend further into the channel. Increased macrophyte cover and shallower depths will slow current speeds in the small-craft channel, forcing more of the river's discharge into the main shipping channel to the south. Furthermore, more of the mid-river islands will be joined, and the shallow areas between them filled with macrophytes. This will act to protect the small-craft channel from waves generated by ships in the main shipping channel.

The physical and biological changes outlined above will dramatically affect the retention and biological processing of sewage in this reach. Initial dilution of the sewage effluent is primarily via vertical mixing, so a 25% decrease in mean depth will produce at least a 33% increase in effluent concentration. Slower current will further decrease the degree of dilution. Slower current, less wave action, and more extensive macrophyte beds will all act to increase retention of POM. More extensive macrophyte cover will also increase the retention of

Figure 3. Distribution of depths in the small-craft navigation channel of the St. Lawrence River downstream of Montreal, at long-term mean water levels (upper panel) and under a scenario of 40% lower discharge (lower panel). The fraction of total area potentially colonizable by macrophytes (< 5 m) is hatched and indicated as a percentage.



15
10
5
0
58%
0
2
4
6
8
10
12
Frequency (%)
15
10
5
0
65%
0
2
4
6
8
10
12
Depth (m)

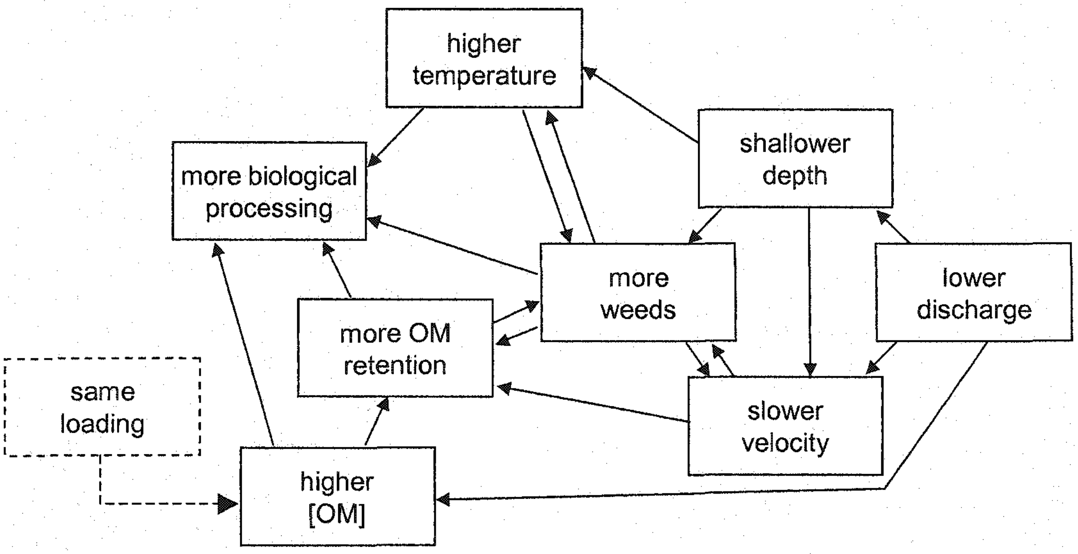
dissolved nutrients, by increasing the surface area of contact between the water column and the benthos. Warm, shallow macrophyte beds, bathed in nutrient-rich sewage effluent, will produce abundant attached algae and heterotrophic bacteria. If these organisms are palatable to macroinvertebrates, this excess production will be readily transformed into fish biomass (Ellis and Gowing 1957; Johnston et al. 1990; A.M.H. deBruyn, unpublished data).

Unfortunately, the changes outlined above (and summarized in Fig. 4) will also increase the likelihood of negative effects. First, higher BOD concentration will increase the rate of oxygen depletion in the water column. Slower current and reduced wave action may also reduce the rate at which oxygen is replenished via vertical mixing, further increasing the frequency of water-column hypoxia or anoxia. Second, if the rate of POM retention exceeds the rate of biological processing, an organic mud will accumulate over the summer. Lower peak flows in spring and fall, further weakened by well-rooted, overwintering macrophyte structures, may be unable to flush this mud each year. Enriched, organic sediment promotes further growth of macrophytes, in a positive feedback loop (Chambers and Prepas 1994). Organic mud is poor habitat for the sediment-dwelling organisms currently abundant in the St. Lawrence, and prone to anoxia and anoxia-induced H_2S toxicity. Finally, it is possible that nutrient enrichment will produce blooms of unpalatable metaphyton (e.g., Murkin et al. 1994; McCormick et al. 1998), reducing the productivity and quality of the habitat for consumers.

Conclusion: management options and research imperatives

Lower water levels will greatly reduce the ability of the small-craft channel to dilute and flush sewage, but will have a much smaller effect on the main shipping channel. An obvious solution to this problem, then, is to move the sewage outfall into the larger channel. Some areas of the main channel are subject to sedimentation, however, and the Canadian Coast Guard dredges about 30,000 m^3 of sediment per year in the fluvial section of the St. Lawrence to maintain an adequate depth for shipping (St. Lawrence Centre 1996). Under lower water

Figure 4. Schematic representation of how lower river discharge can affect retention and processing of sewage organic matter (OM) via physical and biological changes, their interactions and feedbacks. Arrows indicate direct causal relationships. See text for details.


higher temperature
more biological processing
shallower depth
more weeds
lower discharge
more OM retention
same loading
slower velocity
higher [OM]

levels, this dredging will become even more important. Adding 90,000 tonnes of sewage-derived POM to the channel will only exacerbate the sedimentation problem.

Ultimately, the best solution to this problem is improved treatment. Under conditions of extreme low flow (60% below current mean levels; International Joint Commission 1993; Mortsch and Quinn 1996), Montreal's sewage discharge falls in the area of Fig. 1 where anoxic events are likely. The St. Lawrence is a heavily used river. The reach downstream of Montreal supports a wide variety of recreational and commercial users (reviewed in St. Lawrence Centre 1996), as well as a diverse and productive ecosystem. Anoxic events would have catastrophic consequences for many of these uses. The simplest way to avoid this is to reduce the discharge of BOD in proportion to the reduction in river discharge. Unfortunately, the high rate of effluent discharge makes this a considerable engineering problem: a treatment wetland capable of holding 30 m^3/s at 50 cm depth for 5 days would require 25 km^2.

River ecologists have made great progress in understanding how physical forces and biological processes influence material cycling (e.g., Vannote et al. 1980; Ward and Stanford 1983; Minshall et al. 1983, 1985; Junk et al. 1989; Thorp and Delong 1994). The analysis outlined above provides a framework for using these theories to consider the future of Canadian waters subject to sewage loading. Fortunately, much of the work that will need to be done to accomplish this is already underway. Researchers at Environment Canada's St. Lawrence Centre and Canadian Meteorological Society are investigating the effects of reduced water levels and flow on factors such as fine-scale hydrodynamics (Morin et al. 2000), sediment dynamics (Lepage et al. 2000) and patterns of macrophyte development (Hudon 1997). It is a certainty that many Canadian rivers are going to be dramatically altered by climate changes. We hope that this perspective will stimulate discussion of what those alterations will be, and what they will mean for the future of sewage disposal in Canada.

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GENERAL CONCLUSIONS

University researchers are often perceived as having to choose between pure and applied research. I believe that it is possible, even imperative, to include both goals in a research program. Much of what is generally considered "pure" ecology can be expanded to include a consideration of applied issues, and can be usefully brought to bear on applied problems. Conversely, even the most applied work can only benefit from the insights offered by general theory.

The general theory of river ecologists has been based largely on observations of stable, unperturbed systems in forested watersheds. Most rivers, however, are influenced to some extent by human activities. Rivers worldwide are dredged, dammed, diked, channelized, and polluted with excess nutrients and toxic contaminants. These activities alter fundamental physical and biological characteristics, and thus can have dramatic effects on the structure and function of river ecosystems. On the one hand, these activities represent large-scale, uncontrolled experiments which can reveal much about the perturbed ecosystems. At the same time, these activities represent real threats to the integrity of those ecosystems. Our ability to manage those threats hinges on our understanding of how these ecosystems work. This is the strength of general theory.

The general theory addressed in this work concerns how characteristics of an ecological system influence the flow of energy and materials, and how these flows in turn affect the structure and function of a system's biological community. In flowing-water systems, the degree to which nutrients and organic matter can be exploited by the biotic community is a function of retention time within the system, the efficiency with which the local biota can use these materials, and the degree to which other factors limit that use. Large river littoral zones are well suited to exploiting sewage nutrients and organic matter (Chapters 1 and 2), and characteristics that enhance physical retention and biological processing increase the degree of enrichment (Chapter 2). Such localized basal enrichment can perturb a local assemblage away from the regional density-body size relationship

(Chapter 3) via cascading trophic interactions (Chapter 4), mediated by the influence of habitat structure on nutrient uptake (Chapter 2), predator efficiency, and prey vulnerability (Chapter 4). However, the capacity of a system to assimilate the enriching materials in sewage is determined by a complex interplay of physical and biological characteristics; if the rate of sewage loading exceeds that capacity, the system will be subject to gross physical and biological changes (Chapter 5).

The specific case addressed in this work is the effect of Montreal's sewage discharge on the ecology of the St. Lawrence River. Sewage represents a clear perturbation of the ecosystem of this river. Despite the absence of gross negative effects typically associated with sewage pollution, I was able to show that the river is far from being a passive conduit for waste. Sewage-derived carbon and nitrogen are rapidly assimilated by the river's foodweb (Chapters 1 and 2), stimulating dramatic increases in secondary production (Chapter 2). Increased energy flow to higher trophic levels precipitates a shift in community size structure, supporting a relative preponderance of large-bodied fishes (Chapter 3). The identity of these large-bodied organisms depends on whether habitat structure favours the flow of energy to small-bodied invertivorous fishes and their predators, or to large-bodied suckers which have no predators in such shallow water (Chapter 4). All of these changes reflect the great capacity of this river system to physically retain and biologically process the nutrients and organic matter in sewage. Lower river discharge in the next few decades will enhance both retention and processing, and may increase the likelihood of negative effects in the St. Lawrence near Montreal (Chapter 5).

This thesis addresses a specific, relevant problem within the context of general ecological theory, and uses the specific case to verify and extend that body of theory. The St. Lawrence is simultaneously a model system in which to test hypotheses about material cycling and foodweb dynamics, and a great big river with immense social, economic, and ecological value. Ecological problems are best addressed by research that recognizes both aspects of a study system. My hope, then, is that this thesis makes two contributions: I hope that it has value to the managers who work directly with the St. Lawrence, and I hope that it advances the field of river ecology in general, which in turn will improve our ability to cope with threats to all rivers.

APPENDIX 1. Stable isotope signatures of primary consumers from sites in the St. Lawrence River.

Site			Weed	Amphipoda		Trichoptera		Chironomidae (green)		Chironomidae (red)	
code	Site name	Date	cover	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
BB	Ile Bois-Blanc	2-Aug	0.32	-15.8	8.4	-19.9	8.9	-18.1	8.4	-20.8	8.3
BB	Ile Bois-Blanc	19-Aug	0.32	-19.5	7.9	-17.5	8.6	-11.1	7.4	-21.9	8.3
FOI	Ile aux Foins	11-Jul	0.20	-16.1	8.0	-16.5	8.9	-16.1	8.1	-22.8	7.5
FOI	Ile aux Foins	24-Aug	0.20	-16.4	8.1	-16.9	8.2	-12.2	7.2	-15.4	8.4
GRA	Ile de Grace	7-Aug	0.27	-18.1	9.5	-20.3	9.4	-18.0	8.6	-21.6	9.1
GRA	Ile de Grace	4-Sep	0.27	-18.8	8.5	-20.3	9.1	-16.1	8.8	-20.8	8.6
GRO	Ile Grosbois	8-Aug	0.82	-19.2	9.4	-22.5	10.2	-16.1	9.2	-23.6	9.0
GRO	Ile Grosbois	1-Sep	0.82	-14.7	8.7	-17.0	10.1	-14.7	9.3	-15.7	8.3
LAV	Ile Lavaltrie	25-Jul	0.23	-17.7	8.7	-18.1	9.2	-17.6	8.6	-19.1	8.9
LAV	Ile Lavaltrie	31-Aug	0.23	-16.9	8.8	-19.9	8.8	-18.3	8.5	-18.9	9.7
ROB	Iles Robinet	20-Jul	0.28	-17.1	4.5	-16.9	5.1	-17.3	2.8	-18.3	5.5
ROB	Iles Robinet	23-Aug	0.28	-16.2	3.6	-17.1	2.9	-14.8	3.8	-17.7	1.1
RON	Ile Ronde	27-Jul	0.70	-15.2	7.9	-15.9	8.5	-21.9	8.4	-17.1	9.1
RON	Ile Ronde	5-Sep	0.70	-16.0	8.3	-13.4	9.6	-12.3	9.3	-18.3	8.1
STO	Ile St-Ours	25-Jul	0.30	-15.4	8.5	-15.1	8.1	-17.1	9.4	-16.1	6.8
STO	Ile St-Ours	31-Aug	0.30	-13.7	8.5	-14.9	9.4	-15.1	9.4	-14.8	8.5

TEA	Ile Ste-Therese East	19-Jul	0.07	-19.2	8.3	-19.0	8.7	-18.9	7.6	-20.5	8.2
TEA	Ile Ste-Therese East	16-Aug	0.07	-18.6	8.1	-19.2	7.9	-18.1	8.0	-19.2	9.1
THE	Ile Ste-Therese North	19-Jul	0.13	-17.6	1.7	-18.1	3.4	-19.4	0.9	-18.8	0.4
THE	Ile Ste-Therese North	16-Aug	0.13	-18.5	3.8	-20.1	2.8	-19.6	1.4	-19.5	1.5
VAC	Ile aux Vaches	3-Aug	0.50	-14.7	8.5	-15.9	8.6	-18.2	8.3	-17.5	7.6
VAC	Ile aux Vaches	1-Sep	0.50	-17.4	7.9	-17.3	8.8	-21.2	8.0	-18.7	7.4
VER	Ilet Vert	17-Jul	0.62	-15.3	6.6	…	…	-14.3	6.6	-16.6	6.5
VER	Ilet Vert	17-Aug	0.62	-16.3	3.5	…	…	-17.6	4.2	-15.7	5.9

APPENDIX 2. Total seined area (A, m^2) and biomass densities of fish (mg/m^2) at sites in the St. Lawrence River. Species codes are: alew: alewife; bass: smallmouth and largemouth bass; blac: blackchin shiner; bull: brown bullhead; dart: johnny darter; emer: emerald shiner; gold: golden shiner; kill: banded killifish; logp: logperch; perc: yellow perch; pike: northern pike, muskellunge and chain pickerel; pump: pumpkinseed; rock: rock bass; spot: spottail shiner; suck: white sucker and silver redhorse; trou: troutperch; wall: yellow walleye. Site codes as in Appendix 1.

Site	Date	A	alew	bass	blac	bull	dart	emer	gold	kill	logp	perc	pike	pump	rock	spot	suck	trou	wall
BB	2-Aug	938	19.7	67.5	14.0	0.0	4.8	107.3	16.0	0.0	31.8	1158	38.9	226.2	15.4	134.9	6907	0.9	315.7
BB	19-Aug	904	0.0	1.3	0.0	1.7	6.9	2208	9.8	0.0	136.8	802.9	81.5	178.5	354.0	2.6	84.1	1.5	98.7
FOI	11-Jul	840	0.0	0.0	0.0	0.0	1.6	65.8	18.6	47.7	0.0	196.3	0.0	0.0	0.0	46.2	15.5	0.0	0.0
FOI	24-Aug	1593	0.0	2.0	0.0	0.0	5.4	213.1	257.2	0.0	4.9	376.6	0.0	31.2	21.3	24.6	38.2	11.9	0.0
GRA	7-Aug	1261	1.5	51.4	15.9	433.7	20.8	409.9	68.3	7.5	99.3	917.1	0.0	430.1	162.8	389.0	1119	296.2	5.5
GRA	4-Sep	1067	0.0	14.5	21.7	0.0	25.8	108.0	3.7	0.0	212.2	185.0	0.0	0.0	0.0	474.8	1068	960.6	0.0
GRO	8-Aug	973	0.0	284.1	1.0	0.0	23.7	0.0	117.4	10.1	26.4	1862	647.8	981.4	23.3	1.2	1.2	0.0	0.0
GRO	1-Sep	840	0.0	585.2	7.6	0.0	3.5	14.4	0.0	2.5	163.3	1891	1422	114.9	16.9	70.5	14.3	0.0	0.0
LAV	25-Jul	840	133.5	0.0	0.0	0.0	0.0	202.7	0.0	0.0	0.0	172.8	0.0	0.0	0.0	0.0	3217	0.0	0.0
LAV	31-Aug	728	3.0	25.7	5.2	0.0	1.6	360.2	0.0	0.3	35.7	132.0	97.7	12.0	0.0	10.2	493.7	0.0	0.0
ROB	20-Jul	1317	23.6	2013	0.0	315.8	5.1	147.0	2.5	0.0	16.1	566.6	852.6	0.0	0.0	0.0	1879	4.6	29.9
ROB	23-Aug	904	1.1	1112	51.6	0.0	68.3	1037	6.7	0.0	916.4	465.3	2469	0.7	65.8	382.2	10152	31.2	0.0
RON	27-Jul	1585	0.0	6.9	0.0	33.6	4.4	1.3	426.3	66.2	0.0	937.9	1038	281.5	20.8	0.0	1873	0.0	6.4

RON	5-Sep	1071	0.0	14.4	2.3	0.0	1.5	0.0	410.2	8.9	0.0	1539	31.5	89.5	35.8	4.0	96.9	1.6	0.0
STO	25-Jul	840	62.7	0.0	11.8	0.0	9.9	527.6	3.0	176.6	1.6	675.9	0.0	0.0	0.0	27.7	260.3	0.0	0.0
STO	31-Aug	1458	0.0	10.2	0.9	0.0	7.4	18.4	0.0	2.6	12.6	0.0	16.0	0.0	2.7	0.1	21.9	1.0	0.0
TEA	19-Jul	917	1.4	0.0	109.2	0.0	7.3	1.7	0.0	0.0	38.3	198.6	13.4	0.0	4.8	0.0	91.2	5.2	0.0
TEA	16-Aug	1378	0.0	153.0	0.0	0.0	6.8	5.1	0.0	0.0	10.5	30.8	0.0	0.0	0.9	0.4	72.5	5.2	0.0
THE	19-Jul	672	0.0	1213	48.9	0.0	0.1	0.0	0.0	0.0	0.4	159.2	0.0	0.0	0.0	198.4	12572	1.4	325.4
THE	16-Aug	784	3.7	0.0	0.0	1016	3.5	30.1	0.0	0.0	0.0	64.6	7.1	0.0	2.1	12.7	12895	105.5	93.2
VAC	3-Aug	840	167.4	0.0	22.0	494.8	55.4	7.6	345.7	0.0	9.8	1657	942.5	21.3	63.3	663.3	1177	0.0	0.0
VAC	1-Sep	672	0.0	9.5	26.8	53.4	225.1	0.0	222.3	4.5	1.4	1832	278.6	48.4	187.2	15.3	459.1	0.0	0.0
VER	17-Jul	968	0.0	611.4	0.0	59.8	6.9	0.0	0.0	9.9	17.6	493.4	1492	0.0	11.7	0.0	263.2	0.4	11.9
VER	17-Aug	1005	0.0	4.1	1.3	663.8	162.7	12.9	0.0	15.2	120.4	1157	3405	0.0	19.6	2.8	4938	13.2	4.5

APPENDIX 3. Growth parameters of fish from the St. Lawrence River (all sites pooled). Pooled species (basses, pikes, suckers) as in Appendix 2.

	Instantaneous growth rate of age class (slope of log weight vs day)			Mean weight of age class (g)		
species	0+	1+	2+	0+	1+	2+
alewife	0.045	0.022	...	0.097	2.371	...
basses	0.014	0.018	0.018	1.641	32.88	1339
blacknose	0.011	0.012	0.007	0.210	0.762	1.862
bullhead	0.043	0.020	...	0.473	...	...
darter	0.008	0.006	0.006	0.243	1.845	5.623
emerald	0.006	0.008	0.006	0.167	0.953	2.793
common	0.006	0.008	0.006	0.167	0.953	2.793
golden	0.030	0.008	0.007	0.126	3.273	15.34
killifish	0.007	0.003	0.003	0.172	2.089	6.295
logperch	0.013	0.007	...	0.771	5.546	...
perch	0.010	0.004	0.000	2.133	22.64	82.79
pumpkinseed	0.020	0.014	0.000	0.195	6.982	49.20
rockbass	0.020	0.014	0.000	0.195	6.982	49.20
pikes	0.013	0.003	...	10.81	820.3	...
spottail	0.013	0.010	...	0.394	4.529	...
suckers	0.006	0.010	0.005	1.247	32.43	1205
troutperch	0.012	0.005	...	0.655	5.224	...
walleye	0.020	0.010	0.005	3.499	48.52	...

APPENDIX 4. Secondary production of fish in the St. Lawrence River, estimated by Growth Increment Summation (GIS) and Instantaneous Growth Rate (IGR) methods. Site codes as in Appendix 1; species name abbreviations as in Appendix 2.

GIS

site	alew	bass	blac	bull	dart	emer	gold	kill	logp	perc	pike	pump	rock	spot	suck	trou	wall
BB	4.40	24.42	2.01	0.14	13.67	923.2	5.50	0.00	156.8	2480	42.97	85.35	203.06	60.45	5489	0.93	98.37
FOI	0.00	0.48	0.00	0.00	4.63	71.02	177.97	8.92	0.73	359.1	0.00	3.65	25.88	49.72	107.74	3.13	0.00
GRA	0.27	18.92	4.24	0.23	16.55	225.3	52.66	1.68	364.9	1795	0.00	154.83	123.92	595.57	8549	1563	2.10
GRO	0.00	253.33	1.20	0.00	12.82	2.58	72.73	7.24	109.8	2129	3328	970.80	40.53	11.96	4.81	0.00	0.00
LAV	46.34	4.82	0.36	0.00	0.45	64.78	0.00	0.10	23.60	145.2	20.47	1.07	0.00	1.16	3261	0.00	0.00
ROB	11.27	2974	8.56	0.00	64.57	377.6	1.82	0.00	833.9	385.2	799.13	0.12	12.08	100.94	3368	11.48	25.93
RON	0.00	7.64	0.48	25.82	3.93	0.21	866.9	28.74	0.00	1458	723.74	361.40	88.18	0.73	506.3	0.29	4.02
STO	21.25	1.92	2.53	0.00	11.96	31.62	0.83	51.56	3.44	368.1	3.35	0.00	0.35	9.24	128.0	0.21	0.00
TEA	0.66	22.54	15.49	0.00	24.72	1.72	0.00	0.00	17.84	55.36	9.74	0.00	5.53	0.14	84.22	11.12	0.00
THE	0.39	507.44	0.11	0.48	1.11	8.56	0.00	0.00	0.29	52.34	2.30	0.00	0.53	58.35	6993	27.96	119.25
VAC	36.57	1.73	10.55	1.48	189.12	1.28	133.98	1.37	4.10	788.6	1623	25.14	470.39	181.12	681.3	0.00	0.00
VER	0.00	277.36	0.15	92.65	168.19	2.35	0.00	5.92	162.41	932.1	2262	0.00	84.32	0.89	2064	3.97	11.69

IGR

site	alew	bass	blac	bull	dart	emer	gold	kill	logp	perc	pike	pump	rock	spot	suck	trou	wall
BB	0.48	1.38	0.11	0.01	0.08	13.22	0.22	0.00	1.58	9.75	1.26	5.78	1.26	1.55	41.95	0.03	3.66
FOI	0.00	0.02	0.00	0.00	0.05	2.23	2.19	0.21	0.03	1.90	0.00	0.24	0.17	0.80	0.41	0.09	0.00
GRA	0.03	0.63	0.23	0.02	0.30	3.18	0.51	0.03	2.44	7.77	0.00	2.55	1.77	7.64	11.90	9.85	0.10
GRO	0.00	7.99	0.06	0.00	0.17	0.07	1.07	0.05	1.18	10.53	8.40	7.69	0.40	0.35	0.07	0.00	0.00
LAV	4.89	0.16	0.03	0.00	0.01	3.51	0.00	0.00	0.20	0.85	0.60	0.07	0.00	0.06	21.98	0.00	0.00
ROB	1.12	79.20	0.39	0.00	0.35	8.49	0.07	0.00	6.42	0.87	12.69	0.01	0.56	2.97	67.01	0.32	1.22
RON	0.00	0.25	0.01	1.04	0.04	0.01	10.85	0.29	0.00	7.92	4.74	2.30	0.54	0.02	11.38	0.01	0.19
STO	2.29	0.06	0.11	0.00	0.11	3.83	0.03	0.80	0.10	2.81	0.10	0.00	0.02	0.37	1.78	0.01	0.00
TEA	0.07	1.73	1.71	0.00	0.11	0.07	0.00	0.00	0.43	1.10	0.29	0.00	0.13	0.00	1.17	0.08	0.00
THE	0.04	43.98	0.01	0.05	0.02	0.20	0.00	0.00	0.01	1.01	0.07	0.00	0.02	2.88	151.3	0.79	3.10
VAC	3.90	0.06	0.33	0.15	1.57	0.05	4.38	0.02	0.12	13.39	5.13	0.78	2.11	7.34	9.48	0.00	0.00
VER	0.00	24.13	0.01	9.57	1.16	0.09	0.00	0.10	1.43	6.39	18.72	0.00	0.53	0.03	30.88	0.11	0.55

APPENDIX 5. Gut contents (mean volume % of *n* individuals) of fish from reference (ref) and sewage-exposed (sew) sites in the St. Lawrence River. Amph = Amphipoda; Chir = Chironomidae; Clad = Cladocera; Fish = fish; Snai = snails; Terr = terrestial insects (aphids, adult flies); Aqua = aquatic insects (larval mayflies, caddisflies, stoneflies, corixids); Unid = unidentifiable organic material; Sed = sediment; Other = assorted non-insect taxa (clams, ostracods, mites, crayfish).

Species	Age	Sites	*n*	Amph	Chir	Clad	Fish	Snai	Terr	Aqua	Alga	Unid	Sed	Other
alewife	0	sew	5	0	40	54	0	0	0	5	0	0	0	1
alewife	1	ref	11	4	80	0	0	0	10	4	0	0	0	2
alewife	1	sew	7	3	43	0	22	0	0	22	0	0	7	3
bass	0	ref	4	9	5	0	66	0	0	20	0	0	0	0
bass	0	sew	2	5	25	3	33	0	0	10	0	23	3	0
bass	1	ref	7	1	2	0	94	0	0	4	0	0	0	0
bass	1	sew	4	0	0	0	100	0	0	0	0	0	0	0
blacknose	0	sew	1	0	100	0	0	0	0	0	0	0	0	0
blacknose	1	ref	6	0	7	0	0	0	0	0	71	23	0	0
blacknose	1	sew	7	0	61	0	0	0	0	4	0	35	0	0
blacknose	2	ref	17	0	22	0	0	0	0	0	58	19	1	0
blacknose	3	ref	2	0	25	1	0	0	0	0	75	0	0	0
blacknose	3	sew	4	0	83	0	0	0	0	14	0	4	0	0

bullhead	0	ref	2	40	8	0	0	50	0	3	0	0	0	0
bullhead	0	sew	8	15	35	42	0	0	4	2	0	0	0	2
darter	0	ref	14	25	50	10	0	3	0	9	0	3	0	0
darter	0	sew	18	6	82	6	0	0	0	3	0	0	1	2
darter	1	ref	14	36	30	0	0	12	0	0	0	11	0	10
darter	1	sew	10	45	55	0	0	0	0	1	0	0	0	0
darter	2	sew	1	0	100	0	0	0	0	0	0	0	0	0
emerald	1	ref	5	0	0	0	0	0	0	0	26	73	0	1
emerald	1	sew	15	0	7	10	0	0	0	0	5	68	10	0
emerald	2	ref	10	0	55	0	0	0	0	5	11	28	2	0
emerald	2	sew	10	2	20	0	0	0	1	7	23	38	10	0
golden	0	ref	5	0	48	0	0	0	6	0	17	28	0	1
golden	1	ref	16	0	8	6	0	55	0	0	7	19	1	3
golden	1	sew	2	0	0	0	0	0	0	0	100	0	0	0
killifish	0	ref	5	38	22	0	0	31	0	7	0	0	0	2
killifish	1	sew	4	11	45	23	0	19	0	3	0	0	0	0
logperch	0	ref	20	26	52	8	0	3	0	6	1	5	0	0
logperch	0	sew	31	12	68	16	0	3	0	1	0	0	0	0

logperch	1	ref	11	46	37	5	0	0	0	10	0	0	0	1
logperch	1	sew	3	67	28	0	0	0	0	5	0	0	0	0
perch	0	ref	17	17	63	11	0	1	0	5	0	0	2	0
perch	0	sew	5	38	28	33	0	0	0	0	0	0	0	1
perch	1	ref	22	53	13	1	4	15	1	9	0	0	1	3
perch	1	sew	22	54	20	2	9	4	0	0	0	9	0	3
perch	2	ref	1	25	0	0	60	0	0	15	0	0	0	0
perch	2	sew	8	26	24	0	9	15	0	3	14	9	0	0
pikes	0	ref	8	0	0	0	100	0	0	0	0	0	0	0
pikes	0	sew	6	0	0	0	100	0	0	0	0	0	0	0
pumpkinseed	1	ref	11	24	20	3	0	35	0	17	0	0	0	1
rockbass	0	ref	18	10	62	6	0	0	0	15	0	6	0	2
rockbass	0	sew	14	4	81	4	0	0	0	8	0	0	0	3
rockbass	1	ref	11	44	1	0	0	1	0	30	0	2	0	22
rockbass	1	sew	1	40	50	10	0	0	0	0	0	0	0	0
spottail	0	ref	8	0	73	1	0	0	1	3	5	13	0	6
spottail	0	sew	10	0	68	4	0	0	0	2	0	25	0	1
spottail	1	ref	11	0	16	1	0	42	0	0	31	6	4	1

spottail	1	sew	6	0	85	9	0	0	0	0	0	4	0	1
suckers	0	ref	30	1	41	35	0	1	0	1	0	6	9	7
suckers	0	sew	36	4	45	26	0	0	0	0	4	1	14	6
suckers	1	sew	1	0	50	50	0	0	0	0	0	0	0	0
sucker s	1	ref	6	4	44	19	0	1	0	14	8	0	9	0
troutperch	0	ref	7	7	88	4	0	0	0	0	0	0	0	0
troutperch	0	sew	23	2	69	25	0	0	0	0	0	3	0	0
walleye	0	ref	10	0	0	0	59	0	0	0	0	40	1	0
walleye	0	sew	45	0	0	0	83	0	0	0	0	17	0	0
walleye	>0	sew	4	0	0	0	100	0	0	0	0	0	0	0

APPENDIX 6. Mean biomass densities (g dry wt./m^2) of invertebrates sampled in weedbeds (Weed) and on bare sediment/understory at 1 m (Deep) and 0.5 m (Shallow) depths at sites in the St. Lawrence River. Chir = Chironomidae; Amph = Amphipoda; Snai = snails; Tric = Trichoptera; Clam = clams; Cori = Corixidae; Leec = leeches; Mite = mites; Ephe = Ephemeroptera; Clad = Cladocera; Lepi = lepidoptera (caterpillars); Nema = Nematoda; Anis = Anisoptera; Other = assorted taxa. Site codes as in Appendix 1.

Weed

Site	Date	Chir	Amph	Snai	Tric	Clam	Cori	Leec	Mite	Ephe	Clad	Lepi	Nema	Anis	Other
BB	19-Aug	152.1	2.2	5.7	1.1	1.2	0.0	0.0	4.4	0.4	0.4	0.6	0.0	1.0	0.0
BB	19-Aug	96.3	3.9	108.4	18.3	4.1	0.0	0.0	4.8	0.0	1.1	0.0	0.4	0.0	2.2
GRO	8-Aug	26.5	12.8	115.5	56.5	0.0	0.0	0.0	1.2	0.0	0.5	0.5	0.0	0.0	0.6
GRO	8-Aug	63.5	16.6	12.4	3.0	0.0	0.0	0.0	3.8	0.0	0.0	0.0	0.0	0.0	0.0
GRO	1-Sep	53.6	622.3	290.9	7.4	6.0	0.0	86.8	1.2	0.0	0.0	0.0	0.0	0.0	35.7
LAV	25-Jul	458.0	372.5	239.5	34.8	0.0	0.0	0.0	11.1	0.0	0.0	48.0	0.0	0.0	0.0
LAV	25-Jul	48.5	8.1	209.1	6.4	0.0	0.0	0.0	12.4	0.0	0.0	0.0	0.0	0.0	0.0
LAV	31-Aug	94.2	129.1	136.9	0.0	0.0	0.0	0.0	11.1	1.4	0.0	3.0	0.0	0.0	0.0
LAV	31-Aug	117.4	27.7	151.8	0.1	0.0	0.0	0.0	5.3	0.4	0.0	3.4	0.0	0.0	0.0
RON	27-Jul	4.8	160.2	362.0	0.0	0.0	0.0	18.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
RON	27-Jul	13.7	87.6	645.2	6.9	7.9	28.5	0.0	3.8	0.0	2.0	0.0	0.0	3.4	0.0
RON	5-Sep	86.5	216.2	1571.6	0.0	15.3	3.6	47.0	5.2	0.0	0.0	54.9	0.8	27.7	4.1
RON	5-Sep	59.1	226.0	586.8	11.0	21.6	0.0	8.6	15.1	0.0	0.0	30.2	0.0	10.5	0.0

TEA	19-Jul	256.3	15.8	52.5	2.8	3.4	0.0	0.0	0.6	0.0	0.0	0.5	0.0	0.0	0.0
VAC	3-Aug	35.5	1397.8	444.1	27.8	4.0	0.0	10.4	1.4	0.0	0.0	27.5	0.0	0.0	0.0
VAC	1-Sep	8.3	120.4	809.5	45.0	0.0	0.0	8.5	2.5	0.0	0.0	4.7	0.5	1.2	0.0
VAC	1-Sep	52.5	459.9	1730.1	126.5	27.8	4.3	54.7	6.8	0.0	0.0	35.6	0.0	17.9	3.6
ROB	20-Jul	848.4	10.6	10.9	10.5	0.5	0.0	0.0	5.3	0.0	0.0	0.7	0.0	0.0	0.0
ROB	20-Jul	409.5	0.0	54.3	0.0	0.0	0.0	1.0	16.5	0.0	0.0	0.0	0.0	0.0	0.0
ROB	23-Aug	1130.2	1133.1	74.0	266.3	9.5	0.0	20.5	6.2	0.0	0.0	13.4	5.4	0.0	2.5
THE	19-Jul	4822.2	134.3	19.5	9.1	0.0	0.0	40.4	5.1	0.0	3.1	7.8	5.3	0.0	0.0
VER	17-Jul	184.7	6.4	49.3	0.0	3.3	0.6	0.0	0.0	0.0	1.9	1.0	0.0	0.0	0.0
VER	17-Jul	351.8	50.9	90.1	0.0	2.0	0.0	0.0	0.0	0.0	0.0	17.8	0.0	0.0	0.0
VER	17-Aug	320.1	71.3	70.4	16.8	2.3	0.0	1.6	1.1	0.0	1.8	6.3	2.0	0.0	0.0
VER	17-Aug	572.1	438.2	531.5	211.5	2.0	0.0	90.1	3.8	0.0	3.1	42.3	5.5	4.0	0.0

Deep

Site	Data	Chir	Amph	Snai	Tric	Clam	Cori	Leec	Mite	Ephe	Clad	Lepi	Nema	Anis	Other
BB	2-Aug	160.8	220.7	207.7	81.3	1.2	0.0	0.0	2.9	5.8	0.0	21.8	2.7	3.4	1.4
BB	2-Aug	43.2	5.3	13.6	0.2	2.7	1.4	0.0	1.8	0.0	0.0	0.6	0.6	0.0	0.0
BB	19-Aug	91.8	248.3	38.5	3.3	1.8	1.9	0.0	1.1	0.0	1.2	0.0	0.0	0.0	0.0
GRO	8-Aug	57.0	1105.5	75.0	324.7	5.0	7.2	0.0	4.1	0.0	6.4	0.8	1.8	0.0	3.6

GRO	8-Aug	18.4	151.4	57.6	89.5	4.1	10.0	0.0	7.3	0.0	2.4	0.0	1.6	0.1	3.1
GRO	1-Sep	133.8	1358.4	782.4	5.6	16.9	0.0	47.8	10.8	0.0	0.0	4.3	3.3	2.6	68.9
LAV	25-Jul	119.1	25.9	32.0	34.9	18.1	0.0	0.0	6.6	31.7	0.0	0.0	0.4	0.0	0.0
LAV	25-Jul	24.0	43.4	7.1	19.9	6.1	0.0	0.0	17.6	13.4	0.0	0.0	0.3	0.0	0.0
LAV	31-Aug	96.6	103.8	94.5	1.0	9.1	3.0	0.0	11.8	29.8	0.0	0.0	0.8	0.0	0.0
LAV	31-Aug	63.7	169.8	33.2	4.2	6.2	0.0	0.0	8.0	105.2	0.0	0.0	1.0	0.0	0.0
RON	27-Jul	96.6	252.7	155.5	11.7	13.1	10.2	2.0	14.8	0.0	0.0	0.0	0.0	0.3	0.0
RON	27-Jul	88.9	108.3	411.6	153.8	17.5	30.4	0.0	11.4	0.0	0.0	0.0	0.0	0.0	0.0
RON	5-Sep	10.8	126.2	240.0	0.0	16.5	0.0	15.4	7.9	0.0	0.0	47.4	1.5	16.9	3.6
RON	5-Sep	10.3	145.1	1029.3	0.2	6.5	0.0	3.9	2.8	0.0	0.3	14.9	0.0	6.1	1.3
TEA	19-Jul	554.0	13.4	26.9	5.2	9.3	0.3	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0
TEA	19-Jul	591.0	30.6	3.3	0.4	6.0	0.0	0.0	8.0	0.0	0.0	3.9	0.0	0.0	0.0
TEA	16-Aug	13.2	14.8	0.8	6.8	12.5	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0
VAC	3-Aug	7.3	10.8	327.2	23.9	5.8	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0
VAC	3-Aug	6.2	8.3	0.0	91.8	10.1	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	6.3
VAC	1-Sep	13.8	19.5	326.1	0.0	7.7	0.0	5.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
VAC	1-Sep	36.3	37.6	293.1	19.3	3.4	0.1	0.0	1.8	0.8	0.6	1.6	0.5	0.0	0.0
ROB	20-Jul	266.5	0.4	22.0	0.0	3.9	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0
ROB	20-Jul	125.7	2.2	3.5	3.5	0.3	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

ROB	23-Aug	189.6	174.2	74.3	0.2	0.0	0.8	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.2
ROB	23-Aug	83.5	16.4	21.5	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
THE	19-Jul	254.3	63.5	14.5	1.3	105.6	2.1	4.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
THE	16-Aug	29.2	4.9	3.5	0.0	50.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
THE	16-Aug	8.9	0.6	8.0	0.0	62.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
VER	17-Jul	189.0	63.6	54.2	4.5	0.6	0.5	1.2	5.4	0.0	0.0	2.5	0.0	0.0	0.0
VER	17-Jul	43.5	11.5	70.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
VER	17-Aug	500.8	50.7	76.4	1.4	4.1	0.0	3.4	0.0	0.0	0.0	12.4	0.8	0.1	0.0
VER	17-Aug	20.2	9.5	18.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0

Shallow

Site	Data	Chir	Amph	Snai	Tric	Clam	Cori	Leec	Mite	Ephe	Clad	Lepi	Nema	Anis	Other
BB	2-Aug	23.0	17.8	4.9	4.9	2.0	2.4	0.0	2.1	9.1	0.4	0.0	0.0	0.0	0.0
BB	19-Aug	12.1	113.1	0.0	0.7	0.1	1.8	0.0	0.6	0.0	1.2	0.0	0.0	0.0	0.0
BB	19-Aug	11.3	30.3	0.0	0.0	0.0	0.7	0.0	1.9	0.5	0.0	0.0	0.1	0.0	0.0
GRO	8-Aug	30.9	1423.4	0.0	34.7	5.6	4.0	12.0	11.0	0.0	0.0	0.2	0.8	0.0	26.9
GRO	1-Sep	15.9	145.1	488.0	9.4	1.0	0.0	0.0	7.5	0.0	0.0	0.0	0.8	0.0	32.7
LAV	25-Jul	61.6	89.8	110.2	20.2	6.7	0.0	0.0	24.3	72.2	0.0	0.0	2.7	0.0	7.3
LAV	25-Jul	31.2	8.4	2.1	10.1	4.6	0.0	0.0	8.3	24.1	0.0	0.3	0.0	0.0	0.0

LAV	31-Aug	83.1	88.0	27.9	44.7	7.8	3.7	0.0	7.0	15.7	0.0	0.0	0.5	0.0	0.0
LAV	31-Aug	46.3	33.3	41.8	23.4	6.7	0.0	0.0	5.2	4.4	0.0	0.0	0.5	0.0	0.0
RON	27-Jul	20.1	2536.3	577.1	33.8	40.8	42.2	0.0	2.8	0.0	0.0	0.0	0.0	4.9	15.4
RON	27-Jul	8.5	551.5	440.7	23.4	41.2	27.3	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0
RON	5-Sep	1.4	148.7	582.9	0.0	22.5	4.6	0.0	2.4	0.0	0.0	12.3	0.2	0.0	0.4
RON	5-Sep	3.4	135.4	399.1	0.0	17.6	1.6	0.0	3.6	0.0	0.0	0.0	0.2	0.0	0.1
TEA	19-Jul	14.4	0.0	0.3	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TEA	16-Aug	5.5	34.8	9.7	0.2	21.7	0.7	0.0	1.2	0.0	0.0	1.6	0.0	0.0	0.0
TEA	16-Aug	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
VAC	3-Aug	35.7	398.0	484.5	19.4	5.5	75.7	0.0	1.5	0.0	0.0	0.8	0.0	0.6	0.0
VAC	3-Aug	39.0	1028.7	1161.1	35.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
VAC	1-Sep	7.6	209.0	504.2	1.6	9.1	275.3	0.5	0.6	0.0	0.0	2.8	0.0	0.0	22.9
VAC	1-Sep	17.9	121.6	399.8	0.0	2.0	0.0	0.0	1.1	0.0	0.0	8.5	0.0	12.1	0.2
ROB	20-Jul	1555.6	12.6	8.3	0.0	5.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
ROB	23-Aug	204.2	439.6	466.3	20.4	1.3	5.6	1.0	8.9	0.0	0.0	7.0	0.0	0.0	2.1
ROB	23-Aug	93.9	0.0	110.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
THE	19-Jul	373.8	916.6	25.3	0.6	6.8	0.5	4.0	8.8	0.0	0.0	0.0	0.0	0.0	0.0
THE	16-Aug	4.3	59.9	0.0	0.0	1.3	3.0	108.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
THE	16-Aug	3.8	82.4	3.0	0.0	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

VER	17-Jul	30.8	127.9	35.1	2.6	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
VER	17-Jul	57.0	457.4	280.0	5.4	0.0	32.2	0.0	0.0	0.0	2.2	1.1	0.0	0.0	0.0
VER	17-Aug	479.5	42.1	135.5	12.0	6.3	1.3	0.0	1.0	0.0	0.0	18.9	1.7	0.0	0.0
VER	17-Aug	73.8	9.4	18.2	20.8	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0