THE BIOENERGETIC BASIS OF ANADROMY IN BROOK TROUT (*SALVELINUS FONTINALIS*)

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A thesis submitted to McGill University in partial fulfillment of the
requirement for the degree of Doctor of Philosophy

June 2005
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ABSTRACT

Migratory and resident forms of salmonid fishes, including brook trout (*Salvelinus fontinalis*), coexist in many river systems, but little is known about the ecological basis of these important variations in life history. This thesis elucidates the bioenergetic basis of anadromy (migration from freshwater spawning sites to the sea) in populations of brook trout. By focusing on the early stages, I provide support for the idea that variation in energy allocation leads to the adoption of migratory or resident strategies. More specifically, I demonstrate that juvenile anadromous brook trout, in the year(s) prior to migration, exhibit higher food consumption rates but lower growth efficiencies compared to residents indicating that they have higher metabolic costs. Higher metabolic costs of migratory fish are associated with the exploitation of higher current velocity habitats that provide more food but at a higher cost. This conclusion is supported by differences in $\delta^{13}C$ (migrants have more negative $\delta^{13}C$ compared to residents), morphology (migrants are more streamlined than residents), and field observations (brook trout inhabiting streams with both forms exploit a wider range of habitats than those inhabiting 'pure' resident streams). Brook trout thus appear to migrate in response to energetic limitations in their local habitat. The estuary to which they migrate has better feeding opportunities, as the prey spectrum at sea is both larger and wider than that found in freshwater. This permits them to undergo diet shifts to larger prey, reducing their foraging costs, and thus most likely contributes to the trout's rapid growth rates experienced at sea. Importantly, the results of this thesis indicate that the persistence of migrant and resident strategies in the same system suggest a trade-off between local adaptability and the ability to exploit large-scale environmental heterogeneity.

RÉSUMÉ

Plusieurs populations de salmonidés, incluant l'omble de fontaine (*Salvelinus fontinalis*), contiennent des individus qui adoptent une stratégie de migration ou de résidence. Bien que cette coexistence soit étendue, on connaît très peu les bases écologiques sur laquelle elle s'appuie. Cette thèse démontre qu'il existe des mécanismes plausibles contribuant à l'adoption d'anadromie chez l'omble de fontaine en utilisant une approche bioénergétique. Cette étude, en focalisant sur les jeunes stades de vie des ombles, supporte l'idée que selon les variations d'énergie, ils adoptent des stratégies de survie telles la migration ou la résidence. Plus spécifiquement, nous démontrons que les ombles juvéniles anadromes affichent, dans l'année précédant la migration, un taux de consommation plus élevée mais une croissance moins importante que les résidants, à cause de demandes métaboliques plus grandes. Ces demandes métaboliques semblent être le résultat d'un usage différent de l'habitat parce que les migrants exploitent des courants plus rapides nécessitant une plus grande dépense d'énergie que les résidants. Ces résultats sont corroborés par les différences en δ^{13}C (les migrants ont des signatures de δ^{13}C plus négatives que les résidants) et en morphologie (les migrants sont plus élancées que les résidants) et par les observations sur le terrain (les ombles habitant des ruisseaux de migrants et de résidants exploitent une plus grande variété d'habitats que ceux habitant des ruisseaux de résidants 'purs'). Les poissons semblent migrer parce qu'ils encourent des sources limitées d'énergie dans leurs habitats locaux. Dès leur arrivée en mer, ils peuvent se procurer la nourriture nécessaire leurs permettant d'atteindre des taux de croissance élevés. Ceci est dû à l'accès à une plus grande gamme de tailles de proies, leur permettant de changer leur diète pour des proies plus grosses. La réduction de dépense d'énergie en rapport avec la recherche de nourriture amène une augmentation efficace de leur croissance. Comme les résidants et les migrants coexistent et se maintiennent dans le même système, les résultats suggèrent qu’il existe un compromis entre la capacité de s’adapter localement et l’habilité d’exploiter l’hétérogénéité environnementale à grande échelle.

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ACKNOWLEDGEMENTS

I would like to acknowledge the numerous funding agencies which provided support for this project including grants provided to J.B.R. by the Natural Sciences and Engineering Research Council of Canada (NSERC; Strategic Grant and Collaborative Special Projects), the Foundation de la Faune du Québec, the Government of Quebec (FAPAQ), the Government of Canada (Economic development), the financial partners of CIRSA Inc., and graduate fellowships to G.R.M. (Vineberg McGill Major, McConnell Family McGill Major, and McGill's Department of Biology graduate fellowship).

My utmost thanks goes to my supervisor, Dr. Joe Rasmussen, an incredibly intelligent person who gave me the opportunity to grow and develop into a real scientist. I will be happy if I become half the scientist he is. The last few years of my schooling, prior to his departure, would not have been as stimulating if he hadn't been there to discuss ideas about just about everything. I especially appreciated all of those long drives to conferences and the field and missed the lack of stimulating discussions during the years following his move to Lethbridge. May he continue to inspire many more students out west!

I would also like to thank my past committee members, Dr. Jim Grant and Dr. Donald Kramer. Their help throughout the years was extremely appreciated. I especially thank Dr. Kramer for his subsequent role as co-supervisor during my last 2 years at McGill after Dr. Rasmussen's departure from McGill. One of my funniest memories with Don occurred during a committee meeting where Don and I argued about whether 'swimmaging' was an appropriate word for describing fish activity. I will never forget that. His attention to detail was always greatly beneficial. However, I still think that 'swimmaging' is a great word!

I appreciated all of the help and support I received from my collaborators, especially Véronique Thériault and Dr. Sophie Lenormand of Projet Truite de Mer. They were there from the beginning; their friendship and help throughout the years was very important for the completion of this study. All of our joined efforts in the field, lab and office, as well as all of those stimulating discussions made the sea trout collaboration a true success and something I will never forget!! I appreciated the numerous discussions with Dr. Julian Dodson, the past director of CIRSA (Centre Interuniversitaire sur le Saumon Atlantique) and lead investigator of the sea trout project. The participation of the fishers of the Saguenay River in the tagging program was an essential contribution to the project.

I would like to acknowledge the importance of CIRSA (Centre Interuniversitaire sur le Saumon Atlantique), a research centre permitting the exchange of multiple partners including scientists from various universities, government and fishers. I hope that this centre will be able to persist through time. The experience I gained from being part of CIRSA was incredible. The amount of support this centre provided both in terms of dedicated staff and 'emplacement' was irreplaceable. Françoise Colombani did a great job in organising the yearly 'colloques' and preparing all of those reports. I enjoyed the numerous tarot games with Danny Bussières and the arrival of the new biologist, Jean-François Bourque was a welcome addition. His friendship was greatly appreciated during my last few years at CIRSA and will always remember our bond with Pépito.

Je remercie aussi énormément André Boivin (Mononke) pour son aide technique et son amitié pendant toutes mes années au CIRSA. Tu étais un élément important pour que je ne perde pas la tête, surtout pendant mes deux dernières années de terrain. Merci pour toutes les belles soirées de tarot et pour m'avoir donner la chance d'utiliser tes multiples outils.

J'aimerais également remercier l'ensemble des cuisinières au CIRSA, et surtout Albertine et Colette pour leur accueil exemplaire. Par contre, je ne vous remercie pas pour les 25 lbs de trop que j'ai gagné pendant ces années. La nourriture était simplement exquise et a rendu notre séjour au CIRSA des plus merveilleux. Jamais je n'ai eu le ventre vide sur le terrain!

Un grand merci également à Claude Poirier, directeur du club de pêche d'Alcan, pour m'avoir permis de goûter au meilleur saumon fumé au monde. Ta recette est simplement sublime! Je te remercie également pour m'avoir permis de contribuer à de nombreuses sessions d'information pour les pêcheurs séjournant au club.

I would like to express my deepest thanks to all of my great lab/field assistants over the years including Greg Kramer for being there during my first and last field/lab season, Lucas Rasmussen, Caroline Mimeault, Kristin Lunn, Stéphanie Marchal, Marc Dunn, Alain DuCap, Sonja Bodmer-Roy, Myriam Bélanger, Ji-hae Kim and Lillian Harris. The work could not have been all done without your help! J'aimerais aussi remercié tous les assistants de mes collaborateurs incluant Annie, Fannie, Jean-Guillaume, Christian, François et feu Louis-Philippe. They were always willing to lend me a hand in the field.

I would like to thank all of my past and current lab mates, including Ivano Pazzia, Jennifer Kovecses, Jake Vander Zanden, Marc Trudel, Strahan Tucker, Adrian Debruyn, Graham Sherwood, Alison Iles, Veronique Trudeau, Rebecca Ng and David Browne. You made my years in Joe's lab truly unforgettable. Your friendship and support was especially appreciated. Jake, Marc, Strahan and Graham were great role models and really contributed to my development in my early graduate years. I will always remember your neck curling! The most recent remnants of Joe's lab (you know who you are) were an incredible support group, allowing me to finally finish this thesis. I had a great time playing curling and hockey with Rebecca in addition to stitch'n'bitching with Véronique and Alison. Thank you Dave for supporting me in the last few months. I appreciated all of our discussions and your attitude kept me motivated even during the final days.

I would also like to express thanks to Dr. Irene Gregory-Eaves who shared her office/lab space with Dave and myself after we lost our office space following the dissolution of the Rasmussen lab. I don't know where we would have ended up if she hadn't been so generous. A big thanks also to Dr. Rajinder Dhindsa for giving me bench space in his lab, especially since he had no direct ties to my work. I appreciated the welcoming attitude from his post-docs, Dr. Nick and Dr. Qaiser. In addition, I would like to thank Drs. Fréderic Guichard and Andy Gonzalez for providing me some lab space so that I could finish our work. It was greatly necessary and appreciated.

In addition, the secretaries of the biology department, notably Susan Bocti for taking care of us so well, and Linda Morai for all of my budget crises in the last couple of years were especially helpful.

The greatest thanks to the bio 'nerds' including Alison, Inge, Julia, Kristen, Leslie, Robyn and Victoria for their friendship throughout the years. Thanks also to the boys, including Jamie, Rob dog and Josh. You made my times in Montreal very memorable and I thank you all for all of those fun dinners, potlucks, movies and parties. I unfortunately lost many of you over the years but when you were here it was definitely a blast. I especially thank Robyn for being there during all of my university years and being the last of the 'bio nerds' to remain in Montréal. You can't imagine how much your friendship means to me and I will truly miss you when we will no longer be living in the same city. Thanks for all of your support in the final days of my thesis submission. I couldn't have done it without you!

I would also like to thank my other friends including Sandrine and Walter for those wonderful evenings and for all of that coffee which allowed me to stay up late and finally finish my thesis. I also enjoyed the many dinners and movies with Marie-Annick and Vad. Un gros merci à mon amie Julie pour son support ainsi qu'aux amis de Mathieu pour les diverses soirées inoubliables.

I would also like to thank R. Petch for his amazing positive attitude during my time in the arctic! Thanks for helping me to stay up late in order to prepare for my talk in the week prior to my defence.

Un merci sincère à mes parents, Denise et Raymond, de m'avoir aidé à vouloir toujours poussé au-delà de mes capacités. Merci aussi à mes grandes sœurs, Anne et Véronique, pour lesquelles j'ai toujours senti un grand respect. Tous vos accomplissements m'ont permit de foncer et de rester motivé. Je remercie aussi mes deux beaux-frères, Mike et Mike, pour leur sens d'humour à travers les années.

Merci aussi à ma nouvelle belle-famille, incluant mes beaux-parents, Carole et Pierre, ainsi que Marie-Josée et Patrick, pour leurs énergies positives et les nombreuses soirées inoubliables, incluant certaines discussions assez chaudes!

À mes nouvelles nièces, Kiara, Zoe, Aimée, Fée, et neveu, Patrick, pour leurs simples joies, et de me faire ré-réaliser qu'il y a tellement de choses importantes à vivre dans une vie. Je vous aime tous.

Un gros merci à mon mari Mathieu pour m'avoir accompagné et supporté pendant toutes les années de mon doctorat, particulièrement pendant tous les moments de gros stress. Je t'aime énormément. Les nombreuses visites sur le terrain pendant les nombreux étés étaient formidables et je n'aurais pas pu continuer sans toi aussi longtemps. J'ai hâte à notre prochaine étape de vie.

And last but not least, to brook trout, the most beautiful temperate freshwater fish of all! The anadromous form captivated my utmost attention, leading me to dedicate over 7 years of my life to it and in the process, unravel a part of its mystifying nature. I hope that my discoveries will ensure your existence…

GUIDELINES FOR THESIS PREPARATION

The Faculty of Graduate Studies and Research of McGill University requires that the following statements be made in order to inform the reader of Faculty regulations:

1. Candidates have the option of including, as part of the thesis, the text of one or more papers submitted, or to be submitted, for publication, or the clearly-duplicated text (not the reprints) of one or more published papers. These texts must conform to the “Guidelines for Thesis Preparation” with respect to font size, line spacing and margin sizes and must be bound together as an integral part of the thesis. (Reprints of published papers can be included in the appendices at the end of the thesis.)

2. The thesis must be more than a collection of manuscripts. All components must be integrated into a cohesive unit with a logical progression from one chapter to the next. In order to ensure that the thesis has continuity, connecting texts that provide logical bridges preceding and following each manuscript are mandatory.

3. The thesis must conform to all other requirements of the “Guidelines for Thesis Preparation”. The thesis must include the following (1) a table of contents; (2) an abstract in both English and French; (3) an introduction which clearly states the rationale and objectives of the research; (4) a comprehensive review of the literature (in addition to that covered in the introduction to each paper); (5) a final conclusion and summary; (6) a thorough bibliography; (7) Appendix containing an ethics certificate in the case of research involving human or animal subjects, microorganisms, living cells, other biohazards and/or radioactive material.

4. As manuscripts for publication are frequently very concise documents, where appropriate, additional material must be provided (e.g. in appendices) in sufficient detail to allow a clear and precise judgement to be made of the importance and the originality of the research reported in the thesis.

5. In general, when co-authored papers are included in a thesis the candidate must have made a substantial contribution to all papers included in the thesis. In addition, the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent. This statement should appear in a single section entitled “Contributions of Authors” as a preface to the thesis. The supervisor must attest to the accuracy of this statement at the doctoral oral defence. Since the task of the examiners is made more difficult in these cases, it is in the candidate’s interest to clearly specify the responsibilities of all the authors of the co-authored papers.

CONTRIBUTION OF AUTHORS

This thesis consists of four chapters prepared as distinct manuscripts for publication in peer-reviewed scientific journals. All the work presented in this thesis was designed and executed by myself in collaboration with my supervisor, Dr. J.B. Rasmussen (currently at University of Lethbridge, Department of Biological Sciences). All the chapters of the thesis were written by myself, and were co-authored by my supervisor who, in addition to providing technical advice and editorial comments, contributed to the development of the ideas presented in these chapters. Chapter 1 has been published in the *Canadian Journal of Fisheries and Aquatic Sciences* (Can J. Fish Aquat. Sci 60: 401-410), Chapter 2 has been submitted to *Environmental Biology of Fishes*, Chapter 3 has been submitted to *Journal of Animal Ecology* and Chapter 4 was prepared for submission to the *Canadian Journal of Fisheries and Aquatic Sciences*.

CLAIMS FOR ORIGINALITY

Despite the large amount of work previously published on salmonid fishes (including many species of trout and salmon), this is the first study characterizing the intraspecific energy allocation strategies of coexisting juvenile anadromous (freshwater spawning and migration to sea) and resident forms. Bioenergetic differences in growth, consumption and metabolic costs have only been reported between species exhibiting diverse life history strategies such as resident brook trout (*Salvelinus fontinalis*) and anadromous Atlantic salmon (*Salmo salar*) (Tucker and Rasmussen 1999), or within species (brown trout; *Salmo trutta*) shown to migrate between a stream and a lake (Forseth et al. 1999). By focusing on the early life stages of brook trout, this study provides evidence suggesting that variation in energy allocation leads to the adoption of migratory or resident strategies within a species. The migration to a new habitat provides them with better feeding opportunities as the prey spectrum at sea is both larger and wider than that found in freshwater. This thesis provides the most complete investigation of the bioenergetic basis of anadromy in salmonids by demonstrating that the strategies of the two forms are associated with variation in habitat use and morphology. Importantly, given the similarity between many salmonid species, the findings are likely to apply to other salmonids exhibiting both migratory and resident forms, including Arctic charr (*Salvelinus alpinus*) and rainbow trout (*Oncorhynchus mykiss*).

The specific contributions of each chapter are listed below:

Chapter 1. This is the first study demonstrating that differences in energy allocation strategies (growth, consumption and metabolic costs) lead to anadromous and resident forms within a salmonid population. Specifically, those adopting a migratory strategy have lower growth efficiency (ratio of growth to consumption) than those adopting a resident strategy. This is likely associated with differential habitat use, with migrants exploiting faster current velocities (more energetically costly) than residents. Contrary to earlier studies, growth or body size is not the most important determinant of migration. Rather it is how a fish acquires its energy in its local habitat prior to the adoption of migration or residency as life-history strategies. These results thereby indicate that fish adopting a migratory strategy are inefficient at acquiring energy in their local habitat but efficient at exploiting large-scale environmental heterogeneity, consistent with the two aforementioned studies. The results thus demonstrate that a link exists between metabolic costs and the adoption of life-history strategies.

Chapter 2. Previously, no method was available to distinguish between coexisting juvenile anadromous and resident forms of brook trout. The lack of obvious differences between forms of the same species at juvenile stages has also been commonly reported for other salmonids, and as a consequence, has limited the direct study of intraspecific interactions. This is the first study (1) describing the morphological differences between juvenile anadromous (prior to migration) and resident brook trout inhabiting streams, and (2) develops a predictive model for distinguishing future migrants from residents. Such models will now allow the development of future studies involving the juvenile life stages of coexisting forms. Furthermore, the observation that migrants are more streamlined than residents supports the expected habitat use differences deduced from the results of Chapter 1.

Chapter 3. This study provides the best evidence that differential habitat use within a salmonid species leads to the adoption of anadromous and resident life-history strategies. Specifically, brook trout inhabiting streams containing both anadromous and resident forms occupy a wider range of habitats than those inhabiting a ‘pure’ resident stream. These results, combined with those presented in Chapters 1 and 2, further indicate that migrants adopt a more inefficient strategy compared to residents when inhabiting freshwater. The results thus suggest the mechanism by which the evolution of alternative life-history strategies may arise within a population.

Chapter 4. Few studies investigating the biology of anadromous brook trout (sea trout) populations have been conducted. Sea trout are becoming more interesting in the eyes of anglers and fishery managers due to declines of Atlantic salmon returning to rivers. Thus, the information obtained in this study contributes to the creation of sustainable management plans for brook trout. This is the first comprehensive description of the ontogenetic and seasonal marine feeding patterns of anadromous brook trout (sea trout) inhabiting estuarine waters. In the process, I demonstrate that the migration to a new habitat provides sea trout with better feeding opportunities as the prey spectrum at sea is both larger and wider than that found in freshwater. I also document the size at which trout undergo a diet shift to piscivory in the sea and elucidate the important feeding grounds of sea trout in the Saguenay River, Quebec using an extensive diet and stable isotope data set collected over 5 years. Importantly, the methodology employed in this study will be applicable to other studies that wish to achieve a better understanding of seasonal sea trout feeding patterns across marine feeding grounds.

PROLOGUE

I decided to take a very broad approach when writing the general introduction to my thesis. The larger context of my research, animal migration, can be considered quite extensive. Most animal taxa exhibit some type of migration during their life stages and the extent of these migrations can be quite variable, both in time and in distance. For my own personal interest, I wanted to review the phenomenon of migrations across multiple taxa, not simply focussing on fish (and salmonids), by highlighting some of my favourite examples and summarizing some of the generalities leading to these migrations. However, the introduction does gradually focus towards my specific research topic, understanding the bioenergetic basis of migration (anadromy) in brook trout. I also wanted readers to get a sense of the progression of my understanding of the field during my graduate training. Some of the topics will only be briefly touched upon because they will be addressed in detail in my chapters. Others were expanded mostly in the introduction since papers aimed for submission to scientific journals are very concise. Overall, I hope that this introduction will arouse your curiosity to read further and will provide sufficient background information for understanding and enjoyment of the chapters to come.

“Many men go fishing all of their lives without knowing that it is not fish they are after”.
Henry David Thoreau

GENERAL INTRODUCTION

Animal migration…a fascinating phenomenon

Animal migrations can be observed in many animal taxa including birds, insects, fish and mammals. Most migrations involve taxa that can either swim or fly (Baker 1978). Common examples include monarch butterflies that travel thousands of kilometres from North America to their overwintering grounds in Mexico and Cuba (Brower and Malcolm 1991; Dockx et al. 2004); Canada geese take journeys leading them back to northern destinations every spring (Malecki et al. 2001); whales migrate large distances between feeding and calving/breeding grounds (Reeves et al. 2004; Mate et al. 1999); and salmon, who travel impressive distances to feeding grounds only to return to their natal river to spawn, passing through often very steep and long river courses, with many never reaching their final goal (Fleming 1996; Thorpe 1988). These are only a few examples of animal migrations out of thousands that have been acknowledged.

Migrations can occur both on short and long timescales and on variable spatial timescales. For examples, mysid shrimp inhabiting lakes undergo diel vertical migrations in the water column to evade predators (Beeton 1960), whereas sea turtles can migrate great distances, upwards of thousands of kilometres, between feeding and spawning/nursery grounds across spanning multiple years (Luschi et al. 2003).

These types of remarkable migrations have captivated the attention of many. Old historical accounts of salmon entering New England waters have been documented dating back to the 1600s (Wood 1977) and whaling expeditions dating back from the late 1800s capitalized on the whales’ migratory behaviour (Burch 1966, 1981). Although a vast amount of information exists on animal migrations, much remains to be discovered about the patterns and mechanisms of migration.

Why did migration evolve?

" … Should I stay or should I go now? If I go there will be trouble. An' if I stay it will be double…" The Clash 1982 (Combat Rock)

Various explanations have been proposed to explain why animals undertake migrations. The tight interaction between species and their environment appears to be a major contributor. Density effects, where the carrying capacity of a given area is surpassed, has been acknowledged as triggering the migration of animals into new territories, such as the notorious locust outbreaks (Gunn 1960; Uvarov 1961). Animals also migrate to areas permitting them to live within their optimal temperature range (Hinke et al. 2005; Perry et al. 2005), to follow a food supply (Ballard et al. 1997; Frank 1998) or to attain spawning grounds located away from feeding areas (Luschi et al. 2003; Solmundsson et al. 2005).

In addition, migrations may have evolved as a response to less favourable environmental conditions such as temperature fluctuations (Cossette and Rodriguez 2004), severe drought conditions (Adis and Junk 2002; Herremans 2004) or periods of food shortages (Hirche 1996; Whitehead 1996), which are often triggered on a seasonal basis. Such types of situations can directly affect the well being of animals by affecting their normal functioning, leading to various behavioural responses like migration. Other responses may be at the level of the organism, leading to physiological transformations. Many may adapt to such unfavourable conditions by entering a dormant state. For example, bears unable to cope with food shortages during winter hibernate, lowering their metabolism and consequently, their energetic requirements permitting them to survive the winter months (Hilderbrand et al. 2000). Other animals, such as temperate-zone insects, enter diapause where water within the individuals is either chemically bound or reduced in quantity to prevent freezing during winter (Hochachka and Somero. 1973, Tauber et al. 1986).

Even humans have undertaken extensive migrations throughout their history (Little and Mascie-Taylor 2004). The reasons for migrating have been comparable, to cope with fluctuating environments including the avoidance of extreme temperatures and variations in food distribution (Masserli et al. 2000).

Although responses to environmental conditions and the mechanisms leading to migration are species-specific, overall they all strive to achieve one main purpose: to increase or maintain an individual's reproductive output, and in the process, increase an individual's chance at survival.

Partial migration…

In some animals, populations are composed of both migratory and resident counterparts. That is, within a single population, individuals may adopt either a migratory or resident approach, the latter remaining in the same habitat throughout all life stages. This phenomenon is commonly referred to as partial migration and has been documented in birds, mammals and fish (Ball et al. 2001; Jonsson and Jonsson 1993; Lundberg 1988).

Most of our understanding of partial migration has been developed from the study of bird populations (Chan 2001; Kaitala et al. 1993; Lundberg 1988). These studies tend to suggest that it is a consequence of natural selection (Chan 2001; Lundberg 1988). Migratory habits may have a genetic basis (Berthold 1984; Berthold and Querner 1982), where the expressions of two coexisting strategies exist, each specifying a single tactic, irrespective of changes in the environment (Biebach 1983). This theory assumes that the lifetime reproductive success of both forms in the population is balanced over their entire life cycle (Berthold 1984) and is thus a mixed "evolutionary stable state".

Alternatively, some researchers have suggested that individual asymmetries are at play (Lundberg 1988). For instance, partial migration may be a pure evolutionary stable strategy with two condition-dependent tactics, residency and migration (Lundberg 1987). An individual would adopt the tactic providing the best cost-benefit return, and the proportion of migrants and residents within a population could in turn fluctuate from year-to-year, depending on environmental conditions. Support for this mechanism is largely observed in partially migrant bird populations occurring in intermediate latitudes where winter conditions permit a proportion of the population to overwinter. Increasing depletions of winter resources result in stronger intraspecific competiton leading to emigration of the inferior individuals (Berthold 1978). In this situation, the two forms do not necessarily perform equally well but change their strategy to make the 'best of a bad situation' (Lundberg 1988).

Data from the literature continue to support the aforementioned mechanisms (Adriaensen and Dhondt 1990; Alonso and Morales 2000; Pulido et al. 1996). Thus, at present generalities about the specific mechanisms leading to the evolution of partial migration cannot be fully established or confirmed. Certain limitations including our inability to distinguish between migratory and non-migratory forms may hinder future advances (Chan 2001).

It's a wonderful world…of fish

Most fish undergo migrations at some point during their life, although the extent can vary largely both spatially and temporally. Migrations can occur between freshwater habitats, such as the downstream migration from streams to rivers for spawning, commonly reported in species such as longnose dace (*Rhinichthys cataractae*) and between marine habitats, such as herring migrations occurring between offshore spawning grounds and estuarine nurseries (Maes et al. 2005).

The most impressive of migrations occur between fresh and saline waters, otherwise known as diadromy (McDowall 1987), necessitating osmoregulative capacities to enable adaptions to the different salinities (Gross 1987). The majority of research studying diadromous migrations has targeted Salmonidae and Anguillidae species (McDowall 1987). Eels

(Anguillidae) are catadromous, spending most of their lives in freshwater, to later return to the sea as mature adults to breed. Interestingly, two Atlantic eels*, Anguilla anguilla* and *Anguilla rostrata*, leave freshwater streams and rivers of Europe and North America, respectively, to spawn panmictically in the Sargasso sea (Schmidt 1925).

Anadromy, the most recognized form of diadromy, pertains to fish that spend a portion of their life at sea feeding, but return to freshwater for breeding. Salmonids, probably the most well known example, and other fishes including lampreys (Petromyzontidae), shads (Clupeidae), sticklebacks (Gasterosteidae) are all anadromous, varying in time spent at sea. Life cycles can differ tremendously across species; some enter the sea immediately after hatching while others migrate to the sea only after spending many years in freshwater as juveniles (Randal et al. 1987; McDowall 1987).

Why the evolution of anadromy?

It has been suggested that for a migratory life-history pattern to exist, the gain in fitness from moving to a new habitat, minus the costs of moving, must be higher than staying in only one habitat (Gross 1987; for a recent review see Hendry et al. 2004). Relative food availability between freshwater and marine habitats appears to be the most important biological variable explaining the occurrence of anadromous species (Gross et al. 1988). At temperate latitudes, marine systems tend to be more productive than freshwater ones, thereby supporting the direction of migration of salmonids (Power 1987; Gross et al. 1988). As such, anadromy has mostly evolved in the northern latitudes, and has been referred to as a cool temperate phenomenon (Baker 1978).

To migrate or not to migrate…

The advantages of anadromy are clear. Indeed, mature migrants upon return from sea are usually larger than mature residents and benefit from higher age-specific fecundity (Gross 1987; Lenormand 2003; Lenormand et al. 2004). Nevertheless, many fish species exhibit partial migration where individuals become either migratory or resident, spending all of their life stages in freshwater (Jonsson and Jonsson 1993). This is commonly observed in salmonids, including populations of Arctic charr (*Salvelinus alpinus*), brown trout *(Salmo trutta*), Atlantic salmon (*Salmo salar*) and brook trout *(Salvelinus fontinalis*).

As only a fraction of the population migrates, the decision most likely involves a balance between the growth, reproductive and mortality potential (such as predation and/or disease) of the two habitats. Indeed, evidence suggests the existence of a trade-off between the manifestation of migration and sexual maturation in fish populations exhibiting partial migration (Hansen et al. 1989; Jonsson and Jonsson 1993; Thorpe 1987). For instance, Atlantic salmon parr that mature early (precocious males) do not smolt and migrate whereas smolts do not mature sexually the same year they migrate.

It has been difficult to demonstrate that specific genetic differences exist between residents and migrants within a population as larger variations often exist between localities than between coexisting life-history types (Hindar et al 1991). Some studies support the presence of a genetic predisposition to migration where migrant parents are more likely to produce migrant offspring (Nordeng 1983; Zimmerman and Reeves 2000, 2002). Variations in aggressive behaviour and its link to metabolic rates between migratory and resident individuals imply a genetic basis to migration (Lahti et al. 2001; Metcalfe and Thorpe 1992; Metcalfe et al. 1995). Genetic influences can also be inferred from observations in the field. For example, individuals inhabiting a stream above a waterfall do not migrate, suggesting that the influx of migrant spawners and thus genes is important for maintaining a migrant population (Jonsson 1982).

Fish that migrate may also differ in traits such as body size, growth or energy status, suggesting the presence of a conditional reproductive strategy (Bohlin et al. 1996; Økland et al. 1993; Thériault and Dodson 2003). The adoption of one strategy over another most likely involves the interplay of both genetic and environmental influences. For instance, genetically predetermined thresholds, such as growth or energy status, may have to be surpassed for anadromy to be initiated (Hendry et al. 2004).

Although, it still remains unclear what causes individual fish within a population to adopt one particular strategy over another, it is generally accepted that the ‘decision’ to migrate includes some kind of bioenergetic basis (Jonsson and Jonsson 1993). This has been largely inferred from the high growth benefits (and subsequent reproductive outputs) achieved at sea, and the results of studies investigating differences in body size and growth between those that migrate or delay migration. One major limitation to these studies is that growth and body size (Bohlin et al. 1996; Økland et al. 1993) cannot fully explain why certain fish adopt migration. The size threshold hypotheses are inadequate because many fish surpass these thresholds and still do not migrate. This stems from the difficulty in evaluating the actual energetic status of the fish, which requires knowing both the inputs (consumption) and outputs (growth), allowing for metabolic costs to be estimated. A better understanding of the potential link between metabolic costs and life-history strategies (Metcalfe and Thorpe 1992; Metcalfe et al.1995) may provide some insights about the evolution of partial migration in fish populations.

Given the potential important link between bioenergetics and anadromy, the amount of effort required to estimate *in situ* consumption rates of fish in the field using traditional methods (Gingras and Boisclair 2000) has no doubt limited the advancement of our understanding of fish populations exhibiting partial migration. However, recent advances in the development of consumption models using ^{137}Cs (Forseth et al. 1992; Rowan and Rasmussen 1996) now permit a simpler estimation of bioenergetic budgets, providing the basis for the investigation of mechanisms (bioenergetic) leading to partial migration.

The bioenergetic basis of anadromy in brook trout

Brook trout are indigenous to aquatic systems of northeastern North America (Power 1980; Scott and Crossman 1973) and anadromous forms occur in systems having an open access to the sea (Castonguay et al. 1982; Dutil and Power 1980; Montgomery et al. 1990; White 1940). Individuals from southern anadromous populations recolonized the more northern distributions about 10 000 years ago following the last glaciation (Castric and Bernatchez 2003; Power 2001). Like other *Salvelinus* species, their migration is restricted to coastal waters, and they generally experience a short (2-4 months) but seasonally determined sea residence, returning to freshwater for the winter (Castonguay et al. 1982; Dutil and Power 1980; Lenormand et al. 2004; Power 1980; Smith and Saunders 1958).

Few studies have been conducted on anadromous brook trout (sea trout) populations, limiting our understanding of the mechanisms leading to their migratory patterns. Thus, the overall goal of this thesis was to investigate the bioenergetic mechanisms leading to the occurrence of anadromy in a population of brook trout exhibiting partial migration. The first step of this process involved characterizing the bioenergetic differences that exist between juvenile anadromous and resident brook trout during their coexistence in streams (Chapter 1). As bioenergetics are tightly linked to morphology and habitat use in stream fish, Chapters 2 and 3 investigate how these factors are linked to anadromy. Finally, Chapter 4 describes the marine feeding patterns of sea trout permitting them to achieve high growth returns almost immediately upon sea entry.

References

Adis, J., and W.J. Junk. 2004. Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: a review. Freshwater Biology 47: 711-731.

Adriensen, F. and A.A. Dhondt. 1990. Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. Journal of Animal Ecology 59: 1077-1090.

Alonso, J.C., and M.B. Morales. 2000. Partial migration, and lek and nesting area fidelity in female great bustards. The Condor 102: 127-136.

Baker, R.R. 1978. The Evolutionary Ecology of Animal Migration. Holmes and Meier, New York.

Ball, J.P., C. Nordengren, and K. Wallin. 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alce*s ranges in northern Sweden. Wildlife Biology 7: 39-47.

Ballard, W.B., L.A. Ayres, P.R. Krausman, D.J. Reed, S.G. Fancy. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildlife Monographs 135: 5-47

Beeton, A.M. 1960. The vertical migration of *Mysis relicta* in Lakes Huron and Michigan. Journal of the Fisheries Research Board of Canada 17: 517-539.

Berthold, P. 1978. Endogenous control as a possible basis for varying migratory habits in different bird populations. Experientia 34: 1451.

Berthold, P. 1984. The control of partial migration in birds: a review. Ring 10: 253-265

Berthold, P. and U. Querner. 1982. Partial migration in birds: experimental proof of polymorphism as a controlling system. Experientia 38: 805-806

Beibach, H. 1983. Genetic determination of partial migration in the European Robin (*Erithacus rubecula*). Auk 100: 601-606

Bohlin, T., Dellefors, C., and Faremo, U. 1996. Date of smolt migration depends on body size but not age in wild sea-run trout. Journal of Fish Biology 49: 157-164.

Brower, L.P. and S.B. Malcolm. 1991. Animal migrations: endangered phenomena. American Zoologist 31: 265-276

Burch, E.S., Jr. 1966. Authority, aid, and affection: the structure of Eskimo kin relationships. Ph.D. thesis, Univ. Chicago, Chicago, Ill., 336 p.

Burch, E.S., Jr. 1981. The traditional Eskimo hunters of Point Hope, Alaska: 1800-1875. North Slope Borough [Barrow, Alaska]. 89 p.

Castonguay, M., G.J. Fitzgerald, and Y. Côté. 1982. Life history and movements of anadromous brook charr, *Salvelinus fontinalis*, in the St-Jean River, Gaspé, Québec. Canadian Journal of Zoology 60: 3084-3091

Castric, V. and L. Bernatchez. 2003. The rise and fall of isolation by distance in the anadromous brook charr (*Salvelinus fontinalis* Mitchill). Genetics 163: 983-996

Chan, K. 2001. Partial migration in Australian landbirds: a review. Emu 101: 281-292.

Cossette, C. and M.A. Rodriguez. 2004. Summer use of a small stream by fish and crayfish and exchanges with adjacent lentic macrohabitats. Freshwater Biology 49: 931-944

Dockx, C., L.P. Brower, L.I. Wassenaar, and K.A. Hobson. 2004. Do North American monarch butterflies travel to Cuba? - Stable isotope and chemical tracer techniques. Ecological Applications 14: 1106-1114

Dutil, J.D., and Power, G. 1980. Coastal populations of brook trout, *Salvelinus fontinalis*, in Lac Guillaume-Delisle (Richmond Gulf), Québec. Canadian Journal of Zoology 58: 1828–1835.

Flemming, I.A. 1996. Reproductive strategies of Atlantic salmon: Ecology and evolution. Reviews in Fish Biology and Fisheries 6: 379-416.

Forseth, T., B. Jonsson, R. Naeumann, O. Ugedal. 1992. Radioisotope method for estimating food consumption by brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 49: 1328-1335.

Frank, D.A. 1998. Ungulate regulation of ecosystem processes in Yellowstone National Park: direct and feedback effects. Wildlife Society Bulletin 26: 410-418.

Gingras, J., and Boisclair, D. 2000. Comparison between consumption rates of yellow perch (*Perca flavescens*) estimated with a digestive tract model with a radioisotope approach. Canadian Journal of Fisheries and Aquatic Sciences 57: 2547-2557.

Gross, M.A. 1987. Evolution of diadromy in fishes. American Fisheries Society Symposium 1: 14-25.

Gross, M.A., R.M. Coleman, R.M. McDowall. 1988. Aquatic productivity and the evolution of diadromous fish migration. Science 239: 1291-1293.

Gunn, D.L. 1960. The biological background of locust control. Annual Reviews in Entomology 5: 279-300.

Hansen, L.P., Jonsson, B., Morgan, R.I.G., and Thorpe, J.E. 1989. Influence of parr maturity on emigration of smolting Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 46: 410-15.

Hendry, A.P., T. Bohlin, B. Jonsson, and O.K. Berg. 2004. To sea or not to sea? Anadromy versus non-anadromy in salmonids. *In* Evolution Illuminated. Salmon and their relatives. *Edited by* A.P. Hendry and S.C. Stearns. Oxford University Press, New York. pp. 92-125

Herremans, M. 2004. Effects of drought on birds in the Kalahari, Botswana. Ostrich 75: 217-227

Hilderbrand, G.V., C.C. Schwartz, C.T. Robbins, and T.A. Hanley. 2000. Effect of hibernation and reproductive status on body mass and condition of coastal brown bears. Journal of Wildlife Management 64: 178-183.

Hinke, J.T., G.M. Watters, G.W. Boehlert, P. Zedonis. 2005. Ocean habitat use in autumn by Chinook salmon in coastal waters of Oregon and California. Marine Ecology-Progress Series 285: 181-192

Hirche, H.G. 1996. Diapause in the marine copepod, *Calanus finmarchicus*—A review. Ophelia 44: 129-143.

Hochachka, P.W. and G.N. Somero. 1984. Biochemical Adaptation. Princeton University Press, Princeton, New Jersey.

Jonsson, B. 1982. Diadromous and resident trout *Salmo trutta*: is their difference due to genetics? Oikos 38: 297-300.

Jonsson, B. and Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3: 348-365.

Kaitala, A., V. Kaitala, and P. Lundberg. 1993. A theory of partial migration. The American Naturalist 142: 59-81.

Hindar, K, B. Jonsson, N. Ryman, and G. Ståhl. 1991. Genetic relationships among landlocked, resident, and anadromous brown trout, *Salmo trutta* L. Heredity 66: 83-91

Lahti, K., A. Laurila, K. Enberg, J. Piironen. 2001. Variation in aggressive behaviour and growth rate between populations and migratory forms in the brown trout, *Salmo trutta*. Animal Behaviour 62: 935-944

Lenormand, S. 2003. Évolution de l'anadromie et stratégie de reproduction chez l'omble de fontaine (*Salvelinus fontinalis*). PhD thesis, Université Laval, Québec.

Lernomand, S., J.J. Dodson and A. Ménard. 2004. Seasonal and ontogenetic patterns in the migration of anadromous brook charr (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 61: 54-67.

Lundberg, P. 1987. Partial bird migration and evolutionary stable strategies. Journal of Theoretical Biology 125: 351-360.

Lundberg, P. 1988. The evolution of partial migration in birds. Trends in Ecology and Evolution 3: 172-175.

Luschi, P, G.C. Hays, F. Papi. 2003. A review of long-distance movement by marine turtles, and the possible role of ocean currents. Oikos 103: 293-302.

Little, M.A., and C.G.N. Mascie-Taylor. 2004. Human migration and mobility - Demographic, environmental, and evolutionary issues. American Journal of Human Biology 16: 363-364

Maes, J., K.E. Limburg, A. Van de Putte, and F. Ollevier. 1995. A spatially explicit, individual-based model to assess the role of estuarine nurseries in the early life history of North Sea herring, *Clupea harengus*. Fisheries Oceanography 14 (1): 17-31

Malecki, R.A., B.D.G. Batt, and SE Sheaffer. 2001. Spatial and temporal distribution of Atlantic population Canada geese. Journal of Wildlife Management 65: 242-247

Masserli, B., M. Grosjean, T. Hofer, L. Nunez, and C. Pfister. 2000. From nature-dominanted to human-dominated environmental changes. Quaternary Science Reviews 19: 459-479

Mate, B.R., B.A. Lagerquist, J. Calambokidis. 1999. Movements of North Pacific blue whales during the feeding season off southern California and their southern fall migration. Marine Mammal Science 15: 1246-1257.

McDowall, R.M. 1987. Evolution and importance of diadromy. The occurrence and distribution of diadromy among fishes. American Fisheries Society Symposium 1: 1-13.

Metcalfe, N.B., Taylor, A.C., and Thorpe, J.E. 1995. Metabolic rate, social status and life-history strategies in Atlantic salmon. Animal Behaviour 49: 431-436.

Metcalfe, N.B., and Thorpe, J.E. 1992. Early predictors of life-history events: the link between first feeding date, dominance and seaward migration in Atlantic salmon, *Salmo salar* L. Journal of Fish Biology 41 (Supplemental B): 93-99.

Montgomery, W.L., S.D. McCormick, R.J. Naiman, F.G. Whoriskey, and G. Black. 1990. Anadromous behaviour of brook charr (*Salvelinus fontinalis*) in the Moisie River, Québec. Polskie Archiwum Hydrobiologii 37: 43–61.

Nordeng, H. 1983. Solution to the “char problem,’ based on Arctic charr (*Salvelinus alpinus*) in Norway. Canadian Journal of Fisheries and Aquatic Sciences 40: 1372-1387.

Økland, B., Jonsson, B., Jensen, A.J., and Hansen, L.P. 1993. Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon? Journal of Fish Biology 42: 541-550.

Perry, A.L., P.L. Low, J.R. Ellis, and J.D. Reynolds. 2005. Climate Change and Distribution Shifts in Marine Fishes. Science 308: 1912-1915.

Power, G. 1980. The brook charr, *Salvelinus fontinalis*. *In* Charrs: salmonids fishes of the genus *Salvelinus*. *Edited by* E.K. Balon. W. Junik, The Hague, Netherlands. pp. 141-203.

Power, G. 2001. Charrs, glaciation and seasonal ice. 2002. Environmental Biology of Fishes 64: 17-35.

Pulido, F., P. Berthold, and A.J. Van Noordwijk. 1996. Frequency of migrants and migratory activity are genetically correlated in a bird population: Evolutionary implications. Proceedings of the National Academy of Sciences 93: 14642-14647

Randal, R.G., M.C. Healey, and J.B. Dempson. 1987. Variability in length of freshwater residence of salmon, trout, and char. American Fisheries Society Symposium 1: 27-41.

Reeves, R.R., T.D. Smith, E.A. Josephson, P.J. Clapham, G. Woolmer. 2004. Historical observations of humpback and blue whales in the North Atlantic Oceans: Clues to migratory routes and possibly additional feeding grounds. Mammal Science 20: 774-786.

Schmidt, J. 1922. The breeding places of the eel. Annual reports of the Smithsonian Institute 1924: 279-316

Solmundsson J., J. Palsson, and H. Karlsson. Fidelity of Icelandic plaice (*Pleuronectes platessa*) to spawning and feeding grounds. ICES Journal of Marine Science 62: 189-200

Smith, M.W., and Saunders, J.W. 1958. Movements of brook trout, *Salvelinus fontinalis* (Mitchill), between and within fresh and salt water. Journal of the Fisheries Research Board of Canada 15: 1403–1449.

Tauber, M.J., C.A. Tauber, and S. Masaki. 1986. Seasonal adaptations of Insects. Oxford University Press, Oxford.

Thériault, V. & J. J. Dodson. 2003. Body size and the adoption of a migratory tactic in brook charr. Journal of Fish Biology 63:1-16.

Thorpe, J.E. 1987. Smolting versus residency: developmental conflict in salmonids. American Fisheries Society Symposium 1: 244-52.

Thorpe, J.E. 1988. Salmon migration. Science Progress Oxford 72: 345-370.

Uvarov, B.P. 1961. Quantity and quality in insect populations. Proceedings of the Royal Entomological Society of London C 25: 52-59.

White, H.C. 1940. Life history of the sea-running brook trout (*Salvelinus fontinalis*) of Moser River, N.S. Journal of the Fisheries Research Board of Canada 5: 176-186

Whitehead, H. 1996. Variation in the feeding success of sperm whales: Temporal scale, spatial scale and relationship to migrations. Journal of Animal Ecology 65: 429-438.

Wood, W. 1977. *New England's Prospect* (orig published 1634, London) Vaughan, A.T. ed. Amherst, MA: University of Massachusetts Press, p56.

Zimmerman, C.E. and G.H. Reeves. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. Canadian Journal of Fisheries and Aquatic Sciences 57: 2152-2162.

Zimmerman, C.E. and G.H. Reeves. 2002. Identification of steelhead and resident rainbow trout progeny in the Deschutes River, Oregon, revealed with otolith microchemistry. Transactions of the American Fisheries Society 131: 986-993.

CHAPTER 1: Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*)[1]

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[1] contribution to the program of CIRSA (Centre Interuniversitaire de Recherche sur le Saumon Atlantique)

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Canadian Journal of Fisheries and Aquatic Sciences 60: 401-410.

“*The beginning is the most important part of the work*.” Plato

Abstract

Many salmonids, including brook trout (*Salvelinus fontinalis*), contain both anadromous (migrant) and non-anadromous (resident) forms within a population (partial migration). Although partial migration is commonly observed, the mechanisms governing the adoption of migration or residency are poorly understood. We used field estimates of fish growth with in situ estimates of food consumption rates to demonstrate that a trade-off exists between the ability to efficiently exploit local environments (resident approach) and the capacity to capitalize from large-scale environmental heterogeneity (migrant approach). We demonstrate that in the year prior to migration, migrant brook trout have 1.4 times higher consumption rates than resident brook trout. However, migrants have lower growth efficiencies (ratio of growth to consumption) than residents indicating that migrants have higher metabolic costs. Residents and migrants also differed in their stable carbon isotope signatures ($\delta^{13}C$), a time-integrated measure that has been linked to habitat use. Fish muscle $\delta^{13}C$ of migrants was depleted by 1 ± 0.1 ‰ compared to residents and this could not be explained by any biases introduced by the time of sampling or the size of fish sampled. Our findings thus agree with the notion that a link exists between metabolic costs (efficiency) and the adopted life-history strategy.

Résumé

Plusieurs espèces de salmonidés, incluant l’ombre de fontaine (*Salvelinus fontinalis*), présentent des formes résidantes et anadromes, au sein de la même population. Ce phénomène de migration partielle est fréquemment observé mais peu de connaissances existent concernant les mécanismes déterminant l’adoption de l’anadromie ou de la résidence. Nous avons utilisé des estimés de croissance de poissons en milieu naturel couplés à des estimées de taux de consommation *in situ* pour démontrer qu’il y existe un compromis entre l’habilité à exploiter l’environnement local (approche des résidants) et la capacité a profiter de l’hétérogénéité environnementale à grande échelle (approche des migrants). Nous démontrons que les truites migrantes ont des taux de consommation 1.4 fois plus élevées que les truites résidantes et des efficacités de croissance (le rapport de la croissance sur la consommation) plus faibles que les résidants au cours de l’année précédant la migration. Les coûts métaboliques sont donc plus élevés chez les migrants. De plus, les valeurs d’isotopes stables (δ^{13}C), une mesure intégrant le temps et reliée à l’utilisation d’habitat, diffèrent entre migrants et résidants. Dans les tissus musculaires de migrants les valeurs δ^{13}C sont inférieurs de 1 ± 0.1 ‰ comparativement à ceux des résidants. Cette différence ne peu pas être expliquée par une analyse biaisée découlant de la période d’échantillonnage ou de la taille des poissons. Nos résultats supportent donc l’idée qu’il existe un lien entre les coûts métaboliques (l’efficacité) et la stratégie de vie qui est adoptée.

Introduction

The diverse patterns of animal migration between geographically separated habitats have generated a widespread interest among biologists. In fish, migrations may occur between freshwater habitats, marine habitats or between fresh and saline waters (diadromy). Anadromy, a specialized form of diadromy, involves the migration of juveniles from freshwater into seawater and the return to freshwater as mature adults for spawning. Interestingly, a population may be composed of individuals adopting migration or residency as life-history strategies (partial migration) (Jonsson and Jonsson 1993). This is commonly observed in most salmonids including Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), Arctic char (*Salvelinus alpinus*) and brook trout (*Salvelinus fontinalis*).

It has been suggested that for a migratory life-history pattern to exist, the gain in fitness from moving to a new habitat, minus the costs of moving, must be higher than staying in only one habitat (Gross 1987). At first glance, the advantages of migration are evident; mature migrants are usually larger than mature residents and benefit from higher age-specific fecundity (Gross 1987). However, because only a fraction of a population migrates, the decision most likely involves a cost-benefit analysis, balancing the growth, reproductive and mortality potential (such as predation and/or disease) of the two habitats. Indeed, there is evidence to suggest the existence of a trade-off between the manifestation of migration and sexual maturation in fish populations exhibiting partial migration (Thorpe 1987; Hansen et al. 1989). For example, Atlantic salmon smolts do not mature sexually the same year they migrate and those parr that do mature early do not smolt and migrate. However, it remains unclear as to what causes individual fish within a population to adopt one particular strategy over another (i.e., residency and early maturation versus migration and delayed maturation) (Jonsson and Jonsson 1993).

Bohlin et al. (1996) proposed that a critical threshold in body size must be reached for migration to be initiated. At this threshold, fish will either mature in their present niche or leave (delaying maturity) to seek better feeding opportunities (Jonsson and Jonsson 1993). Gross (1987) has suggested that the most important biological parameter in explaining the occurrence of diadromous migration in fish populations is the relative availability of food in freshwater versus marine habitats. Studies have shown that by changing food availability, the proportion of fish emigrating from a system can be altered (Nordeng 1983; Tipping and Byrne 1996). A lowering of food resources results in an increase in the proportion of fish adopting migration. In this situation, body size or growth is limited by food supply (Forseth et al. 1994) and the migration to areas of higher food availability could allow for a continuation of growth.

It has also been observed that within populations, fast growers often migrate at younger ages than do slow growers (Jonsson 1985; Økland et al. 1993; Forseth et al. 1999). Food supplies in the natal habitat may limit fast growers sooner than slow growers, thus switching to richer feeding habitats earlier may serve to ensure continued growth (Jonsson and Jonsson 1993). However, the opposite has also been documented. Ricker (1938) showed that faster growing sockeye salmon (*Oncorhynchus nerka*) matured earlier and did not migrate to sea, whereas the slower growing fish matured only after migrating to sea. A threshold size of migration or growth rate is a plausible hypothesis; however, the explanation is incomplete as most fish surpass the threshold size or achieve high growth rates and still do not migrate. Thus, simply investigating growth rates has been proved inadequate in explaining the divergence of life-history forms.

Estimating the energy intake (i.e., consumption rate) and coupling this with growth may allow for a more complete analysis of the energetic performance of fish and how this may relate to differences in life-history strategies of anadromous fish. For example, Forseth et al. (1999) investigated the partial migration pattern (stream to lake) of brown trout. In their study, brown trout began to migrate at the age of 2+. They found that age 2+ migrants consumed significantly more than residents however a larger proportion of the consumed energy was allocated towards metabolic costs, thereby leaving less energy for growth compared to age-2+ residents. The migrants were possibly leaving because of their poor energetic performance (low growth efficiency) resulting from increased metabolic costs but not necessarily low growth since age-2+ migrants grew faster because of their much higher consumption rate.

Other studies have also shown indirectly that a link may exist between metabolic costs and life-history strategies (Metcalfe and Thorpe 1992; Metcalfe et al.1995). Increased metabolic costs could be the result of higher standard metabolic rates (SMRa) and (or) activity costs. It has been shown that Atlantic salmon with higher SMRa migrated sooner than those with lower SMRa (Metcalfe and Thorpe 1992; Metcalfe et al. 1995). Fish residing in fluvial environments may require a higher SMRa (higher aerobic scope) to feed in areas of higher food flux and may also exhibit increased activity rates if they are associated with costly habitats, such as those characterized by fast current velocity. Other fish may opt for reducing costs to a minimum when feeding by associating with energy-efficient habitats, e.g., slow currents or pools. Indeed, salmonids tend to position themselves in current velocities at which net energy benefits are maximized, balancing the trade-off between swimming costs and the delivery of drifting prey (Fausch 1984; Hughes and Dill 1990; Hill and Grossman 1993), leading to a spectrum of habitat preferences. Because different species of salmonids vary in their metabolic capacity for swimming in currents and distribute themselves accordingly, it is very likely such differences may also be found within a species exhibiting different life-history strategies. Finlay et al. (2002) showed that (δ^{13}C) signatures of juvenile steelhead trout, a migrant form of *Oncorhynchus mykiss* that lives and feeds predominantly in fast water, were more negative than those of rainbow trout, a resident form of the same species that obtains its food mainly from pools. It thus appears that carbon signatures may help to elucidate the links between velocity regimes, metabolic costs, and life-history variation in the field.

In this study, given a potential link between metabolic costs and life-history strategies, we propose a trade-off between the ability to efficiently exploit a local environment throughout life (resident approach) and the energetic scope required to exploit large-scale environmental heterogeneity (migrant approach). We thus expect to see migrant brook trout exhibiting higher feeding rates than resident brook trout, but experiencing lower growth efficiencies, a consequence of higher metabolic costs. In addition, we expected that we might find similar differences in δ^{13}C between migrants and residents as those found in resident rainbow trout and steelhead by Finlay et al. (2002)—that is, migrants will have lighter $\delta^{13}C$ signatures (indicative of feeding in faster waters) than those of residents.

Materials and methods

This study was conducted in Morin creek, a tributary of the Ste-Marguerite River system in the Saguenay region of Quebec (Figure 1.1). The Ste-Marguerite River is home to the most important anadromous brook trout population of the Saguenay River basin (Lesueur 1993). Populations of anadromous Atlantic salmon and brook trout, as well as resident brook trout co-occur in this region. The watershed area of Morin creek is ~ 18 km^2. Habitats range from riffles to pools, to shallow, laminar flow areas. Average water velocity during the summer is ~ 0.30 $m \cdot s^{-1}$.

Fish collection

The anadromous brook trout of Morin creek have been observed to migrate as young as age-1+ (G.R. Morinville, personal observation) to the estuarine Saguenay River. The genus *Salvelinus* exhibits the least pronounced anadromy of salmonids (Power 1980). No obvious smoltification occurs in migrant brook trout (McCormick et al. 1985) making it very difficult to differentiate a migrant from a resident until the moment of migration. Thus, fish captured in a downstream trap were considered migrants, whereas those captured in streams following the migration period were defined as residents. Migrant brook trout were captured from mid May to mid June 1999. Resident brook trout were captured by electrofishing immediately following the end of migration, in late June 1999. Both fork length (FL; to the nearest mm) and total mass (to the nearest 0.01 g) were measured.

Age analysis and growth rates

All trout collected in the summer of 1999 were aged using sagital otoliths and the biological intercept method (Campana 1990) was used to back-calculate lengths (Thériault 2001). Because the trout were not captured at the same time in the spring, lengths were back-calculated to the end of the last winter for age-1+ and age-2+ trout and to one year earlier at the end of the previous winter for initial sizes of age-2+ trout. Because of size-selective mortality, the estimated back-calculated size of age-1+ trout at emergence (age 0+) corresponded to the average of the top 10% size of age-0+ brook trout captured in early June. An emergence date of June 1 was assumed. Regressions between length and weight for both migrant and resident brook trout were performed to convert back-calculated lengths to weights for subsequent growth calculations.

Specific growth rates (G; $g \cdot g^{-1} \cdot d^{-1}$ or d^{-1}) were estimated for individual 1999 trout following Ricker (1979):

$$(1) \qquad G = \frac{1}{t} \ln\left(\frac{w_t}{w_0}\right)$$

where w_t is the final weight (g) at time t (days) and w_0 is the back-calculated initial body weight (g).

Consumption rates

Annual consumption rates (C; $g \cdot g^{-1} \cdot day^{-1}$ or day^{-1}) of migrant and resident brook trout (summer 1999) were estimated using a ^{137}Cs mass-balance model (Rowan and Rasmussen 1996). This method of estimating consumption rates is less labour-intensive, requires fewer fish sacrifices, and results in comparable feeding estimates to more traditional methods of estimating consumption rates based on gut clearance models (Gingras and Boisclair 2000). The model is defined as follows:

$$(2) \qquad C = \frac{\left(Q_t - Q_0 \cdot e^{-(E+D) \cdot t} + Q_g\right)}{\alpha \cdot [{}^{137}Cs_p] \cdot w_o \cdot (e^{Gt} - e^{-(E+D) \cdot t})} \cdot \left(G + E + D\right)$$

where Q_t is the total quantity of ^{137}Cs in fish, or burden (Bq) at time t (days), Q_0 is the initial ^{137}Cs burden (Bq), Q_g is the gonadal ^{137}Cs burden released at spawning, G, E is the elimination rate of ^{137}Cs (Bq·Bq^{-1}·day^{-1}or day^{-1}), D is the radioactive decay of ^{137}Cs (Bq·Bq^{-1}·day^{-1} or day^{-1}), [^{137}Cs$_p$] is the concentration of ^{137}Cs in the diet (Bq·kg^{-1}), α is the assimilation efficiency of ^{137}Cs from the diet (fraction), and w_0 is the initial body weight (kg).

^{137}Cs concentration in individual fish was measured by gamma spectrometry with a Coaxial Germanium Detector (Canberra Industries, Inc., Meriden, Connecticut, USA). To concentrate samples and reduce the time required to perform analyses, entire fish were ashed at 450 °C for 48 hours. The initial ^{137}Cs burden for age-1+ fish was assumed to be negligible (~0 Bq) at emergence, as the ^{137}Cs burden can increase several orders of magnitude in fish during their first year as a result of an increase in mass of several orders of magnitude. Initial ^{137}Cs burdens for age-1+ and age-2+ fish were back-calculated from ^{137}Cs body burden versus body weight relationships (see Tucker and Rasmussen 1999). Body burden models were determined independently for residents and migrants. The gonadal ^{137}Cs contribution was ignored because only juvenile fish were examined.

Daily water temperature (T) of Morin tributary was modelled with a Gaussian function as

$$(3) \qquad T = -0.24 + 19e^{\frac{-(JD-209)^2}{71.95^2}}$$

where JD is the Julian day.

Elimination rates of ^{137}Cs were obtained using a species independent model, described by a function of body size and temperature (Rowan and Rasmussen 1995). Morin tributary specific prey ^{137}Cs concentrations (6 Bq·kg^{-1}), determined on undigested gut contents, and assimilation efficiency (α = 0.23) were obtained from a previous study conducted in the same system (Tucker and Rasmussen 1999). The Atlantic salmon value was used because negligible differences exist between brook trout and Atlantic salmon assimilation efficiencies (Tucker and Rasmussen 1999).

Food consumption rates were estimated on a daily basis by interpolating fish size and ^{137}Cs burden between two adjacent age classes. Annual food consumption rates were then determined by summing the daily ration values obtained during these intervals.

Growth efficiency and total metabolic costs

Growth efficiency (*K1*, %) for individual resident and migrant brook trout was calculated as:

$$(4) \qquad K1 = \left(\frac{G}{C}\right) \cdot 100$$

Fish with the lowest growth efficiencies will have the highest maintenance costs defined as the amount of energy required to neither gain or lose weight (Tucker and Rasmussen 1999).

Total metabolic costs (TMC) were determined by incorporating the independently obtained estimates of growth and consumption, and solving by difference the following bioenergetics model (Hewett and Johnson 1992):

$$(5) \qquad G = C - (TMC) - F - U$$

where G is somatic and gonadal growth ($J \cdot d^{-1}$), C is the total energy consumed ($J \cdot d^{-1}$), and F (15% of C) and U (10% of C) are fecal (not assimilated) and urinary losses, respectively (Hewett and Johnson 1992). *TMC* incorporates specific dynamic action, the energy expenditure of digesting and processing food, standard metabolic rates (SMRa) and activity costs related to swimming, foraging and other behavioural activities (unitless). All parameters were converted to energy units with a conversion factor of 3429 J·g wet weight^{-1} for fish tissue (Cummins and Wuycheck 1971; Hartman and Brandt 1995) and 3176 J·g wet weight^{-1} for food items of aquatic invertebrates (Cummins and Wuycheck 1971). The relative energy allocation to the various components of the model could thus be computed.

Stable carbon signatures

Stable carbon signatures ($\delta^{13}C$) were measured for a sample of migrant and resident brook trout. In addition, resident trout sampled later in the summer were also analysed to determine whether the signature changed throughout the summer as the fish grew larger. This would allow us to remove any biases associated with small differences in size and time of sampling between the migrants and residents at the time of capture. Samples of white muscle tissue were oven-dried at 75 °C for approximately 48 hours and individual samples were ground into a fine powder with mortar and pestle. The stable carbon isotope analyses were performed using a mass spectrometer (G.G. Hatch Isotope Laboratories, University of Ottawa, Ottawa, Ontario, Canada). The stable carbon isotope ratios are reported relative to a standard (Pee Dee Belemnite) and are expressed as the parts per thousand (‰) deviation from the standard.

Statistical analyses

Brook trout were divided according to trout that migrated at 1+ (1+MIG), trout that were resident at age 1+ (1+RES), trout that migrated at age 2+ (2+MIG) and trout that were resident at age 2+ (2+RES). In addition, the first year of life (age 1) of both 2+MIG and 2+RES were also considered to form another 2 groups, identified as 1+(2+)MIG and 1+(2+)RES, respectively.

To compare ^{137}Cs concentrations and $\delta^{13}C$ signatures of combined (all ages) migrants and residents, *t* tests were performed. An analysis of covariance (ANCOVA) was performed to compare the relationship of weight and ^{137}Cs body burden for combined migrants and residents.

ANCOVAs were also performed to compare the relationship between $\delta^{13}C$ as a function of time, and as a function of weight for both migrants and residents combined. A one-way-analysis of variance (ANOVA) was conducted to compare size at age for combined migrants and residents. ANOVAs were performed to compare specific growth rates, consumption rates and growth efficiency between migrant and resident trout at age 1. Tukey's tests were also conducted for specific comparisons between groups at age 1. Comparisons between 2+ migrants and residents were performed using t-tests. Non-parametric tests were also performed and revealed the same conclusions as parametric tests and thus the results are not presented. We also used *t* tests to compare $\delta^{13}C$ between migrants and residents.

Results

Specific growth rates

Migrant and resident brook trout collected from Morin tributary followed different growth trajectories (mean size at age) over time (Figure 1.2) prior to migration ($F = 11.6$, $p < 0.001$, $n = 130$). By age 2, residents are 1.3 times larger in size than migrants.

Growth rates for resident brook trout ranged from 0.0033 - 0.0067 $g \cdot g^{-1} \cdot d^{-1}$ (Table 1.1, Figure 1.3). Growth rates for migrant brook trout ranged from 0.0030 $g \cdot g^{-1} \cdot d^{-1}$ to 0.0066 $g \cdot g^{-1} \cdot d^{-1}$. There was an overall significant difference in growth between age 1 fish (Table 1.2). Growth rates for 1+RES were similar to those of 1+(2+)RES ($p = 0.99$) suggesting that growth rates for residents at age 1 did not vary between cohorts. Tukey's tests also revealed no differences between 1+MIG and 1+RES ($p = 0.99$) or 1+(2+)RES ($p > 0.99$). However, 1+(2+)MIG had significantly lower growth rates than 1+(2+)RES ($p < 0.001$) and 1+RES ($p < 0.001$). In addition, 1+(2+)MIG had lower growth rates than 1+MIG ($p < 0.001$). There were also no significant differences in growth between 2+MIG and 2+RES (Table 1.2) even though residents are larger by age 2. This indicates that 2+MIG had the lowest growth rate compared to all other groups in their first year of life and thereafter.

Fish ^{137}Cs body burden relationships

^{137}Cs concentration in resident brook trout varied from 2.7 to 3.1 Bq·kg^{-1}, whereas migrant brook trout had significantly higher ^{137}Cs concentrations, ranging from 3.9 Bq·kg^{-1} to 4.8 Bq·kg^{-1} (t = 3.56, df = 86, p = 0.001) (Table 1.1). Migrants had a higher ^{137}Cs body burden as a function of weight compared to residents (F = 4.74, p = 0.032, n = 88; Fig. 4). These migrant and resident specific regressions were subsequently used to assign ^{137}Cs body burdens to individual fish for their respective back-calculated sizes.

Consumption rates

Consumption rates of migrants ranged from 0.017 to 0.019 g·g^{-1}·d^{-1}, whereas residents ranged from 0.011 g·g^{-1}·day^{-1} and 0.013 g·g^{-1}·day^{-1} (Table 1.1, Figure 1.5). Migrants consumed more than residents at age 1 regardless of the cohort (Table 1.2). Specifically, 1+MIG had similar consumption rates to 1+(2+)MIG (p = 0.91) and consumed 1.4 times more than 1+RES (p = 0.011) and 1+(2+)RES ($p < 0.001$). 1+(2+)MIG also had consumption rates 1.4 times higher than both 1+(2+)RES (p = 0.012) and 1+RES (p = 0.001). Migrants also consumed more than residents at age 2 (Table 1.2). Overall, migrants consumed more than residents in the year(s) prior to migration.

Growth efficiencies and total metabolic costs

Migrants had growth efficiencies ranging from 19.9 to 40.1% (Table 1.1, Figure 1.6). In contrast, residents had higher growth efficiencies than migrants, ranging from 27.6 to 60.2%. There was a significant difference in growth efficiencies between migrants and residents of age 1 regardless of cohort (Table 1.2). More specifically, 1+(2+)MIG had significantly lower growth efficiencies than 1+RES ($p < 0.001$) and 1+(2+)RES ($p < 0.001$). 1+MIG also had lower growth efficiencies than both 1+RES (p = 0.004) and 1+(2+)RES ($p < 0.001$), but had higher growth efficiencies than

1+(2+)MIG ($p = 0.02$). In addition, 2+MIG had significantly lower growth efficiencies than 2+RES (Table 1.2).

Both age-1+ (both cohorts) and age-2+ migrants allocated a higher proportion of their consumed energy to metabolism (38% and 53%, respectively) than residents (25% and 45%, respectively) (Fig. 7). The proportion of energy lost to excretion and egestion was considered the same across all fish types (25% of C). Age-1+ and age-2+ residents thus allocated a higher proportion of the energy consumed to growth (62% and 30%, respectively) compared to migrants (36% and 21%, respectively).

Stable carbon signatures

There was no relationship between δ^{13}C and weight for either migrants ($F_{1,15} = 0.20$, $r^2 = 0.014$, $p > 0.5$), or resident brook trout ($F_{1,33} = 1.9$, $r^2 = 0.057$, $p = 0.17$) in the size range concerned. There was also no relationship between δ^{13}C and sampling date in our study for either migrants ($F_{1,19} = 0.18$, $r^2 = 0.010$, $p > 0.5$) or residents ($F_{1,41} = 0.32$, $r^2 = 0.0080$, $p > 0.5$). There were no significant differences in δ^{13}C between age-1+ and age-2+ migrants ($t = 0.47$, $df = 18$, $p > 0.5$) or between age-1+ and age-2+ residents ($t = 0.48$, $df = 32$, $p > 0.5$); therefore age classes were pooled. As expected, δ^{13}C signatures of migrants were significantly lighter than residents by 1 ± 0.1‰ ($t = -4.6$, $df = 52$, $p < 0.001$) (Fig. 8).

Discussion

Migrant and resident brook trout bioenergetic budgets

The results obtained from Morin tributary indicate that, as predicted, migrant brook trout have noticeably different energy budgets than resident brook trout from the same system. No differences in specific growth rates were found between migrants and residents of the same age class, although age-2+ migrants had lower specific growth rates than both age-2+ residents and age-1+ migrants in their first year of life. Moreover, 2+ migrants were smaller than both age-1+ migrants and age-2+ residents in their first year of life and were thus the smallest part of their cohort at age

1 (Thériault 2001). This contrasts the findings of Forseth et al. (1999) where age-2+ migrant brown trout were larger (faster growing) than age-2+ resident brown trout. However, no differences in size existed between 3+ migrant and resident brown trout.

Within migrants, our study supports previously reported findings that faster growing individuals migrate sooner than slower growing individuals (Jonsson 1985; Forseth et al. 1999) because age-1+ migrants grew faster at age 1 than brook trout that migrated at 2+. However, when comparing residents to migrants, no differences in growth rates were observed. In addition, the larger age-2+ trout remained residents, whereas the smaller migrated. The inconsistencies regarding size and growth may not be surprising as these are measures of excess acquired energy that ignores any underlying minimum amount of energy required to meet the physiological demands of the fish and ensure survival.

The analyses performed in this study showed that migrant brook trout consumed, on average, 1.4 times more than resident brook trout. As there were no differences in growth rates observed between migrants and residents, the results indicate that migrants require more food to grow the same amount. Migrants thus have lower growth efficiency, a consequence of higher total metabolic costs. As indicated previously, results regarding growth were not consistent between this study and that of Forseth et al. (1999). However, when consumption is included in the analysis, the results agree with those of Forseth et al. (1999) as age-2+ migrant brown trout had lower growth efficiencies than age-2+ resident brown trout. Our bioenergetic results, consistent with those observed by Forseth et al. (1999) for resident and migrant brown trout, highlight the importance of coupling growth rates with consumption rates when interpreting growth differences (or lack thereof) of fish in the wild.

According to the bioenergetic model, growth efficiency differences are the consequence of variations in energy losses related to metabolism. In salmonids, there appears to be a link between metabolic rates, behaviour and life-history strategies. Variations in metabolic rates may be the result of differences in SMRa and/or activity. Lahti et al. (2001) recently found that migratory forms of brown trout (*Salmo trutta*) were more aggressive than resident forms. In addition, it has been found that Atlantic salmon possessing the highest SMRa migrated earlier than those with low SMRa (Metcalfe and Thorpe 1992; Metcalfe et al. 1995). These early migrating individuals also exhibited more aggressive and dominant behaviours. Because both Atlantic salmon and migrant brook trout adopt migration as a life-history strategy it may be argued that there exists a strong behavioural similarity between them. It is thus possible that migrant brook trout, like early migrating salmon, have the highest SMRa compared to their non-migrating counterparts. This is reasonable to assume because Atlantic salmon also have lower growth efficiencies and higher total metabolic costs compared to resident brook trout (Tucker and Rasmussen 1999).

In fluvial systems, fish tend to position themselves in current velocities at which net energy benefits are maximised (Fausch 1984; Hughes and Dill 1990; Hill and Grossman 1993). Swimming in a fast current is more costly than swimming in a slow current (Beamish 1980), however, because a positive correlation exists between current velocity and drift (Hughes and Dill 1990), a higher food flux is possible in fast current velocities. In general, stream-dwelling brook trout are usually observed in low current velocities, around 25 $cm \cdot s^{-1}$ (Griffith 1972; Fausch and White 1981), whereas Atlantic salmon inhabit faster current velocities around 50 $cm \cdot s^{-1}$ in the wild (Heggenes 1996; Booth et al. 1997). If migrant brook trout are similar to Atlantic salmon in their behaviour and habitat use then we might expect differences in food sources between the two life-history strategies as a result of differences in habitat use. According to Finlay et al. (1999), feeding in riffles or fast current will result in a depleted $\delta^{13}C$ signature (more negative) relative to feeding in pools or slow currents which will result in an enriched (less negative) $\delta^{13}C$

signature. This interpretation is based on significant differences in algal $\delta^{13}C$ between riffle and pool habitats. Because there is the potential for drift feeding fish to obtain food from a mixture of food sources as a result of the continuous downstream movement of aquatic invertebrates, detecting significant differences in stable isotopes requires low mixing of drift between pool and riffle habitats. High mixing of food sources would result in small or insignificant differences in observed signatures. In Morin Creek, $\delta^{13}C$ in migrants was depleted by 1‰ compared to residents. This difference, although small, was highly significant and could not be explained by any time or size biases. The observed difference in $\delta^{13}C$ is also consistent with expected isotopic differences between riffles and pools. Furthermore, this difference is similar in both magnitude and direction to that reported by Finlay et al. (2002) for steelhead and rainbow trout. Given the three lines of evidence – increased consumption rates, increased metabolic costs, and depleted $\delta^{13}C$ – we hypothesize that migrants, like salmon, utilize faster current velocities than residents. This is a plausible explanation because similar differences in $\delta^{13}C$ are observed between Atlantic salmon and resident brook trout in Morin Creek (G.R. Morinville, unpublished data).

Bioenergetic role in partial migration: from stream to sea

This study, by focussing on the early life stages of brook trout, provides support for the idea that variations in energy allocation lead to the adoption of migration or residency as life-history strategies. Although it appears that migrants obtain more food, the fact that they migrate suggests that they do not receive enough energy to satisfy their higher metabolic demands. They most likely enter growth bottlenecks (although not necessarily apparent by simple size measurements) sooner than residents. Migrating, although potentially risky because of increases in predation threats or mortality, could serve to improve energetic performance (lowering total metabolic costs without reducing energy intake) and allow energy needs to be met. This may be similar to when fish make ontogenetic diet shifts to larger prey (Sherwood et al. 2002). This is reasonable to assume as anadromous fish grow faster in the sea than resident fish do in freshwater (Gross 1987; Rikardsen et. al. 2000).

The findings suggest that migrants adopt migration most likely as a consequence of energetic limitations. It is thus reasonable to assume that residents are better adapted to living in streams than migrants as they exhibit a more energy efficient life-history strategy. Residents can be considered ‘winners’ in streams as they perform well energetically in their immediate surroundings and are thus not required to leave their local environment. The consequence of their more efficient strategy is a lower food intake and limited growth over their life-cycle. On the other hand, migrants possess the energetic scope to capitalize on better feeding opportunities and are thus better adapted to profit from large-scale heterogeneous environments. Migration can thus initially be considered a ‘losing’ strategy as the residents manifest higher growth efficiency in freshwater but ultimately a ‘winning’ strategy because migrants returning from sea to spawn are larger and more fecund. Nonetheless, for the two strategies to coexist, it seems unlikely that overall either strategy wins or loses. Thus the fitness benefits and costs of migration compared to those of residency should balance over the entire life-cycle (Jonsson and Jonsson 1993). This most likely involves a balance between growth, and predation and mortality risk in the two habitats (Gross 1987).

Interestingly, it was found that brook trout that migrated at age 2+ were the most constrained (lowest growth efficiency), however possibly because of their small size at age 1, they delayed migration. This would support the notion that a critical threshold in body size must be reached for migration to be initiated (Bohlin et al. 1996). This delay is most likely related to the fact that smaller individuals have higher costs associated with mortality and osmoregulation in the marine environment (Svenning et al. 1992; Økland et al. 1993). However, even though most individuals surpass a critical size, not all individuals adopt migration. Thus it appears that growth efficiency and size may both play a role in determining whether a fish adopts migration over residency.

In conclusion, the present study demonstrates a link between metabolic costs and life-history strategies. In addition, the study supports the idea that a trade-off exists between the ability to efficiently exploit a local environment throughout life (resident approach) and the energetic scope required to capitalize from large-scale environmental heterogeneity across the entire life-cycle (migrant approach). This trade-off is an important factor to be considered in conservation and management as a population composed of individuals able to exploit either the local environment or large-scale diverse environmental heterogeneity may be better positioned to persist through unpredictable events such as climate shifts and habitat degradation.

Acknowledgments

We thank A. Boivin, A. Du Cap, S. Lenormand, K. Lunn, C. Mimeault, V. Thériault for field assistance and laboratory work. We are grateful to D. Browne, G. Sherwood, S. Tucker, and Y. Vadeboncoeur for their helpful comments on earlier versions of this manuscript. This study is a contribution to the program of CIRSA (Centre Interuniversitaire de Recherche sur le Saumon Atlantique) and GRIL (Groupe de Recherche Interuniversitaire en Limnologie et en Environnement Aquatique). Funding for this project was provided to J.B.R. by NSERC of Canada (Strategic Grant and Collaborative Special Projects), the Fondation de la Faune du Québec, the Government of Quebec (FAPAQ), the Government of Canada (Economic development), the financial partners of CIRSA Inc, and a Graduate Fellowship to G.R.M. from the Vineberg family.

References Cited

Beamish, F.W.H. 1980. Swimming performance and oxygen consumption of the charrs. *In C*harrs: Salmonid fishes of the genus *Salvelinus*.

Edited by E.K. Balon. W. Junik, The Hague, The Netherlands. pp. 739-748.

Bohlin, T., Dellefors, C., and Faremo, U. 1996. Date of smolt migration depends on body size but not age in wild sea-run trout. J. Fish Biol. 49: 157-164.

Booth, R.K., Bombardier, E.B., McKinley, R.S., Scruton, D.A., and Goosney, R.F. 1997. Swimming performance of post spawning adult (kelts) and juvenile (smolts) Atlantic salmon, *Salmo salar*. Can. Manuscr. Rep. Fish. Aquat. Sci. No. 2406: v +18p.

Campana, S.E. 1990. How reliable are growth back-calculation based on otoliths? Can. J. Fish. Aquat. Sci. 47: 2219-2227.

Cummins, K.W., and Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. Int. Assoc. Theor. Appl. Limnol. Proc. No. 18.

Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Can. J. Zool. 62: 441-451.

Fausch, K.D., and R.J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Can. J. Fish. Aquat. Sci. 38: 1220-1227.

Finlay, J.C., Power, M.E., and Cabana, G. 1999. Effects of water velocity on algal carbon isotope ratios: Implications for river food web studies. Limnol. Oceanogr. 44(5): 1198-1203.

Finlay, J.C., Khandwala, S., and M.E. Power. 2002. Spatial scales of carbon flow in a river food web. Ecology, 83: 1845-1859.

Forseth, T, Ugedal, O., and Jonsson, B. 1994. The energy budget, niche shift, reproduction and growth in a population of Arctic charr, *Salvelinus alpinus*. J. Anim. Ecol. 63: 116-126.

Forseth, T., Næsje, T.F., Jonsson, B., and Hårsaker, K. 1999. Juvenile migration in brown trout: a consequence of energetic state. J. Anim. Ecol. 68: 783-793.

Gingras, J., and Boisclair, D. 2000. Comparison between consumption rates of yellow perch (*Perca flavescens*) estimated with a digestive tract model with a radioisotope approach. Can. J. Fish. Aquat. Sci. 57: 2547-2557.

Griffith, J.S., Jr. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. J. Fish. Res. Board. Can. 29: 265-273.

Gross, M.A. 1987. Evolution of diadromy in fishes. American Fisheries Society Symposium 1: 14-25.

Hansen, L.P., Jonsson, B., Morgan, R.I.G., and Thorpe, J.E. 1989. Influence of parr maturity on emigration of smolting Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 46: 410-15.

Hartman, K. J., and Brandt, S.B. 1995. Estimating energy density of fish. Trans. Am. Fish. Soc. 124: 347-355 .

Heggenes, J. 1996. Habitat selection by brown trout (*Salmo trutta*) and young Atlantic salmon (*Salmo salar*) in streams: static and dynamic hydraulic modelling. Regul. Rivers 12: 155-169.

Hewett, S.W., and Johnson, B.L. 1992. A generalized bioenergetics model of fish growth for microcomputer. Tech. Rep. No. WIS-SG-92-250. University of Wisconsin Sea Grant Program, Madison, Wis.

Hill, J., and Grossman, G.D. 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. Ecology, 74: 685-698.

Hughes, N.F., and Dill, L.M. 1990. Position choice by drift-feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Can. J. Fish. Aquat. Sci. 47: 2039-2048.

Jonsson, B. 1985. Life history patterns of freshwater and sea-run migrant brown trout in Norway. Trans. Am. Fish. Soc. 114: 182-194.

Jonsson, B. and Jonsson, N. 1993. Partial Migration: niche shift versus sexual maturation in fishes. Rev. Fish Biol. and Fish. 3: 348-365.

Lahti, K., Laurila, A., Enberg, K., and Piironen, J. 2001. Variation in aggressive behaviour and growth rate between populations and migratory forms in the brown trout, *Salmo trutta*. Anim. Behav. 62: 935-944.

Lesueur, C. 1993. Compte rendu des résultats obtenus lors de l'étude de l'Omble de fontaine anadrome de la rivière Ste-Marguerite (Saguenay) en 1992. Rapport réalisé dans le cadre du Programme de subvention aux projets à caractères fauniques du ministère du Loisir, de la Chasse et de la Pêche. Association de la rivière Ste-Marguerite. Canada.

McCormick, S.D., Naiman, R.J., and Montgomery, E.T. 1985. Physiological smolt characteristics of anadromous and non-anadromous brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 42: 529-538.

Metcalfe, N.B., Taylor, A.C., and Thorpe, J.E. 1995. Metabolic rate, social status and life-history strategies in Atlantic salmon. Anim. Behav. 49: 431-436.

Metcalfe, N.B., and Thorpe, J.E. 1992. Early predictors of life-history events: the link between first feeding date, dominance and seaward migration in Atlantic salmon, *Salmo salar* L. J. Fish Biol. 41 (Suppl. B): 93-99.

Nordeng, H. 1983. Solution to the "char problem,' based on Arctic charr (*Salvelinus alpinus*) in Norway. Can. J. Fish. Aquat. Sci. 40: 1372-1387.

Økland, B., Jonsson, B., Jensen, A.J., and Hansen, L.P. 1993. Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon? J. Fish. Biol. 42: 541-550.

Power, G. 1980. The brook charr, *Salvelinus fontinalis*. *In* Charrs: salmonids fishes of the genus *Salvelinus*. *Edited by* E.K. Balon. W. Junik, The Hague, Netherlands. pp. 141-203.

Ricker, W.E. 1938. ‘Residual’ and kokanee salmon in Cultus Lake. J. Fish. Res. Board Can. 4: 192-218.

Ricker, W.E. 1979. Growth rates and models. *In* Fish Physiology, vol III. Bioenergetics and growth. *Edited by* W.S. Hoar, D.J. Randall, and J.R. Brett. Academic Press, NY. pp. 677-743.

Rikardsen, A.H., Amudsen, P.A., Bjorn, P.A., Johansen, M. 2000. Comparison of growth, diet and food consumption of sea-run and lake-dwelling Arctic charr. J. Fish Biol. 57: 1172-1188.

Rowan, D.J., and Rasmussen, J.B. 1995. The elimination of radiocesium from fish. J. Appl. Ecol. 32: 739-744.

Rowan, D.J., and Rasmussen, J.B. 1996. Measuring the bioenergetic cost of fish activity *in situ* using a globally dispersed radiotracer (^{137}Cs). Can. J. Fish. Aquat. Sci. 53: 734-745.

Sherwood, G., Pazzia, I., Moeser, A., Hontela, A., and Rasmussen, J.B. 2002. Shifting gears: enzymatic evidence for the energetic advantage of switching diet in wild-living fish. Can. J. Fish. Aquat. Sci. 59: 229-241.

Svenning, M.-A., Smith-Nilsen, A., and Jobling, M. 1992. Sea water migration of Arctic charr (*Savelinus alpinus* L.). Correlation between freshwater growth and seaward migration based on back-calculations from otoliths. Nord. J. Freshwat. Res. 67: 18-26.

Thériault, V. 2001. Anadromie et résidence chez l’omble de fontaine (*Salvelinus fontinalis*): présence d’une stratégie conditionelle basée sur la croissance? M.Sc. thesis, Laval University, Ste-Foy, Canada.

Thorpe, J.E. 1987. Smolting versus residency: developmental conflict in salmonids. Am. Fish. Soc. Symp. 1: 244-52.

Tipping, J.M., and Byrne, J.B. 1996. Reducing feed levels during the last month of rearing enhances emigration rates of hatchery-reared steelhead smolts. Prog. Fish-Cult. 58: 128-130.

Tucker, S., and Rasmussen, J.B. 1999. Using ^{137}Cs to measure and compare bioenergetic budgets of juvenile Atlantic salmon (*Salmo* *salar*) and brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. 56: 875-887.

Table 1.1 Mean (± 1 standard error) growth rates (G), [^{137}Cs], consumption rates (C), and growth efficiency (GE) for groups of resident and migrant brook trout from Morin tributary.

Type	Age	N	G ($g \cdot g^{-1} \cdot d^{-1} \times 10^{-2}$)	[^{137}Cs] ($Bq \cdot kg^{-1}$)	C ($g \cdot g^{-1} \cdot d^{-1} \times 10^{-2}$)	GE (%)
Resident	1+	16	0.67 ± 0.022	2.9 ± 0.34	1.3 ± 0.083	57 ± 3.5
	1+ (2+)	18	0.67 ± 0.029	2.7 ± 0.34	1.1 ± 0.055	60 ± 2.6
	2+	18	0.33 ± 0.0079	3.1 ± 0.42	1.2 ± 0.062	28 ± 1.2
Migrant	1+	38	0.66 ± 0.014	4.3 ± 0.24	1.8 ± 0.081	40 ± 2.2
	1+ (2+)	14	0.44 ± 0.023	4.8 ± 0.24	1.9 ± 0.12	25 ± 2.1
	2+	14	0.30 ± 0.012	3.9 ± 0.31	1.7 ± 0.11	20 ± 1.4

Note: 1+(2+) refers to the first year of fish aged 2+.

Table 1.2 Statistical comparison of the energy budget of migrants and residents using one-way analysis of variance (ANOVA; age 1) and t-test (age 2).

	Age[a]	*F* (ANOVA)	*t* (t-test)	*df*	*p*
Growth rates ($g{\cdot}g^{-1}{\cdot}d^{-1}$)	1	12.9	--	82	< 0.001
	2	na	-1.24	30	0.24
Consumption rates ($g{\cdot}g^{-1}{\cdot}d^{-1}$)	1	9.4	--	82	< 0.001
	2	na	2.66	30	0.012
Growth efficiency	1	16.6	--	82	< 0.001
	2	na	-3.2	30	0.003

na: not applicable

[a] Age 1 includes migrants and residents captured at age 1 and the back-calculated age 1 of fish captured at age 2.

Age 2 includes migrants and residents captured at age 2.

Figure 1.1 The Ste-Marguerite River system in the Saguenay region of Quebec, Canada.

Migrant and resident brook trout (*Salvelinus fontinalis*) were obtained from Morin tributary.

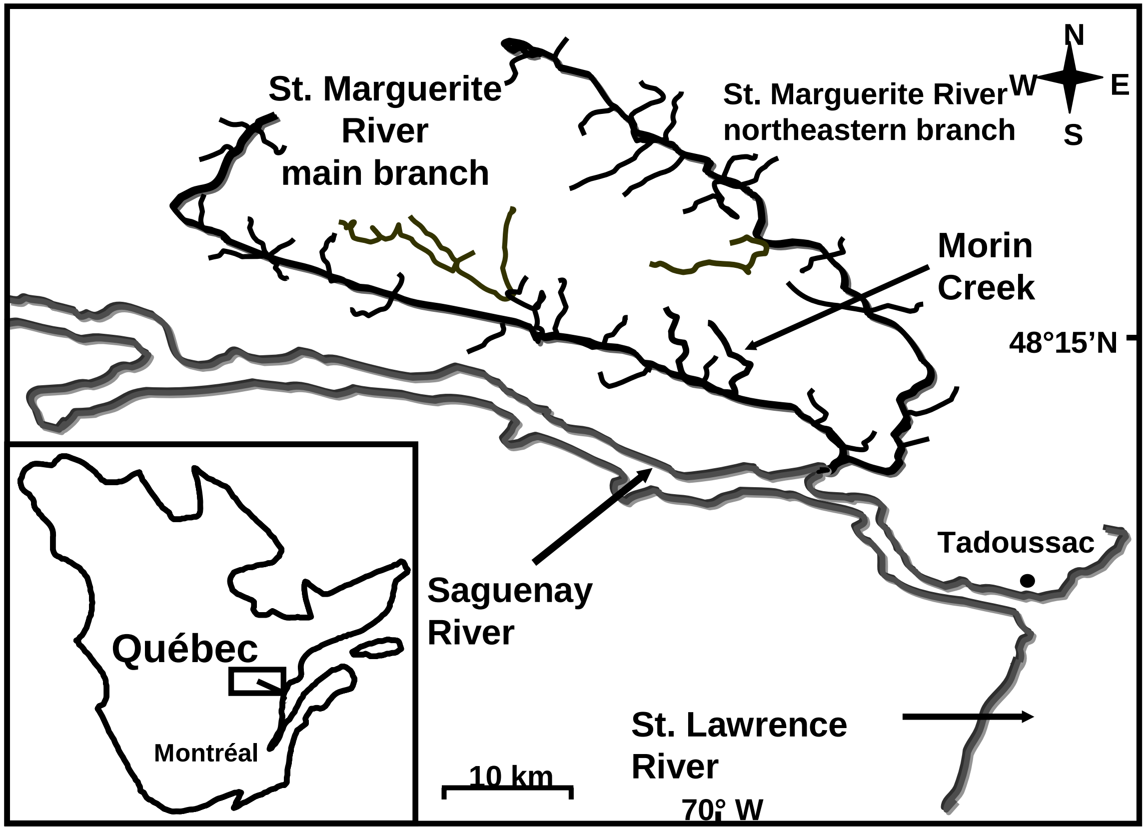
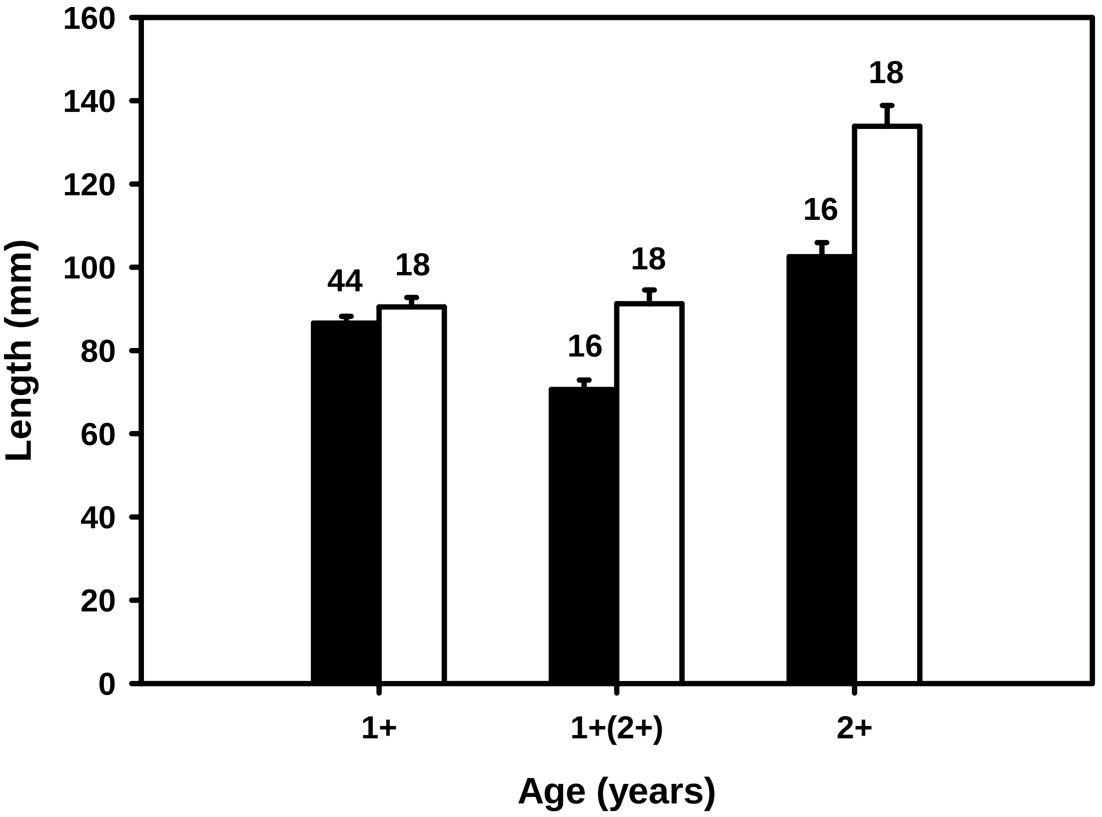

St. Marguerite River main branch
St. Marguerite River northeastern branch
N
W
E
S
Morin Creek
48°15'N
Tadoussac
Saguenay River
Québec
Montréal
St. Lawrence River
10 km
70° W

Figure 1.2 Mean size at age (+ 1 standard error) for migrant (solid bars) and resident brook trout (*Salvelinus fontinalis*) (open bars).

1+(2+) refers to the first year of life of fish aged 2+. Numbers above bars represent sample size.



160
140
120
100
80
60
40
20
0
Length (mm)
44
18
16
18
16
18
1+
1+(2+)
2+
Age (years)

Figure 1.3 Growth rates for migrant (solid bars) and resident (open bars) brook trout (*Salvelinus fontinalis*).

1+(2+) refers to the first year of life of fish aged 2+. The error bars represent +1 standard error. Numbers above bars represent sample size.

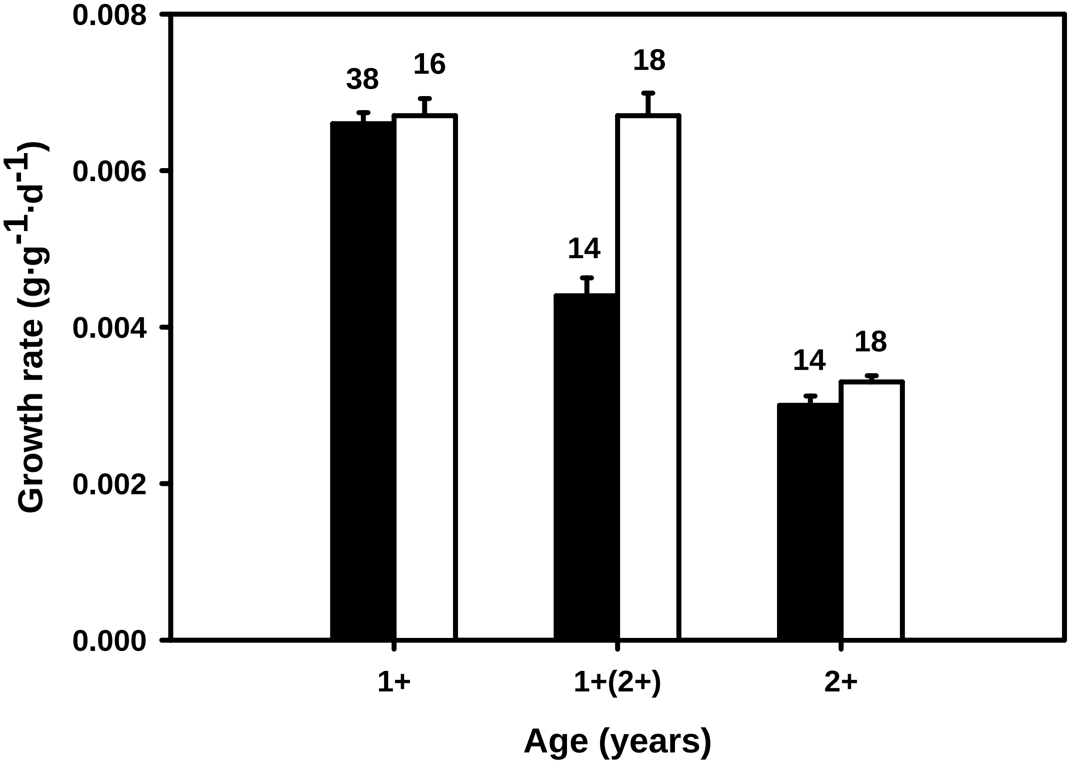

0.008
0.006
0.004
0.002
0.000
Growth rate ($g \cdot g^{-1} \cdot d^{-1}$)
38
16
18
14
14
18
1+
1+(2+)
2+
Age (years)

Figure 1.4 Weight-^{137}Cs body burden relationships for individual migrant ($F_{1,52}$ = 63.5, $p < 0.001$, $r^2 = 0.55$, n = 54; closed circles) and resident ($F_{1,32}$ = 156.3, $p < 0.001$, $r^2 = 0.83$, n = 34; open circles) brook trout (*Salvelinus fontinalis*) from Morin tributary.

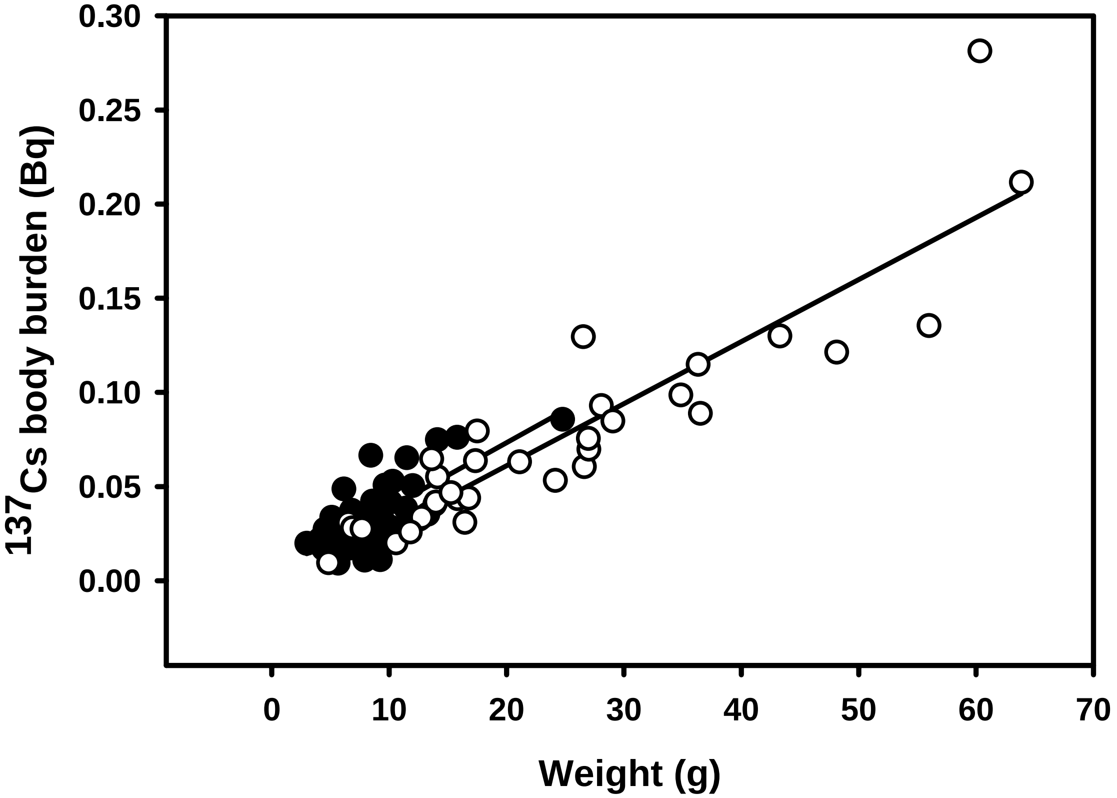

0.30
0.25
0.20
0.15
0.10
0.05
0.00
^{137}Cs body burden (Bq)
0
10
20
30
40
50
60
70
Weight (g)

Figure 1.5 Consumption rates for migrant (solid bars) and resident (open bars) brook trout (*Salvelinus fontinalis*).

1+(2+) refers to the first year of life of fish aged 2+. The error bars represent +1 standard error. Numbers above bars represent sample size.

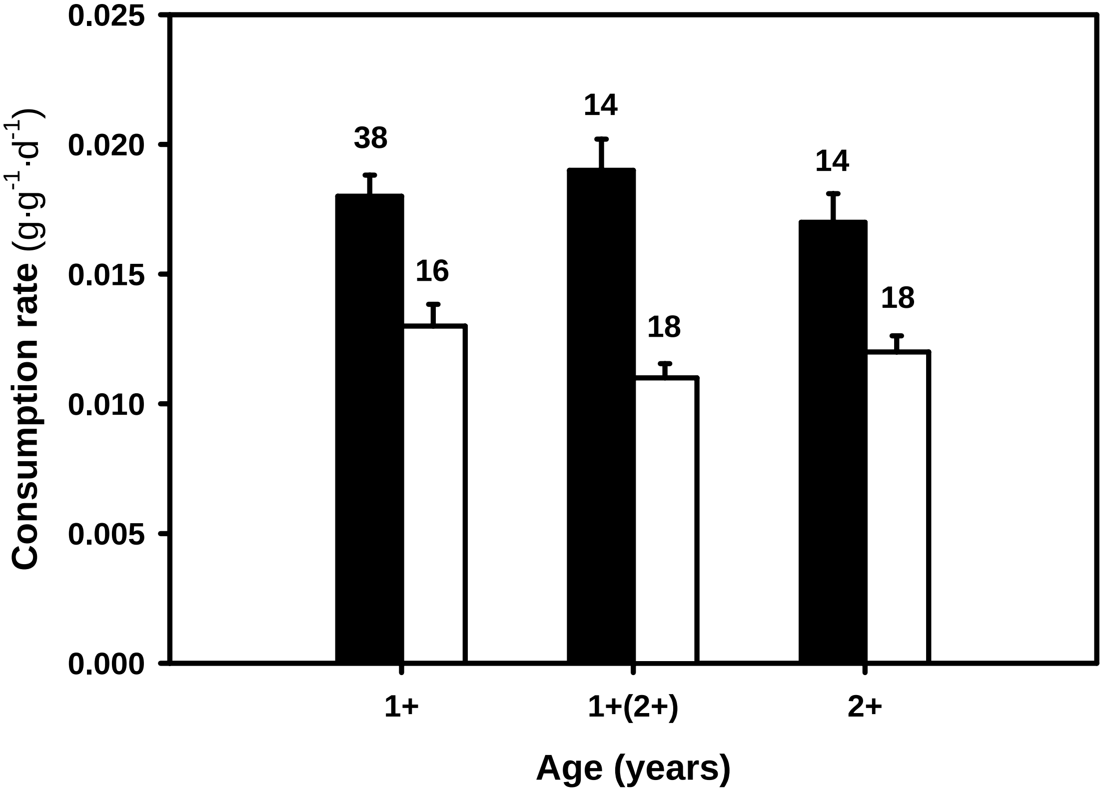

Consumption rate (g·g-1·d-1)
0.025
0.020
0.015
0.010
0.005
0.000
38
16
14
18
14
18
1+
1+(2+)
2+
Age (years)

Figure 1.6 Growth efficiency for migrant (solid bars) and resident (open bars) brook trout (*Salvelinus fontinalis*).

1+(2+) refers to the first year of life of fish aged 2+. The error bars represent +1 standard error. Numbers above bars represent sample size.

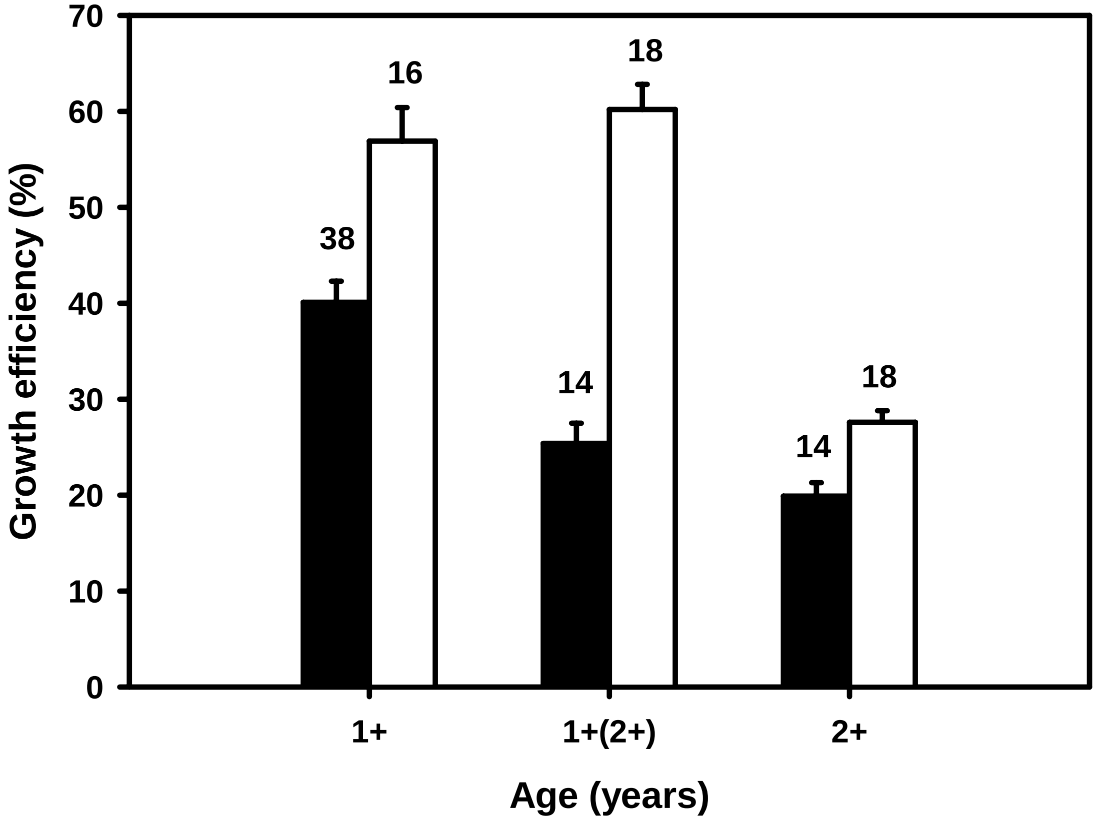

70
60
50
40
30
20
10
0
Growth efficiency (%)
16
18
38
14
18
14
1+
1+(2+)
2+
Age (years)

Figure 1.7 Relative allocation of energy consumed to the various compartments of the bioenergetic budget of migrant (MIG) and resident (RES) brook trout (*Salvelinus fontinalis*).

1+(2+) refers to the first year of life of fish aged 2+. Solid bars refer to growth, open bars refer to fecal and urinary losses, and shaded bars refer to total metabolic costs including standard metabolic rates, activity and specific dynamic action.

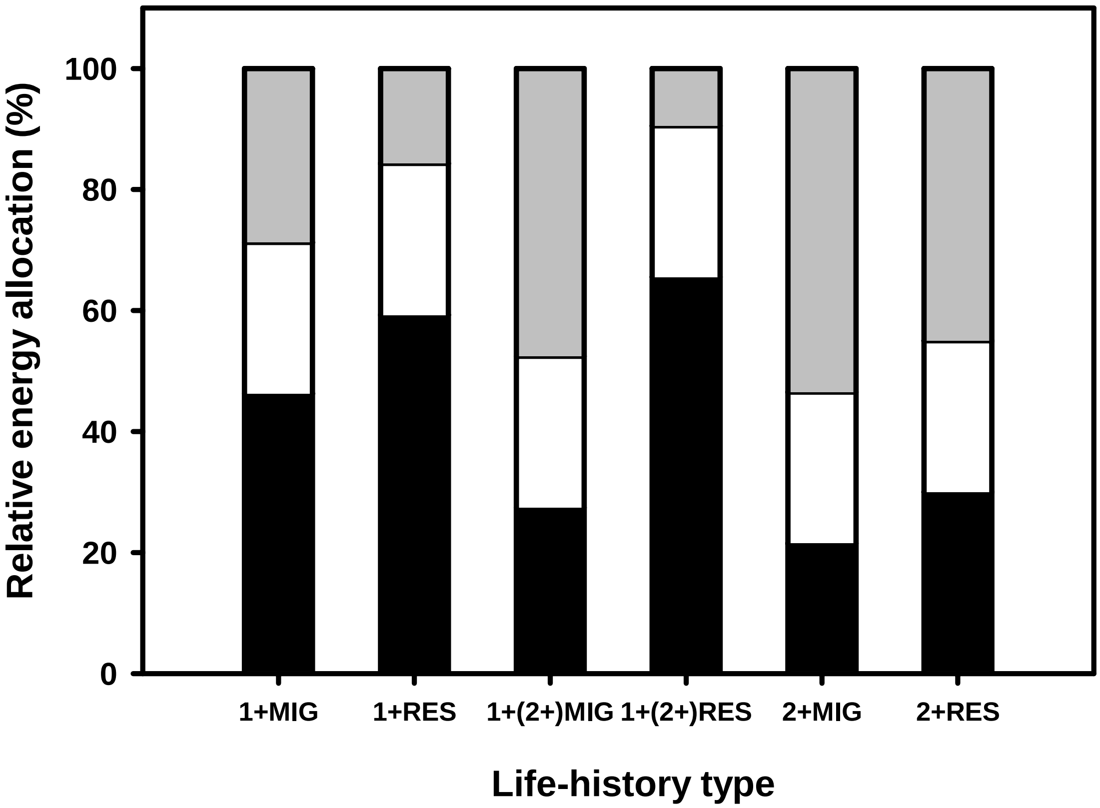
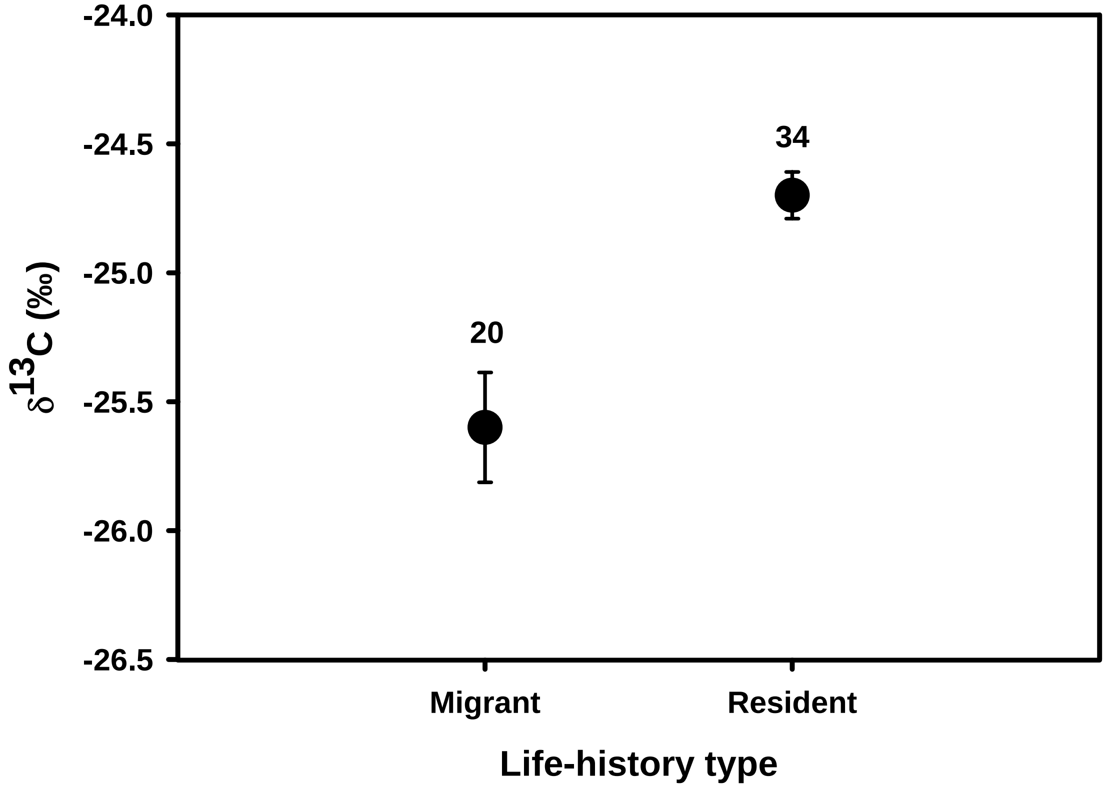

Relative energy allocation (%)
100
80
60
40
20
0
1+MIG
1+RES
1+(2+)MIG
1+(2+)RES
2+MIG
2+RES
Life-history type

Figure 1.8 δ^{13}C for migrant and resident brook trout (*Salvelinus fontinalis*).

Migrants have signatures reflecting use of faster current velocities than residents. The error bars represent ± 1 standard error. Numbers above circles represent sample size.



-24.0
-24.5
-25.0
-25.5
-26.0
-26.5
δ^{13}C (‰)
34
20
Migrant
Resident
Life-history type

CONNECTING STATEMENT: bridging Chapter 1 and 2

Interestingly, the results of Chapter 1 suggest that coexisting juvenile anadromous and resident brook trout exploit different habitats due to their differences in metabolic costs and stable isotope signatures. Given these results and the tight link between fish morphology and habitat use, variations in body morphology between anadromous and resident brook trout are expected. This would provide additional support to the results presented in Chapter 1.

Furthermore, in Chapter 1, we distinguished migrants as trout captured in trap nets during the downstream migration period, whereas those captured in streams following the migration periods were defined as residents, since no obvious morphological differences exist between the two forms. Chapter 1 thus exposes our inability to distinguish future migrant brook trout from residents during their coexistence as juveniles in streams prior to the migration period. This greatly hinders the potential for studying directly the feeding and behaviour of the two forms, in addition to their habitats, limiting our understanding of the two forms.

For these reasons, Chapter 2 describes the variations in body morphology between anadromous and resident brook trout, presents a tool for differentiating between the two forms in the field and links them to the bioenergetic differences shown in Chapter 1.

"*Everyone ought to believe in something; I believe I'll go fishing*." Unknown

CHAPTER 2: Distinguishing between juvenile anadromous and resident brook trout (*Salvelinus fontinalis*) using morphology[1]

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Submitted to *Environmental Biology of Fishes*

Synopsis

Phenotypic variation linked to habitat use has been observed in fish, both between and within species. In many river systems, migratory and resident forms of salmonids coexist, including anadromous and resident brook trout (*Salvelinus fontinalis*). It has been suggested from bioenergetics and stable carbon isotope signatures, that in such populations, juvenile anadromous (migrant) brook trout, prior to migration, inhabit regions of higher current velocity than residents. As it is more costly to occupy fast currents than slow currents, differences in morphology minimizing the effects of drag are expected. This study determined whether migrant and resident brook trout differ in body morphology in a manner consistent with their hypothesized habitat use differences. Based on 7 body measurements collected on populations of migrant and resident brook trout, migrant brook trout were found to be more streamlined (narrower and shallower bodies) than resident brook trout, and these differences persisted into the marine life of the fish. Migrants also exhibited shorter pectoral fins, which facilitate pelagic swimming, indicating that migrants, prior to their migration to the sea, possess the appropriate morphology for swimming in open water habitats. The reported differences between migrants and residents were powerful enough to derive discriminant functions allowing for accurate classification of brook trout as either migrants or residents using only five of the seven traits with an overall correct classification rate of 87%. A modified function was also applied to young-of-the-year (YOY) stages to predict future migrant-like and resident-like forms. Although the accuracy of this classification could not be verified, stable isotope signatures of predicted YOY migrant-like and resident-like forms were consistent with previously reported values between known juvenile migrants and residents, providing support to the validity of these models as predictive tools.

Introduction

Phenotypic variation in morphological traits implicated in predator evasion and feeding have been commonly reported in the literature. For example, crucian carp (*Carassius carassius*) are known to increase their body depth as a defense mechanism against gape-limited piscivores (Holopainen et al. 1997, Pettersson & Brönmark 1999) and Arctic charr from an Icelandic lake have developed morphological adaptations in mouth and snout shape according to their benthivorous or planktivorous-piscivorous feeding behaviors leading to four sympatric morphs (Skúlason et al. 1989).

Phenotypic variation linked to habitat use has also been observed, both in warm-water stream fishes including cyprinids and percids (Wood & Bain 1995), and in salmonids, both within and between species (Riddell & Leggett 1981, Bisson et al. 1988, Swain & Blair 1989). Bisson et al. (1988) demonstrated that differences in fin size and body shape predicted the stream channel locations utilized by juvenile salmonids. Coho salmon (*Oncorhynchus kisutch*), which prefer pools, possessed a deep and laterally compressed body with large median and paired fins, facilitating transitory maneuvering ability. In contrast, steelhead (*Oncorhynchus mykiss*) possessed a fusiform body shape with short median fins and large paired fins, allowing for efficient swimming in fast water, and cutthroat trout morphology was intermediate between the two other salmonid species (*Salmo clarki clarki*).

Riddell & Leggett (1981) showed within-species morphological differences in Atlantic salmon by linking river flow conditions to variations in body shape. They demonstrated that a river with higher average flow velocities contained salmon that were more streamlined in shape and had larger paired fins than those inhabiting a river with lower average flows. Taylor & McPhail (1985) also found heritable morphological differences between interior and coastal populations of juvenile coho salmon. Interior populations were more streamlined in shape and possessed smaller median fins than coastal populations, most likely the result of their greater need for efficient swimming during migrations, as a greater amount of distance separates these interior populations from the sea.

Thus, it is commonly observed that fish inhabiting faster currents are more streamlined (shallow-bodied versus deep-bodied) than those inhabiting slow currents. A more streamlined morphology in fast water reduces swimming costs by minimizing the effects of drag (Pettersson & Brönmark 1999). Drag is influenced by fish shape, the square of the current speed and the Reynolds number (Re) of the fish (Vogel 1994). Re is positively related to fish size, the undisturbed velocity, and water temperature (kinematic viscosity). Pressure drag predominates at high velocities such that changes to a more streamlined body morphology, as indicated by the fineness ratio (ratio of standard length to body depth), leads to a reduction in the drag coefficient (Webb 1975, Blake 1983). A high ratio between span and length of their caudal fin ('aspect ratio') also reduces the effects of drag (Webb 1984, Webb 1988).

In the wild, brook trout tend to swim actively and feed in the water column and continue to swim against the current even in fast waters (Keenleyside 1962). It should thus be more efficient for trout inhabiting fast currents, to possess a more streamlined morphology. Indeed, YOY brook trout inhabiting faster currents in the wild are more streamlined than those inhabiting slow currents, exhibiting shallower body depths, shorter caudal peduncle depths and larger caudal fin heights (McLaughlin and Grant 1994), although the differences may not persist over time (Imre et al. 2001).

Brook trout populations in some rivers are a mixture of anadromous (migratory) and resident forms (Thériault & Dodson 2003). It has been suggested that in such populations juvenile anadromous (migrant) brook trout, prior to migration, inhabit regions of higher current velocity in freshwater than residents (Morinville & Rasmussen 2003). This was predicted based on the finding that migrants exhibit higher consumption rates but lower growth efficiencies (ratio of growth to consumption), the consequence of higher metabolic costs. In addition, migrants had muscle tissues that were more negative in δ^{13}C than residents, suggesting the use of faster currents because algal δ^{13}C depletes with increasing water velocity (Finlay et al. 1999, Trudeau & Rasmussen 2003).

The objectives of this study are (1) determine whether anadromous (migrant) and resident brook trout of the Ste. Marguerite River system, Quebec, Canada differ in body morphology, (2) whether the observed differences coincide with habitat use expectations, and (3) whether any observed differences can be used for field identification. It is predicted that within migrant-resident streams (streams with resident and anadromous forms), migrant brook trout will be more streamlined than residents. Specifically, it is predicted that resident brook trout will have wider and deeper bodies (higher drag morphology) compared to migrant brook trout. Fin sizes including caudal, pelvic and pectoral are also expected to differ between migrants and residents. Furthermore, it is predicted that resident fish from migrant-resident streams will be less streamlined than those of resident-only streams. We also expected that any pre-migratory morphological differences that we observed between migrants and residents would persist (carry over) into the marine life of the fish. That is, sea trout migrants will continue to differ morphologically from residents throughout their life.

Study Site and Methods

Study site

This study was conducted in the Ste. Marguerite River (SMR) system in the Saguenay region of Quebec, Canada (48º27’N, 69º95’W). The SMR flows into the estuarine Saguenay River that further empties into the St. Lawrence River. The SMR system is home to the largest anadromous brook trout population of the Saguenay River basin (Lesueur 1993). Populations of anadromous Atlantic salmon and brook trout, as well as resident brook trout, co-occur in the region. Streams containing such populations of coexisting brook trout and Atlantic salmon will be referred as ‘migrant-resident’ streams. Anadromous brook trout down-migrate from mid-May to early-June, as early as age 1+ to the estuarine Saguenay River (Thériault & Dodson 2003). Stream reaches above man-made barriers, such as poorly constructed culverts and natural barriers, such as waterfalls, will be referred as ‘resident-only’ streams as these only contain resident brook trout. Sea trout have never been observed in the resident-only streams and outmigrations have never been recorded.

Fish collection

The genus *Salvelinus* exhibits the least pronounced anadromy of salmonids (Power 1980). No obvious smoltification occurs in migrant brook trout (McCormick et al. 1985) making it very difficult to differentiate a migrant from a resident until the moment of migration. In migrant-resident streams, we distinguished migrants as trout captured in trap nets during the downstream migration period, whereas those captured in streams following the migration period were defined as residents. Although the trout remaining in the system after migration are considered residents, an unknown proportion of these trout may actually consist of future migrants.

Migrants were captured from two migrant-resident streams, Morin (2001-2003) and Portage (2002). Migrants were also captured upon sea entry in the Saguenay River estuary every two to four weeks from the Ste. Marguerite Bay or from nearby Anse-de-Roche between May and October of 2001 and 2002. These trout will be referred to as sea trout.

All resident brook trout were captured using a backpack electro-fisher (Smith-Root, Inc. model 12A) following the migration period beginning mid-June. Residents were sampled in three migrant-resident streams including Morin (2001-2003), Portage (2002) and Édouard (2002), and in two resident-only streams including Épinette (2002) and La Prairie (2002). Young-of-the-year (YOY) from Morin stream were also captured and measured in early September 2000 and 2001.

Morphological trait measurements

All fish morphological trait measurements were performed in the field. Both fork (FL; to the nearest mm) and standard length (SL; to the nearest mm) was measured for each trout. Previously reported empirical evidence and theory, in addition to logistical constraints, guided the selection of morphological traits to be measured. Morphological traits included maximum body depth, maximum body width, peduncle depth, caudal fin height, pectoral fin length and pelvic fin length (Imre et al. 2001, Peres-Neto & Magnan 2004). A needlepointed divider was employed to measure the length of each body trait. This involved stretching the divider to the desired length, placing of the divider on paper, and tracing the distance between the two needle ends. These lines were then subsequently measured using calipers (to the nearest 0.05mm). The same person (G.R. Morinville) took all measurements.

Morphological comparisons

Regressions of individual morphological trait measurements as a function of size (standard length) were conducted for both migrants and residents of Morin streams for years 2001 to 2003. Trait-specific regressions were then compared between migrants and residents using analysis-of-covariance (ANCOVA) for Morin stream for all years.

Regressions of individual morphological trait measurements as a function of size were conducted for residents captured in migrant-resident streams (Édouard, Morin and Portage) and for residents captured in resident-only streams (Épinette, La Prairie) in 2002. Trait-specific regressions were subsequently compared between pooled migrant-resident stream residents and resident-only residents using ANCOVAs.

Discriminant function analysis (DFA) was conducted to assess whether the overall differences observed between (1) pooled migrants, (2) pooled residents of migrant-resident streams, and (3) pooled residents of resident-only streams using all measured traits were powerful enough to accurately predict the life-history group to which an individual fish belonged. Residuals obtained from group-specific linear regressions of each morphological trait as a function of fish size were retained for DFA, and all fish were reclassified according to the model generated by DFA to obtain the correct reclassification rate.

Finally, comparisons between residents of migrant-resident streams and sea trout were conducted using ANCOVA to evaluate whether the morphological differences observed between migrants and residents persist post-migration, that is whether the differences persist over time. All statistical analyses were conducted using SYSTAT (Version 10.2).

Overall morphological comparisons between life-history forms

Form drag was estimated for the different life-history forms including migrant-resident migrants and residents, resident-only residents and sea trout captured in 2002 using two surrogate measures: (1) fineness ratio (ratio of standard length to maximum body depth, and (2) circular ratio (ratio of maximum body depth to maximum body width) indicative of prolonged swimming (Webb 1975, Sibbing & Nagelkerke 2001). A higher fineness ratio indicates a more elongated body shape with a ratio of about 5 indicating low drag. A lower circular ratio indicates a more circular shaped body with a ratio of 1 indicating a perfect circle. Both the fineness and circular ratio were compared between residents from migrant-resident and resident only streams, migrants and sea trout using one-way analysis-of-variance (ANOVA) and subsequent pairwise Tukey comparisons.

Three fin length ratios were calculated for the different life-history forms including migrant-resident migrants and residents, resident-only residents and sea trout captured in 2002. The ratios included: (1) caudal fin height to standard length, (2) pelvic fin length to standard length, and (3) pectoral fin length to standard length. These ratios were compared between the life-history forms using ANOVA and subsequent pairwise TUKEY comparisons.

Field identification and validation

An interactive stepping DFA (Alfonso 2004) was conducted using all possible size-free ratios of morphological traits of migrant and resident data from Morin 2002 in order to select the variables that best classified migrants and residents. The purpose of this was to develop a means of discriminating between future migrants and residents prior to the spring outmigration, during the previous summer when fish can be readily caught by electrofishing. The resultant function was then applied to fish captured in Morin in 2001 and 2003 in addition to trout captured in 2002 resident-only streams in order to assess the validity of the model.

Predicting future migrants and residents at young-of-the-year (YOY) stages

Young-of-the year (YOY) captured in 2001 on Morin stream were considered as precursors to trout captured in 2002 on Morin. Comparisons using ANOVAs and Tukey pairwise comparisons were made between 2001 YOY, 2002 migrants and residents using the means of the residuals from the pooled (all groups) linear regressions of each trait. A separate interactive stepping DFA using Morin 2002 migrants and residents was conducted to attempt to classify YOY as either future migrants or residents. This DFA was conducted using size-free ratios derived only from standard length, maximum body depth, caudal fin height and peduncle depth as fewer traits were measured on YOY. The derived model was then applied to 2000 and 2001 Morin YOY using trait means obtained from 2001 and 2002 Morin migrants and residents, respectively. The different morphological traits as a function of length were subsequently compared between predicted ‘future’ migrants and residents using ANCOVAs.

Results

Fish collection

In total, 2561 fish were measured in the field across all sites and years. Migrants captured in traps installed on Morin and Portage stream and measured ranged in size between 93.3 mm and 117.9 mm (Table 2.1). Young-of-the-year (YOY) brook trout captured in Morin stream in 2000 and 2001 had a mean size of 63.3 mm and 55.6 mm, respectively. Residents captured in migrant-resident streams (Édouard, Morin and Portage streams) ranged in size from 96.4 mm to 119.6 mm, while those from resident-only streams (Épinette and La Prairie streams) ranged in size from 101.9 and 113.1 mm. Sea trout captured in the Saguenay River, including sites in the Ste. Marguerite Bay and Anse-de-Roche, were larger ranging in size between 149.7 mm and 164.2 mm.

Morphological comparisons

Migrants versus residents

Significant relationships of morphological trait length as a function of standard length were found for 2001 to 2003 migrant and resident brook trout of Morin stream (Figure 2.1; Table 2.2). Morphological trait lengths differed significantly between Morin brook trout migrants and residents across all years. Specifically, Morin migrants were more streamlined than residents, possessing shallower maximum body depths and peduncle depths, and smaller body widths as a function of size (Table 2.2). In addition, Morin migrants had smaller caudal fins, and shorter pelvic and pectoral fins than residents. These differences were consistently detected over three years, suggesting temporal persistence.

Migrant-resident stream residents versus resident-only stream residents

Significant relationships were found among all morphological trait lengths (Table 2.3) for both migrant-resident stream residents and resident-only residents. Overall, residents from resident-only streams are slightly more deeply-bodied, are wider and have larger peduncle depths than residents from migrant-resident streams, although the differences decrease with increasing size. Residents from migrant-resident streams also had smaller caudal fins and similarly, the differences decreased with increasing size. No differences in pelvic fin size were detected between migrant-resident and resident-only streams. However, migrant-resident stream trout had slightly smaller pectoral fins as a function of length.

Migrants versus migrant-resident and resident-only stream residents

A complete DFA was used with the known a priori separation of migrants, migrant-resident and resident-only stream residents. The three forms showed slightly overlapping but distinct distributions in multivariate space, with residents from both stream types showing the most overlap (U = 0.365, $F_{6,12} = 112.7$, $p < 0.005$; Figure 2.2). The DFA model correctly reclassified (jackknifed classification) 91% of migrants, 65% of resident-only residents and 74% migrant-resident residents for an overall correct classification of 74%. Only 2.3% of migrants were misclassified as resident-only fish and 6.5% as residents from migrant-resident streams. The lower classification rates of residents from resident-only streams indicate that 24.5% were misclassified as residents from migrant-resident streams and only 1.9% as migrants. A proportion of residents from migrant-resident streams were misclassified as migrants (11.7%) and an even larger proportion as residents from resident-only streams (23.8%).

Migrant-resident streams versus Saguenay River

A significant positive relationship exists for all morphological trait lengths as a function of standard length for brook trout captured in the Saguenay River (sea trout) both in 2001 and 2002 (Table 2.4). Morphological differences between migrants and residents appear to persist even once the migrants are living in the sea. Saguenay River sea trout were more streamlined (shallower body depths, smaller widths and shallower peduncles) than Morin stream residents in 2001, and this was also observed in 2002 between pooled migrant-resident residents and sea trout (Table 2.4). In addition, residents were observed, in both years, as having shorter pectoral fins compared to sea trout, as well as smaller caudal fins. The differences in pelvic fin length between residents and sea trout was not as clear across years, although resident trout in 2002 had shorter pelvic fins than sea trout.

Overall comparison of body morphology between life-history forms independent of size

Fineness ratio (standard length to maximum body depth) varied significantly (ANOVA: $F_{3,1354} = 291.9$, $p < 0.001$) between 2002 resident-only stream residents, migrant-resident stream residents, migrants and sea trout (all at $p < 0.001$; Figure 2.3a). Similarly, the bodies of migrants and sea trout are significantly more circular (ratio of maximum body depth to maximum body width is closest to 1) than those of residents from migrant-resident and resident-only streams (ANOVA: $F_{3,1354} = 61.7$ $p < 0.001$; Figure 2.3b). Although no statistically significant differences exist between migrants and sea trout ($p = 0.062$), significant differences do exist between residents from migrant-resident and resident-only streams (both have $p < 0.001$). Overall, migrants and sea trout have the most elongated and circular body form, and thus possess a drag-efficient morphology compared to residents from resident-only streams that possess a less elongated and circular body form.

Caudal fin height to standard length ratios differed significantly between migrant-resident migrants and residents, resident-only residents and sea trout ($F_{3,1225} = 291.6$, $p < 0.001$; Figure 2.3c). Subsequent Tukey comparisons revealed significant differences between all groups at $p < 0.001$. Significant differences also exist for ratios of pelvic fin length to standard length ratio between the groups (ANOVA: $F_{3,1351} = 348.2$, $p < 0.001$; Figure 2.3d). Residents from resident-only streams do not differ from residents of migrant-resident streams ($p = 0.98$), although all other forms differ at $p < 0.001$. Similarly, no differences were found between resident-only residents and migrant-resident residents for pectoral length ($p = 0.55$; Figure 2.3e), although significant differences were found between all other groups (ANOVA: $F_{3,1352} = 394.3$, $p < 0.001$). Overall, residents from both types of streams have the largest caudal, pelvic and pectoral fin length to standard length ratios compared to migrants and sea trout. Migrants have larger pelvic fins but smaller pectoral and caudal fins than sea trout.

Field identification and validation

Using an interactive stepping DFA with Morin 2002 data, three size-free ratios were selected including depth to standard length ratio (DEP_LTH), peduncle to caudal height ratio (PED_CAUD) and pectoral to standard length ratio (PECT_LTH). The following function was derived for Morin 2002 using the standardized within variance canonical discriminant functions, within sample means (m_{year}) and standard deviations (SD_{year}; Table 2.5) to classify brook trout as either migrant or resident:

$$(1)\quad \begin{aligned} F = {} & (0.728)(\text{DEP\_LTH} - m_{year})(SD)^{-1} \\ & + (-0.719)(\text{PED\_CAUD} - m_{year})(SD)^{-1} \\ & + (0.386)(\text{PECT\_LTH} - m_{year})(SD)^{-1} \end{aligned}$$

If $F < 0$, trout are classified as migrant and, if $F > 0$, trout are classified as resident. This function correctly classifies 94.3% of migrants and 81.8% of residents from Morin 2002 brook trout leading to an overall correct classification rate of 86.6% ($U = 0.42$, $F_{3,649} = 298.8$, $p < 0.001$).

The above function was employed to assess its validity for other sampling years, using the same canonical discriminant functions as above but using sample means and standard deviations specific to 2001 and 2003 samples (2.5). In 2001, the function accurately classified 92.2% of migrants and 89.6% of residents, for an overall classification of 90.8%. Similarly, the function accurately classified 90.8% of migrants and 83.7% of residents, for an overall correct classification of 87.2%.

The same function was also applied to 2002 resident-only streams, using the function above, and the 2002 means and standard deviations.

The function correctly predicted 96.3% of the ‘pure’ residents as being residents (n = 160). The function thus appears to work well across years and sites.

Predicting future migrants and residents at young of the year (YOY) stages

Significant positive relationships exist for maximum body depth, caudal fin height and peduncle depth as a function of standard length for Morin 2000 and 2001 YOY (Table 2.6). Residuals of YOY (Table 2.7) compared to those of migrants and residents from the pooled relationship between log body depth and log standard length were found to be intermediate to those of migrants ($p < 0.01$) and residents ($p < 0.01$). Comparisons of the residuals also indicate that YOY caudal fin heights were intermediate between migrants ($p < 0.01$) and residents ($p < 0.01$). In contrast, YOY had peduncle residuals that were more negative than both migrants ($p < 0.01$) and residents ($p < 0.01$). Thus overall, the results suggest the occurrence of convergence at small sizes.

The following function was derived using only two size-free ratios DEP_LTH and PED_CAUD to predict future migrants and residents from YOY stages:

$$(2) \qquad F = (0.872)(\mathrm{DEP\_LTH} - m_{\mathrm{year}})(\mathrm{SD})^{-1} + (-0.682)(\mathrm{PED\_CAUD} - m_{\mathrm{year}})(\mathrm{SD})^{-1}$$

If $F < 0$, YOY are predicted to be migrants and, if $F > 0$, YOY are classified as resident.

YOY in 2000 were classified 62% and 38% as migrants and residents, respectively, while YOY in 2001 were classified 56% as migrants and 44% as residents. Predicted resident YOY (n = 14) captured in 2000 were more deeply bodied (elevation: $F_{1,48} = 6.1$, $p = 0.017$) and had larger caudal fin heights (elevation: $F_{1,48} = 26.1$, $p < 0.001$) as a function of size compared to predicted migrants (n = 37)(Figure 2.4). Significant differences were detected for peduncle depth between predicted migrants and residents both in terms of slope ($F_{1,47} = 5.5$; p = 0.023) and elevation ($F_{1,47} = 5.2$; p = 0.027).

Similarly, significant differences were also detected between predicted 2001 migrant (n = 61) and resident YOY (n = 48) for maximum body depth (elevation: $F_{1,106} = 25.4$, $p < 0.001$) and for caudal fin height (elevation: $F_{1, 106} = 40.5$, $p < 0.001$; Figure 2.4). Predicted residents were more deeply bodied and had larger caudal fin heights as a function of size than predicted migrants. No differences were detected in peduncle depth between predicted YOY migrant and resident ($F_{1,106} = 2.3$, p = 0.13).

Discussion

Morphological differences between anadromous and resident brook trout

The present study compares the body morphology of anadromous (migrant) and resident brook trout of the Ste. Marguerite River system, Quebec, Canada in order to establish a link between morphology, habitat use, bioenergetics and the adopted life-history strategy. Resident brook trout from Morin stream, a migrant-resident stream, were found to be less streamlined as they were wider, more deeply-bodied and had deeper peduncles than migrant brook trout, supporting initial predictions. These differences were observed across all years on Morin stream indicating temporal persistence, and not the result of year-to-year variation. The morphological variations concur with inferred anadromous and resident brook trout habitat use and bioenergetics (Morinville and Rasmussen 2003), such that migrants, by possessing a more streamlined morphology, minimize their energetic costs when swimming in fast water (Sagnes et al. 2000, Boily & Magnan 2002). Similarly, Taylor & McPhail (1986) also found that anadromous threespine sticklebacks (*Gasterosteus aculeatus*) had less robust bodies (narrower bodies and heads, and shorter caudal peduncle depths) and fatigued less quickly than resident ones, coinciding with habitat requirements.

Morphological differences among brook trout using different habitats have been detected as early as age 0+ in resident populations (McLaughlin & Grant 1994). They observed shallower body depths for young-of-the-year (YOY) brook trout using faster current velocities compared to those using slower currents, giving support to the morphological differences observed in older trout (older than 0+) in this study and the expected variations in habitat use. However, contrary to our findings, YOY utilizing fast currents in the wild (McLaughlin & Grant 1994) and YOY raised in fast waters (Imre et al. 2002) had larger caudal fin heights than those using slow currents. Although larger caudal fin heights were detected for YOY using faster currents in the wild, the observation did not persist over time (Imre et al. 2001), suggesting that other mechanisms may be present to offset a change in caudal fin height. Such mechanisms may include differences in developmental rates (Martin 1949), physiology (such as standard metabolic rates) or behaviour, whereby certain adaptations may be important at small sizes but not necessarily so at large sizes.

We found that migrants, assumed to be using faster currents in freshwater, to have shorter pectoral fins and shorter pelvic fins compared to residents. In contrast, Imre et al. (2002) found no differences in pelvic or pectoral fin length between YOY brook trout (lake strain) reared under slow and fast flow conditions. Observations from resident brook trout populations may not apply to populations comprising both migratory and resident phenotypes as developmental tradeoffs may vary between forms.

The slower pelvic and pectoral fin growth of migrants may allow for immediate adaptation to pelagic swimming upon sea entry, as sea trout continue to exhibit short pelvic and pectoral fins throughout their ontogeny. Pectoral fins of lacustrine benthic-feeding brook trout are longer than those of pelagic-feeding ones (Bourke et al. 1997), the former facilitating slow and precise maneuvering (Webb 1984). Short pectoral fins, important for cruising, are required for searching efficiently for prey in open water habitats (Ehlinger 1990). Shorter pectoral fins also reduce drag (Drucker & Lauder 2003). Similarly, benthic feeding Arctic charr, characterized by stocky bodies, also have longer fins compared to streamlined piscivorous-planktivorous feeders (Skúlason et al. 1989, and references therein). It therefore appears that anadromous brook trout, prior to their migration to the sea, possess the appropriate morphology for swimming in the open water habitats of the sea, by being more streamlined in shape and having short pectoral and pelvic fins.

It is important to mention that differential sampling periods could have contributed to the observed differences in body condition (body depth and width) as migrants were sampled in early spring following winter, a period associated with low feeding and growth. However, our results show that residents from migrant-resident streams are also more streamlined than residents from resident-only streams, possessing narrower and shallower bodies, and thereby supporting our initial predictions. The observation that the morphological differences among residents become less apparent at large sizes, which results in a steeper relationship between trait length and size, is logical as the older and larger brook trout of migrant-resident streams are most likely ‘true’ residents, since the majority of trout that migrate leave by the age of 2+. In addition, the differences in body condition are also not due to smoltification since brook trout do not experience physiological transformations prior to migration (Hoar 1976, McCormick et al. 1985, Beeman et al. 1995).

Linear discriminant function analysis revealed significant discernable and predictable differences between migrants and residents from both migrant-resident and resident-only streams using the morphological traits. The model accurately classified over 90% of migrants as migrants while residents from migrant-resident and resident-only streams were correctly classified at 74% and 65%, respectively. The misclassification is mostly the result of residents from migrant-resident streams being misclassified as residents from resident-only streams, and vice-versa. Only 1.9% of resident-only residents were classified as migrants while 11.6% of residents were classified as migrants. Given the high correct classification rate, and the presence of future migrants within the brook trout population of migrant-resident streams we interpret this to mean that the migrant-resident residents that were misclassified as migrants, probably were fish that would migrate in future years. Larger fish, older than >2+ which is the oldest age of migration, would be expected to be true residents, while many of the smaller fish, younger than 2+, might still be future migrants. Interestingly, the migrant-resident stream residents misclassified as migrants were smaller (82.6 mm ± 16.4 S.D.) than those misclassified as resident-only stream residents (106.8mm ± 30.9 mm S.D.). Even so, this interpretation for the higher rate at which migrant-resident residents were misclassified as migrants, remains to be confirmed.

The morphological differences observed between migrants and residents reported in this study were found to persist over time. Migrant trout captured out at sea continued to be more streamlined in shape than residents from migrant-resident streams in 2002 and residents from Morin stream in 2001, having narrower and shallower body depths and peduncle depths, and shorter caudal, pectoral and pelvic fin lengths. Similar differences were observed in a Nova Scotia population of migrant and resident brook trout where newly returning sea trout to freshwater possessed more cylindrical bodies and shorter fins than freshwater trout (Wilder 1952). This same pattern was observed even though the trout were larger (average size of 170 mm) and older than SMR fish (80% of migrants are at age 3+ compared to SMR system where almost 100% migrate before the age of 3+). The adaptations leading to anadromy thus seem consistent across populations, regardless of the age or size at migration.

Efficient prolonged swimming requires a streamlined body shape of about equal depth and width, and a length/depth ratio around 5 to minimize drag (Sibbing & Nagelkerke 2001)). Thus brook trout exhibiting all life-history forms have hydrodynamically efficient body forms, although trout captured during outmigration and at sea had the highest fineness ratio (ratio of standard length to maximum body depth), in addition to having the most circular body shape compared to residents from migrant-resident and resident-only streams, suggesting that their morphology would produce the lowest drag. Thus overall, the variations in body shape reported here are consistent with previously reported studies regarding morphology and habitat use.

Field identification

A function using three size-free ratios including depth to standard length ratio (DEP_LTH), peduncle to caudal height ratio (PED_CAUD) and pectoral to standard length ratio (PECT_LTH) was derived from Morin 2002 data that significantly differentiates between migrants and residents of Morin stream leading to a high classification rate. Only four morphological trait measurements are required for accurate classification of migrants and residents. Cross-validation further indicated that the function could be employed to accurately classify fish from other sampling years. As mentioned earlier, the misclassified residents as migrants could indeed be future migrants.

Applying the discriminant function using only two size-free ratios, DEP_LTH and PED_CAUD, allowed us to predict future migrants and resident from YOY. With such separations, we detected two significantly different forms, where predicted migrants were less deep-bodied and had small caudal fins as a function of size than predicted residents, consistent with older trout. Subsequent stable isotope analyses revealed small but significant differences in δ^{13}C (t = -2.5, df = 40, p = 0.017) between predicted future 2000 YOY migrants (-25.06‰; n = 31) and residents (-24.59‰; n = 11), consistent with those reported by (Morinville &

Rasmussen 2003) between known migrants and residents. In addition, predicted future migrants also had higher $\delta^{15}N$ than residents, again consistent with known migrants and residents (G.R. Morinville & J.B. Rasmussen, unpublished data). These results not only provide further support to the strength of the above discriminant function, but that the development of such a tool to discriminate migrants from residents will allow for more detailed investigations of coexisting life forms within a single species.

Early morphological development and the adoption of anadromy

Overall, this study demonstrates that morphological differences can be detected within a species exhibiting two life-history strategies, residency and anadromy. Importantly, these differences are powerful enough to develop predictive models for discriminating trout as either migrant or resident by measuring only a few morphological traits. Furthermore, the results agree with the expected habitat use of anadromous and resident brook trout, where the former is believed to exploit faster habitats and is more morphologically adapted for doing so than the latter.

Although morphological variations related to habitat use have been observed in the wild, uncertainties remain as to how they arise. In particular, it is still not fully understood whether fish that are morphologically pre-adapted for swimming in fast water prefer and select faster habitats or whether fish modify (phenotypic plasticity) their shape according to the habitat in which they experience. In addition, it has not been established whether early differences in physiological traits (such as higher aerobic metabolism) contribute to initial habitat preference and selection, although morphological variations between morphs have been found to be both heritable and related to physiological performance (Proulx & Magnan 2002, 2004). Early variations in metabolism and morphology thus suggest the presence of mechanisms involving both environmental and genetic factors.

Perry et al. (2004) found that maternal genetic effects were high for embryonic length, but quickly decreasing for post-resorption length in brook trout bred from anadromous and resident parents. They in turn detected low but significant heritability for brook trout length at the alevin (after yolk sac resorption) stage. In addition, it was also found that maternal genetic differentiation between embryonic anadromous and resident brook trout was high (Qst > 0.5) and was greater than neutral genetic divergence in their study for specific embryonic traits including length and growth rate for length (Perry et al. in press). Maternal Qst for post-resorption morphological traits was almost zero (Perry et al. in press). The work of Perry and colleagues suggest that post-emergence stages are more susceptible to developmental changes induced by early variations in environmental conditions, as maternal effects are greatly weakened. It is thus possible that immediately after emergence, segregations according to size occur in the habitat. The larger post-hatch individuals, possessing the competitive advantage for obtaining better feeding territories (Johnsson et al. 1999), could exploit the faster velocities characterized by high food delivery rates sooner, leading to subsequent morphological adaptations.

Such predictions are likely as body shape may be altered under different current regimes (Pakkasmaa & Piironen 2001, Imre et al. 2002, Peres-Neto & Magnan 2004). Sagnes et al. (2000) demonstrated a shift in body shape and swimming potential during grayling (*Thymallus thymallus*) ontogenesis in relation with habitat use. Grayling, over their ontogeny, develop towards a shape that is more hydrodynamically efficient for swimming at high velocities. Similarly, comparisons between older migrants and residents with pooled YOY revealed that YOY were intermediate both in maximum body depths and caudal fin heights, suggesting that the morphological differences observed between the two forms diverge with increasing size.

Differential habitat use may thus influence fish morphology at young stages, leading to larger and more measurable changes over time. Such early size differences could result in the development of divergent body forms in parallel with the subsequent bioenergetic consequences of habitat use and ultimately to the presence of migrant and resident phenotypes. However with the evidence at hand, it can only be concluded that brook trout adopting the migratory life-history strategy (prior to migration) have higher consumption rates, exhibit more elevated metabolic costs, utilize faster current velocities (Morinville & Rasmussen 2003) and are more streamlined in shape than those adopting the resident life-history. Further studies are required to gain a better understanding of the link between early morphological development, habitat use and the adopted life-history strategy.

Acknowledgements

We thank M. Bélanger, S. Bodmer-Roy, A. Boivin, J-F. Bourque, A. DuCap, L. Harris, G. Kramer, S. Lenormand and V. Thériault for field assistance and laboratory work. We are grateful to D. Browne for his helpful comments on earlier versions of this manuscript and to N. Alfonso for his assistance with the linear discriminant analyses. This study is a contribution to the program of CIRSA (Centre Interuniversitaire sur le Saumon Atlantique). Funding for this project was provided to J.B.R. by the Natural Sciences and Engineering Research Council of Canada (NSERC; Strategic Grant and Collaborative Special Projects), the Foundation de la Faune du Québec, the Government of Quebec (FAPAQ), the Government of Canada (Economic development), the financial partners of CIRSA Inc., and Graduate Fellowships to G.R.M. from McGill’s Department of Biology and the McConnell Family McGill Major.

References Cited

Alfonso, N.R. 2004. Evidence for two morphotypes of lake charr, *Salvelinus namaycush*, from Great Bear Lake, Northwest Territories, Canada. Environmental Biology of Fishes 71: 21-32.

Beeman, J. W., D. W. Rondorf, M. E. Tilson & D. A. Venditti. 1995. Nonlethal meassure of smolt status of juvenile steelhead based on body morphology. Transactions of the American Fisheries Society 124:764-769.

Bisson, P. A., K. Sullivan & J. L. Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile coho Salmon, steelhead, and cutthroat trout in streams. The American Fisheries Society 117:262-273.

Blake, R. W. 1983. Fish locomotion. Cambridge University Press, Cambridge ; New York.

Boily, P. & P. Magnan. 2002. Relationship between individual variation in morphological characters and swimming costs in brook charr (*Salvelinus fontinalis*) and yellow perch (*Perca flavescens*). Journal of Experimental Biology 205:1031-1036.

Bourke, P., P. Magnan & M.A. Rodriguez. 1997. Individual variations in habitat use and morphology in brook charr. Journal of Fish Biology 51:783-794.

Drucker, E. G. & G. V. Lauder. 2003. Function of pectoral fins in rainbow trout: behavioral repertoire and hydrodynamic forces. Journal of Experimental Biology 206:813-826.

Ehlinger, T. J. 1990. Habitat choice and phenotype-limited feeding efficiency in bluegill: individual differences and trophic polymorphism. Ecology 7:886-896.

Finlay, J. C., P. M.E. & C. G. 1999. Effects of water velocity on algal carbon isotope ratios: Implications for river food web studies. Limnology and Oceanography 44:1198-1203.

Hoar, W. S. 1976. Smolt transformation. Journal of the Fisheries Research Board of Canada 33:12344-11252.

Holopainen, I. J., J. Aho, M. Vornanen & H. Huuskonen. 1997. Phenotypic plasticity and predator effects on morphology and physiology of crucian carp in nature and in the laboratory. Journal of Fish Biology 50:781-798.

Imre, I., R. McLaughlin & D. L. G. Noakes. 2001. Temporal persistence of resource polymorphism in brook charr, *Salvelinus fontinalis*. Environmental Biology of Fisheries 60:393-399.

Imre, I., R. L. McLaughlin & D. L. G. Noakes. 2002. Phenotypic plasticity in brook charr: changes in caudal fin induced by water flow. Journal of Fish Biology 61:1171-1181.

Johnsson, J. I., F. Nobbelin & T. Bohlin. 1999. Territorial competition among wild brown trout fry: effects of ownership and body size. Journal of Fish Biology 54:469-472.

Keenleyside, M. H. A. 1962. Skin-diving observations of Atlantic salmon and brook trout in the Miramichi River, New Brunswick. Journal of the Fisheries Research Board of Canada 19:625-634.

McCormick, S. D., R. J. Naiman & E. T. Montgomery. 1985. Physiological smolt characteristics of anadromous and non-anadromous brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 42:529-538.

McLaughlin, R. L. & J. W. A. Grant. 1994. Morphological and behavioural differences among recently-emerged brook charr, *Salvelinus fontinalis*, foraging in slow- vs. fast-running water. Envionmental Biology of Fishes 39:289-300.

Morinville, G. R. & J. B. Rasmussen. 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 60:401-410.

Pakkasmaa, S. & J. Piironen. 2001. Water velocity shapes juvenile salmonids. Evolutionary Ecology 14:721-730.

Peres-Neto, P. R. & P. Magnan. 2004. The influence of swimming demand on phenotypic plasticity and morphological integration: a comparison of two polymorphic charr species. Oecologia 140:36-45.

Perry, G. M. L., C. Audet, & L. Bernatchez. in press. Maternal genetic effects on adaptive divergence between anadromous and resident brook charr during early life history. Journal of Evolutionary Biology.

Perry, G. M. L., C. Audet, B. Laplatte & L. Bernatchez. 2004. Shifting patterns in genetic control at the embryo-alevin boundary in brook charr. Evolution 58:2002-2012.

Pettersson, L. B. & C. Brönmark. 1999. Energetic consequences of an inducible morphological defence in crucian carp. Oecologia 121:12-18.

Power, G. 1980. The brook charr, *Salvelinus fontinalis*. Pages 141-203 *in* E. K. Balon, editor. Charrs, salmonid fishes of the genus Salvelinus. W. Junk, The Hague, Netherlands.

Proulx, R. & P. Magnan. 2002. Physiological performance of two forms of lacustrine brook charr, *Salvelinus fontinalis*, in the open-water habitat. Environmental Biology of Fishes 64:127-136.

Proulx, R. & P. Magnan. 2004. Contribution of phenotypic plasticity and heredity to the trophic polymorphism of lacustrine brook charr (*Salvelinus fontinalis* M.). Evolutionary Ecology Research 6:503-522.

Riddell, B. E. & W. C. Leggett. 1981. Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Science 38:308-320.

Sagnes, P., J.-Y. Champagne & R. Morel. 2000. Shifts in drag and swimming potential during grayling ontogenesis: relations with habitat use. Journal of Fish Biology 57:52-68.

Sibbing, F. A. & L. A. J. Nagelkerke. 2001. Resource partitioning by Lake Tana barbs predicted from fish morphometrics and prey characteristics. Reviews in Fish Biology and Fisheries 10:393-437.

Skúlason, S., D. L. G. Noakes & S. S. Snorrason. 1989. Ontogeny of trophic morphology in four sympatric morphs of Arctic charr *Salvelinus alpinus* in Thingvallavatin, Iceland. Biological Journal of the Linnean Society 38:281-301.

Swain, D. & H. L. Blair. 1989. Differences in morphology and behaviour between juvenile Coho salmon (*Oncorhynchus kisutch*) rearing in a lake and in its tributary stream. Canadian Journal of Fisheris and Aquatic Sciences 46:1406-1414.

Taylor, E. B. & J. D. McPhail. 1985. Burst swimming and size-related predation of newly emerged Coho salmon, *Oncorhynchus kisutch*. American Fisheries Society 114:546-551.

Taylor, E. B. & J. D. McPhail. 1986. Prolonged and burst swimming in anadromous and fresh-water threespine stickleback, *Gasterosteus aculeatus*. Canadian Journal of Zoology 64:416-420.

Thériault, V. & J. J. Dodson. 2003. Body size and the adoption of a migratory tactic in brook charr. Journal of Fish Biology 63:1-16.

Trudeau, V. & J. B. Rasmussen. 2003. The effect of water velocity on stable carbon and nitrogen isotope signatures of periphyton. Limnology and Oceanography 48:2194-2199.

Vogel, S. 1994. Life in moving fluids. Princeton University Press, Princeton, N.J.

Webb, P. W. 1975. Hydrodynamics and energetics of fish propulsion. Department of the Environment Fisheries and Marine Service: available from Information Canada, Ottawa.

Webb, P. W. 1984. Body form, locomotion and foraging in aquatic vertebrates. American Zoology 24:107-120.

Webb, P. W. 1988. Simple physical principles and vertebrate aquatic locomotion. American Zoology 28:709-725.

Wood, B. M. & M. B. Bain. 1995. Morphology and microhabitat use in stream fish. Canadian Journal of Fisheries and Aquatic Science 52:1487-1498.

Table 2.1 Number and mean fork length (± 1 SE) of sampled resident, migrant and young-of-the-year (YOY) brook trout from resident-only (res-only) and migrant-resident streams, and Saguenay River (sea) sampling sites.

Site	Site type	Fish type	Year	Mean fork length (mm)	Range (mm)	N
Épinette	Resident-only	Resident	2002	101.9 ± 1.9	66-155	118
La Prairie	Resident-only	Resident	2002	113.1 ± 4.2	53-184	45
Édouard	Migrant-resident	Resident	2002	97.6 ± 1.9	60-218	175
Morin	Migrant-resident	YOY	2000	63.3 ± 0.82	50-74	51
		YOY	2001	55.6 ± 0.50	35-68	120
		Migrant	2001	93.3 ± 1.4	50-179	197
		Resident		116.8 ± 2.6	53-256	198
		Migrant	2002	96.6 ± 1.3	65-186	285
		Resident		98.2 ± 1.5	58-227	419
		Migrant	2003	100.1 ± 1.4	56-156	226
		Resident		96.4 ± 1.4	62-168	211
Portage	Migrant-resident	Migrant	2002	117.9 ± 3.9	63-264	110
		Resident		119.6 ± 13.9	51-195	11
Saguenay	Sea	Migrant	2001	149.7 ± 3.1	73-311	257
			2002	164.2 ± 3.5	79-275	192

Table 2.2 Regression statistics and statistical comparisons using analysis-of-covariance (ANCOVA) between brook trout migrants (M) and residents (R) of Morin stream from 2001 to 2003 for six morphological traits as a function of standard length.

Different letters indicate significant difference at $p<0.01$ between migrants and residents for slope and/or intercept. All traits were measured in mm.

Site	Trait	Fish type	N	Slope	Intercept	*p*	R^2
Morin 2001	Body depth	M	197	0.191^a	0^a	< 0.01	0.95
		R	198	0.223^b	0^a	< 0.01	0.95
	Body width	M	186	0.111^a	0^a	< 0.01	0.89
		R	198	0.126^b	0.597^a	< 0.01	0.94
	Peduncle	M	175	0.088^a	0.618^a	< 0.01	0.92
		R	198	0.092^a	1.041^b	< 0.01	0.96
	Caudal fin	M	168	0.27^a	1.714^a	< 0.01	0.89
		R	193	0.335^b	1.255^a	< 0.01	0.96
	Pelvic fin	M	172	0.124^a	0.639^a	< 0.01	0.91
		R	198	0.12^a	1.708^b	< 0.01	0.96
	Pectoral fin	M	173	0.153^a	0^a	< 0.01	0.90
		R	197	0.148^a	0.985^b	< 0.01	0.95
Morin 2002	Body depth	M	285	0.174^a	2.523^a	< 0.01	0.90
		R	419	0.230^b	-0.462^b	< 0.01	0.97
	Body width	M	285	0.108^a	1.354^a	< 0.01	0.90
		R	417	0.137^b	-0.381^b	< 0.01	0.96
	Peduncle	M	285	0.073^a	2.84^a	< 0.01	0.84
		R	419	0.095^b	0.851^b	< 0.01	0.97
	Caudal fin	M	248	0.291^a	1.294^a	< 0.01	0.93
		R	401	0.361^b	-1.643^b	< 0.01	0.96
	Pelvic fin	M	285	0.108^a	2.684^a	< 0.01	0.90
		R	417	0.128^b	1.636^b	< 0.01	0.96
	Pectoral fin	M	285	0.126^a	2.78^a	< 0.01	0.91
		R	418	0.154^b	1.176^b	< 0.01	0.96
Morin 2003	Body depth	M	222	0.187^a	0^a	< 0.01	0.95
		R	211	0.233^b	0^a	< 0.01	0.88
	Body width	M	222	0.113^a	0.005^a	< 0.01	0.94
		R	211	0.117^a	1.169^b	< 0.01	0.85
	Peduncle	M	223	0.087^a	0.820^b	< 0.01	0.92
		R	209	0.099^a	1.171^b	< 0.01	0.87
	Caudal fin	M	195	0.31^a	0^a	< 0.01	0.92
		R	205	0.279^a	2.196^b	< 0.01	0.83
	Pelvic fin	M	225	0.107^a	2.522^a	< 0.01	0.89
		R	211	0.125^b	2.419^a	< 0.01	0.88
	Pectoral fin	M	225	0.128^a	2.257^a	< 0.01	0.91
		R	211	0.144^b	2.20^a	< 0.01	0.89

Table 2.3 Regression statistics and statistical comparisons using analysis-of-covariance (ANCOVA) between brook trout residents from 2002 pooled migrant-resident (MR) and pooled resident-only streams (RO) for six morphological traits as a function of standard length.

Different letters indicate significant difference at p < 0.01 between residents from migrant-resident streams and residents from resident-only streams. All traits were measured in mm.

Site	**Trait**	**Fish type**	**N**	**Slope**	**Intercept**	***p***	***R*^{2}**
Migrant-resident and Resident-only	Body depth	MR	604	0.23^a	-0.677^a	< 0.01	0.97
		RO	163	0.215^b	1.838^b	< 0.01	0.92
	Body width	MR	601	0.136^a	-0.431^a	< 0.01	0.95
		RO	162	0.116^b	1.607^b	< 0.01	0.87
	Peduncle	MR	604	0.095^a	0.83^a	< 0.01	0.96
		RO	163	0.088^b	1.959^b	< 0.01	0.92
	Caudal fin	MR	579	0.359^a	-0.937^a	< 0.01	0.95
		RO	160	0.327^b	2.719^b	< 0.01	0.94
	Pelvic fin	MR	601	0.129^a	1.752^a	< 0.01	0.94
		RO	163	0.128^a	1.972^a	< 0.01	0.94
	Pectoral fin	MR	602	0.156^a	1.245^a	< 0.01	0.95
		RO	163	0.164^a	0.826^b	< 0.01	0.95

Table 2.4 Regression statistics and statistical comparisons using analysis-of-covariance (ANCOVA) between brook trout residents from (R) from 2001 Morin stream and 2001 Saguenay (Sag) River sea trout (sea), and between brook trout residents (R) from 2002 migrant-resident streams (MR) and 2002 Saguenay River sea trout (Sea) for six morphological traits as a function of standard length.

Different letters indicate significant difference at p < 0.01 between residents from migrant-resident streams and residents from resident-only streams. All traits were measured in mm.

Site	**Trait**	**Fish type**	**N**	**Slope**	**Intercept**	***p***	***R*^{2}**
Sag 2001	Body depth	Sea	255	0.215^{a}	-1.566^{a}	< 0.01	0.96
and		R	198	0.223^{a}	0^{b}	< 0.01	0.95
Morin 2001	Body width	Sea	253	0.121^{a}	0^{a}	< 0.01	0.95
		R	198	0.126^{a}	0.597^{b}	< 0.01	0.94
	Peduncle	Sea	143	0.089^{a}	0.832^{a}	< 0.01	0.97
		R	198	0.092^{b}	1.041^{b}	< 0.01	0.96
	Caudal fin	Sea	252	0.326^{a}	0^{a}	< 0.01	0.96
		R	193	0.335^{a}	1.255^{b}	< 0.01	0.96
	Pelvic fin	Sea	43	0.112^{a}	2.218_{a}	< 0.01	0.95
		R	172	0.124^{a}	0.639^{b}	< 0.01	0.91
	Pectoral fin	Sea	43	0.144^{a}	0^{a}	< 0.01	0.92
		R	197	0.148^{a}	0.985^{b}	< 0.01	0.95
Sag 2002	Body depth	Sea	192	0.222^{a}	-1.292^{a}	< 0.01	0.96
and		R	604	0.23^{a}	-0.677^{b}	< 0.01	0.97
MR 2002	Body width	Sea	192	0.134^{a}	-0.907^{a}	< 0.01	0.96
		R	601	0.136^{a}	-0.431^{b}	< 0.01	0.95
	Peduncle	Sea	192	0.084^{a}	1.411^{a}	< 0.01	0.97
		R	604	0.095^{b}	0.83^{b}	< 0.01	0.96
	Caudal fin	Sea	184	0.324^{a}	0^{a}	< 0.01	0.97
		R	579	0.359^{b}	-0.937^{a}	< 0.01	0.95
	Pelvic fin	Sea	192	0.102^{a}	3.105^{a}	< 0.01	0.96
		R	601	0.129^{b}	1.752^{b}	< 0.01	0.94
	Pectoral fin	Sea	192	0.129^{a}	1.946^{a}	< 0.01	0.96
		R	602	0.156^{b}	1.245^{b}	< 0.01	0.95

Table 2.5 Within year means, standard deviations and sample sizes for depth to standard length ratio (DEP_LTH), peduncle to caudal height ratio (PED_CAUD) and pectoral to standard length ratios (PECT_LTH) selected in field identification for Morin 2001 to 2003 brook trout.

Ratio	Year	Mean	S.D.	N
DEP_LTH	2001	0.208	0.021	358
	2002	0.216	0.016	647
	2003	0.202	0.034	398
PED_CAUD	2001	0.312	0.031	358
	2002	0.323	0.036	647
	2003	0.343	0.053	398
PECT_LTH	2001	0.156	0.011	358
	2002	0.386	0.012	647
	2003	0.156	0.018	398

Table 2.6 Regression statistics for Morin stream 2001 young-of-the-year (YOY) brook trout for three morphological traits as a function of standard length (mm).

Site	**Trait**	**Fish type**	**N**	**Slope**	**Intercept**	***p***	***R*²**
Morin 2000	Body depth	YOY	51	0.21	0	< 0.01	0.70
	Caudal fin	YOY	51	0.35	0	< 0.01	0.71
	Peduncle	YOY	51	0.085	1.8	< 0.01	0.61
Morin 2001	Body depth	YOY	109	0.22	0	< 0.01	0.80
	Caudal fin	YOY	109	0.33	0	< 0.01	0.66
	Peduncle	YOY	109	0.11	0	< 0.01	0.63

Table 2.7 Residuals (± 1 SE) of pooled relationship between maximum body depth, caudal fin height and peduncle depth as a function of standard length for 2002 Morin stream migrants and residents, and 2001 young-of-the-year (YOY) brook trout.

Different letters indicate significant difference at $p < 0.05$.

Trait	Fish type	N	Mean residual	F	*p*
Body depth	M	285	-0.058 ± 0.0040^{a}	233.1	< 0.01
	R	419	0.040 ± 0.0027^{b}		
	YOY	120	-0.0021 ± 0.0048^{c}		
Caudal fin	M	248	-0.068 ± 0.0043^{a}	183.3	< 0.01
	R	401	0.038 ± 0.0034^{b}		
	YOY	110	0.014 ± 0.0074^{c}		
Peduncle	M	285	0.011 ± 0.0051^{a}	10.2	< 0.01
	R	419	-0.00096 ± 0.0027^{a}		
	YOY	119	-0.023 ± 0.0064^{b}		

Figure 2.1 Linear regressions of a) maximum body depth, (b) maximum body width, (c) peduncle depth, (d) caudal fin height, (e) pelvic fin length, and (f) pectoral fin length as a function of size (standard length) for 2002 Morin stream brook trout migrants (closed circle; dashed line) and residents (open circle; solid line).

For all regressions, $p < 0.01$ and $r^2 > 0.80$. Significant differences ($p< 0.01$) exist between migrants and residents for all morphological traits.

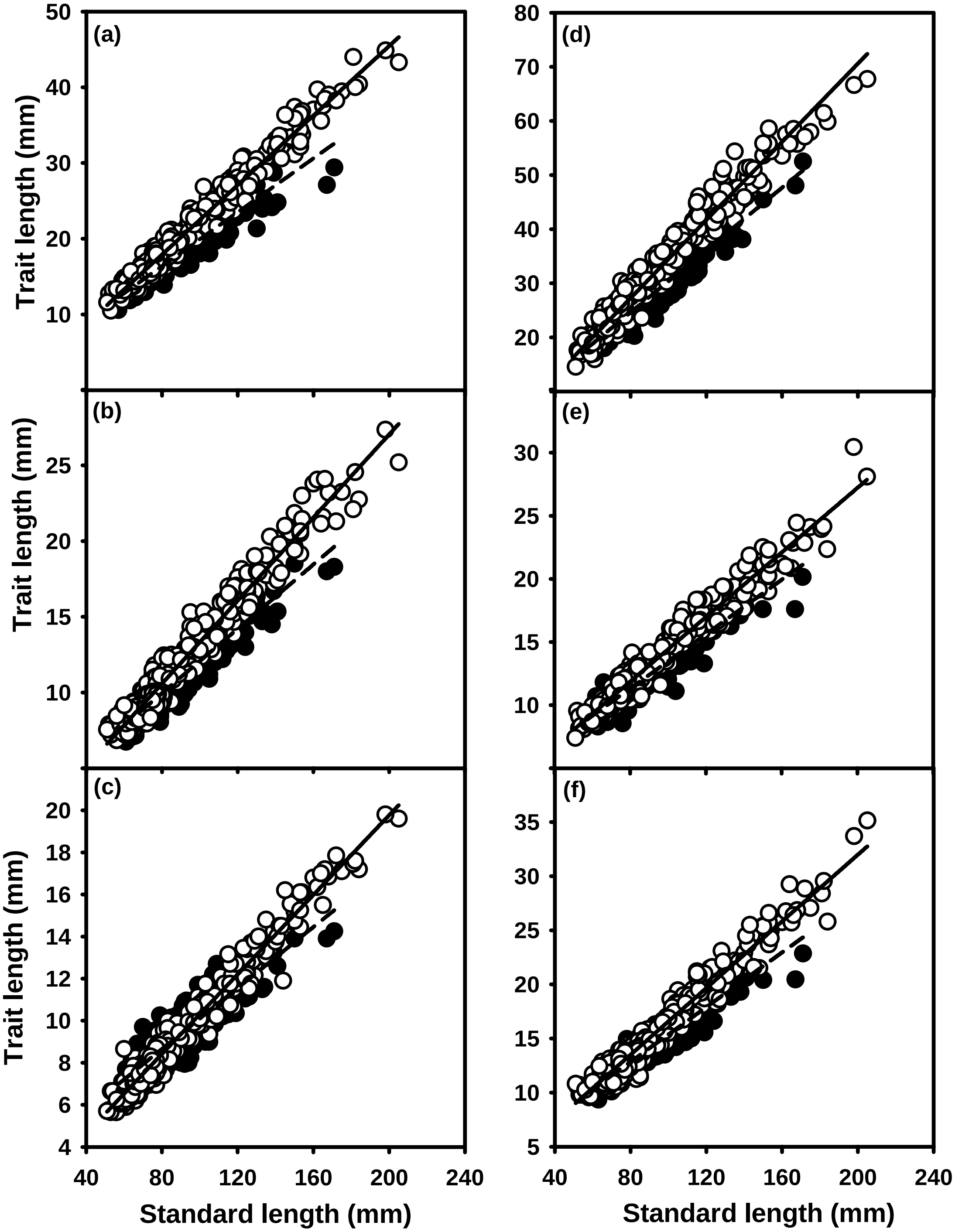

(a)
(b)
(c)
(d)
(e)
(f)
Trait length (mm)
Trait length (mm)
Trait length (mm)
Standard length (mm)
Standard length (mm)
50
40
30
20
10
25
20
15
10
20
18
16
14
12
10
8
6
4
80
70
60
50
40
30
20
30
25
20
15
10
35
30
25
20
15
10
5
40
80
120
160
200
240
40
80
120
160
200
240

Figure 2.2 Bivariate plot of the first two canonical variables of the linear discriminant function performed using migrants (circles, dotted line), resident-only stream residents (diagonal crosses; dashed line) and migrant-resident stream residents (crosses; solid line).

Confidence ellipses are centred on the centroid of each life-history form. The first canonical variable (eigenvalue = 1.486) captures 94% of the difference among the groups. Significant differences exist between the three groups (U = 0.365, $F_{6,12} = 112.7$, $p < 0.005$). The model obtained correctly reclassifies 91% of migrants, 65% of resident-only residents and 74% migrant-resident residents for an overall correct classification of 74%.

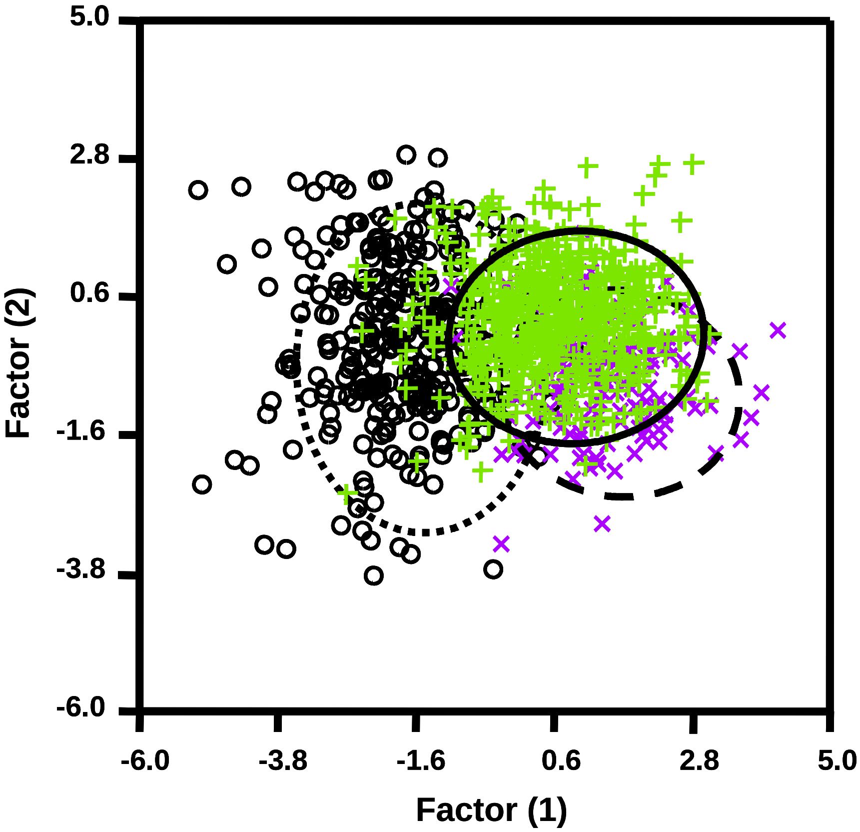

5.0
2.8
0.6
-1.6
-3.8
-6.0
Factor (2)
-6.0
-3.8
-1.6
0.6
2.8
5.0
Factor (1)

Figure 2.3 Ratios of (a) standard length to maximum body depth (SL:BD; fineness ratio), (b) maximum body depth to maximum body width (BD:BW; circular ratio), (c) caudal fin height to standard length (CF:SL), (d) pelvic fin length to standard length (PLF:SL), and (e) pectoral fin length to standard length (PCL:SL) for 2002 resident brook trout from resident-only (RO) and migrant-resident streams (R), migrant brook trout (M) and sea trout (ST).

Different letters above bars indicate significant differences at $p < 0.001$ between life-history forms. Numbers in bars indicate sample size.

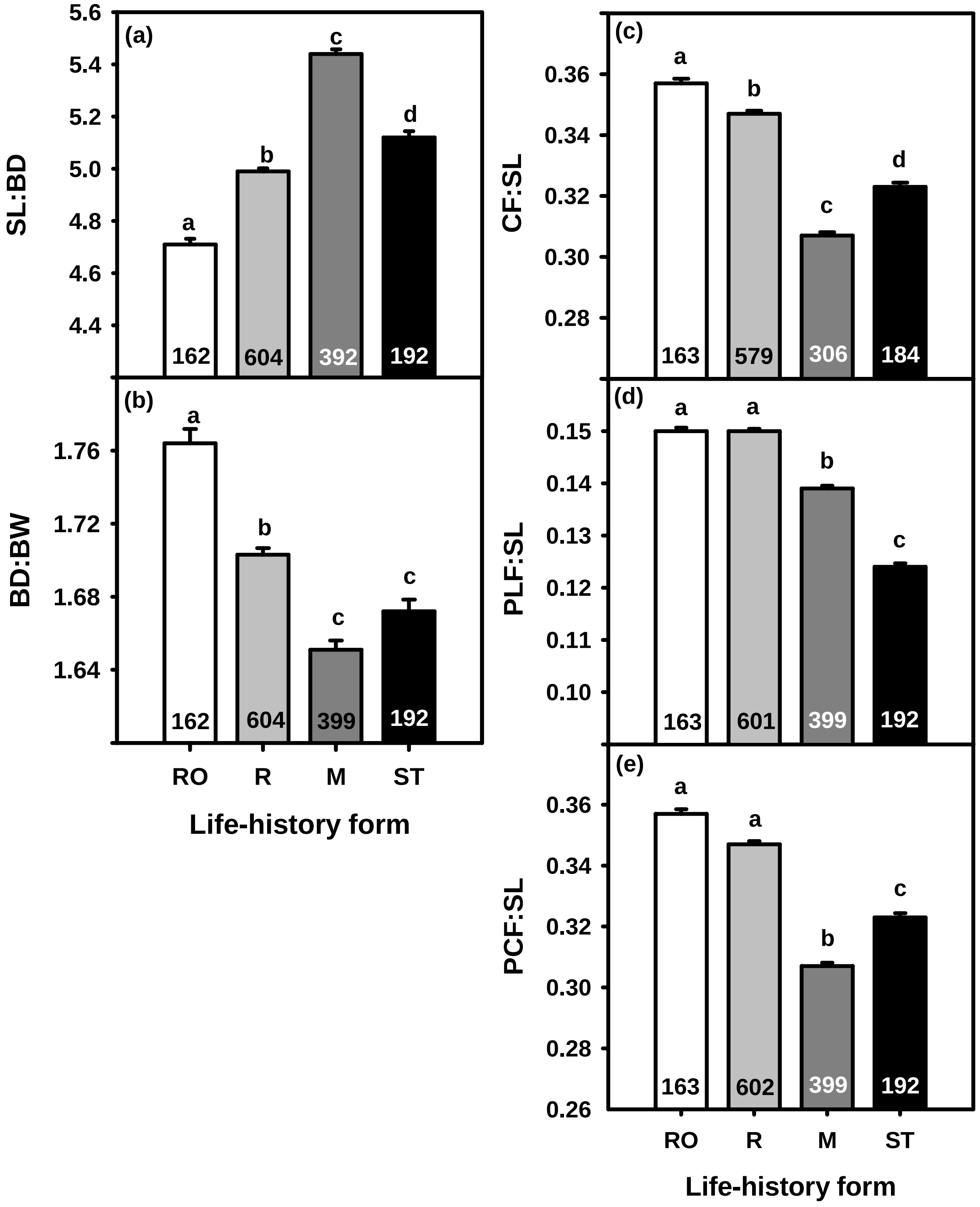
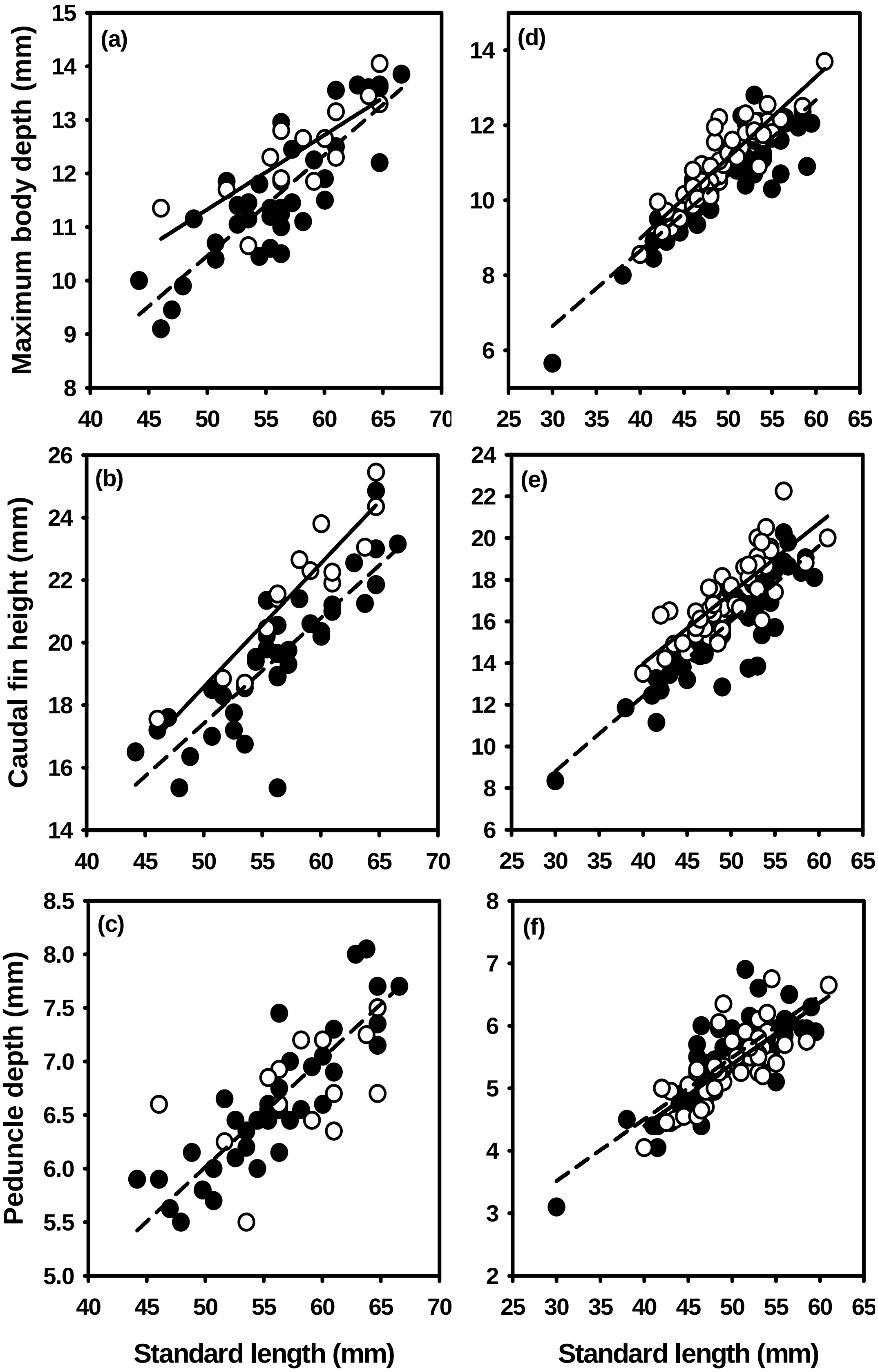

(a)
SL:BD
5.6
5.4
5.2
5.0
4.8
4.6
4.4
a
b
c
d
162
604
392
192
(b)
BD:BW
1.76
1.72
1.68
1.64
a
b
c
c
162
604
399
192
RO
R
M
ST
Life-history form
(c)
CF:SL
0.36
0.34
0.32
0.30
0.28
a
b
c
d
163
579
306
184
(d)
PLF:SL
0.15
0.14
0.13
0.12
0.11
0.10
a
a
b
c
163
601
399
192
(e)
PCF:SL
0.36
0.34
0.32
0.30
0.28
0.26
a
a
b
c
163
602
399
192
RO
R
M
ST
Life-history form

Figure 2.4 Linear regressions of maximum body depth (a, d), caudal fin height (b, e) and peduncle depth (c, f) as a function of size (standard length) for 2000 and 2001 Morin YOY, respectively.

Closed circles (dashed lines) and open circles (solid line) indicate predicted YOY migrants and residents, respectively. All regressions are significant at $p < 0.05$, except for the 2000 resident peduncle depth regression ($p = 0.074$). Predicted 2000 and 2001 migrants differ significantly from residents for maximum body depth and caudal fin height ($p < 0.05$). For peduncle depth, only predicted migrants captured in 2000 differ from residents ($p < 0.05$).


(a)
(b)
(c)
(d)
(e)
(f)
Maximum body depth (mm)
Caudal fin height (mm)
Peduncle depth (mm)
Standard length (mm)
Standard length (mm)
15
14
13
12
11
10
9
8
26
24
22
20
18
16
14
8.5
8.0
7.5
7.0
6.5
6.0
5.5
5.0
40
45
50
55
60
65
70
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35
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22
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6
4
2

CONNECTING STATEMENT- bridging Chapter 2 and 3

The results of Chapter 1 and 2 suggest, as demonstrated by the differences observed between anadromous and resident brook trout in bioenergetic budgets, stable isotopes and body morphology, that the former exploits faster and more costly habitats than the latter during stream coexistence. Chapter 3 describes the habitat use of anadromous and resident brook trout found in streams in order to provide additional support for the predictions generated from the previous chapters.

Directly describing the habitat use of juvenile anadromous and resident brook trout is problematic because as seen in Chapter 2, the morphological differences, although significant, are relatively small, limiting our ability in differentiating future migrants from residents without the use of a discriminant function. As a consequence, the direct study of habitat use was not previously possible. Nonetheless, we addressed this issue by comparing the habitat use of residents in streams only containing resident brook trout to the habitat use of residents from streams containing both migratory and resident individuals. Juvenile residents from such systems are a mixture of both future migrants and residents while those of resident-only streams can be considered true residents. A wider use of habitats is thus expected in streams containing the two forms compared to streams only containing the resident form.

"*Rivers and the inhabitants of the watery elements are made for wise men to contemplate and for fools to pass by without consideration.*" - Izaac Walton

CHAPTER 3: Differential habitat use of salmonids in streams open and closed to anadromy[1]

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Submitted to *Journal of Animal Ecology*

"Often I have been exhausted on trout streams, uncomfortable, wet, cold, briar scarred, sunburned, mosquito bitten, but never, with an (electrofisher) have I been less than in a place that was less than beautiful." Charles Kuralt

Summary

1. Migratory and resident forms of salmonids coexist in many river systems. Although such coexistence is widespread, little is known about its ecological basis and no studies have compared the habitat use of pre-migratory juveniles and residents.

2. We employed a comparative approach to explore the differential habitat use of juvenile anadromous and resident brook trout. This required the investigation of habitat use in streams closed to anadromy, containing only resident brook trout ('resident-only' streams) and streams open to anadromy, containing coexisting Atlantic salmon and anadromous and resident brook trout ('migrant-resident' streams).

3. We demonstrate that fast habitats (riffles) are occupied more frequently in streams with migratory brook trout relative to riffle habitats of streams with only resident brook trout. In contrast, occupation of slow current velocities (pools) was observed in both migrant-resident and resident-only streams since both stream types contain resident juvenile brook trout. The net effect is a wider distribution of occupied habitats (pool and riffles) in migrant-resident streams relative to resident-only streams, resulting in few, if any, unused habitats.

4. These results are consistent with previously reported bioenergetic, morphological and stable isotope differences observed between anadromous and resident brook trout.

5. Our findings suggest that a link exists between juvenile habitat use, metabolic costs and life-history strategies.

Introduction

Intraspecific forms of migratory and resident fish coexist in many river systems. Well known examples include resident rainbow trout (*Oncorhynchus mykiss*) and anadromous steelhead found in Pacific drainages (Scott & Crossman 1973), and in Europe, resident brown trout and sea trout (*Salmo trutta*) commonly coexist (Jonsson 1985, Bohlin, Dellefors & Faremo 1996). Most charrs (*Salvelinus*) also exhibit this pattern throughout their range (Power 1980). Despite the prevalence and the economic importance of this coexistence, little is actually known about its ecological basis and no studies have compared the habitat use of pre-migratory juveniles and residents.

On the one hand, inter-specific comparisons between salmonid species are common (Gibson 1966, 1973, Fausch & White 1981, Fausch 1993, Heggenes, Saltveit & Lingaas 1996). For example, anadromous Atlantic salmon coexist with anadromous and resident brook trout competing for similar resources and habitats leading to territorial and agonistic behaviours, with salmon gaining better feeding opportunities in fast waters (Gibson 1973). Energetic demand for territorial defence can be high (Elliott 1990, Cutts, Adams & Campbell 2001) and swimming in fast currents is more costly than swimming in slow currents leading to increased metabolic costs (Beamish 1980). Although costs may be more elevated when using faster currents, there is the potential for higher consumption rates since a positive correlation exists between current velocity and drift (Hughes & Dill 1990). Salmonids thus tend to position themselves in current velocities at which net energy benefits are maximized, balancing the trade-off between swimming costs and the delivery of drifting prey (Fausch 1984, Hughes & Dill 1990, Hill & Grossman 1993).

Swimming costs experienced in various habitats will be governed, in part, by individual variations in metabolic scope. Laboratory studies have demonstrated that wild Atlantic salmon attain a higher sustained, higher prolonged and a higher maximum swimming speed than brook trout (Peake, McKinley & Scruton 1997, McDonald, McFarlane & Milligan 1998) supporting field observations that Atlantic salmon employ faster currents than brook trout (Gibson 1966, Griffith 1972, Gibson 1973, Heggenes, Saltveit & Lingaas 1996). Fish occupying high cost habitats (fast currents) may thus experience reduced growth efficiencies (the ratio of growth to consumption) in comparison to fish occupying low cost habitats (slow currents or pools). Indeed, anadromous Atlantic salmon (employing fast currents) exhibit higher consumption rates in the wild than resident brook trout (employing slow currents), but lower growth efficiencies, the consequence of higher metabolic costs (Tucker & Rasmussen 1999). Such variations in metabolic costs between species have been linked to differences in life-history strategies such as migration and residency. Interestingly, these variations have also been observed within species where the migrant form exhibits higher metabolic costs than the resident form (Forseth 1999, Morinville & Rasmussen 2003). We would thus expect coexistence between life-history variants to be strongly enhanced if pre-migratory juveniles of anadromous forms occupied different microhabitats than residents in the spawning and nursery stream systems.

Although analysis of stable isotopes and energy budgets suggest that juvenile anadromous brook trout occupy faster current velocities than resident brook trout (Morinville & Rasmussen 2003), direct habitat use observations have not been feasible. Until recently, no method was available to distinguish between migratory and resident brook trout in the field (G.R. Morinville & J.B. Rasmussen, Chapter 2), as no obvious differences exist between the two forms. The genus *Salvelinus* exhibits the least pronounced anadromy of salmonids with migrations limited to a hundred kilometres from river mouths (Power 1980) and no smoltification occurs in juvenile migrants (McCormick, Naiman & Montgomery 1985). As a consequence, migrants could only be differentiated from juvenile residents if they were captured during their outmigration in a trap or at sea

(Morinville & Rasmussen 2003, Thériault & Dodson 2003) thus limiting our ability to directly investigate their habitat use patterns in streams.

Due to these limitations, we employed a comparative approach to explore the differential habitat use of juvenile migrant and resident brook trout to better understand the link between habitat use, metabolic costs and life-history strategies. This required the investigation of habitat use of brook trout in streams closed to migrant fish, containing only resident brook trout ('resident-only' streams) and streams open to migrant fish, containing coexisting juvenile migratory brook trout, Atlantic salmon and resident brook trout ('migrant-resident' streams).

Juvenile anadromous brook trout (migrants) have higher consumption rates than coexisting resident brook trout (residents), but lower growth efficiencies, stemming from higher metabolic rates (Morinville & Rasmussen 2003). Similar to Atlantic salmon, migrants may achieve higher consumption rates if they occupy faster current velocities since the delivery of drifting prey is higher in fast versus slow currents (Grant & Noakes 1987). The observed metabolic differences between migrants and residents could thus be linked to migrants using faster, more costly water velocities. Occupying fast current habitats can result in higher metabolic costs due to higher standard metabolic rates (SMRa) and/or higher activity costs including costs related to foraging and swimming.

Given our earlier work, we predict that fast habitats (riffles) will be occupied more frequently in streams with migratory brook trout than streams with resident brook trout only. In contrast, occupation of slow current velocities (pool habitats) in both migrant-resident and resident-only streams is expected since both stream types contain resident juvenile brook trout. The net effect should be a wider distribution of occupied habitats (pool and riffles) in migrant-resident streams relative to resident-only streams. Because Atlantic salmon have high consumption rates, low growth efficiencies and higher metabolic rates (Tucker & Rasmussen 1999), migrant-resident streams are expected to have juvenile Atlantic salmon occupying riffle habitats at a higher proportion than slow habitats.

Study Area and Methods

This study was conducted in the Ste. Marguerite River watershed (48º27’N, 69º95’W) in the Saguenay region of Quebec, Canada (Morinville and Rasmussen 2003). The Ste. Marguerite River is home to the largest anadromous brook trout population of the Saguenay River basin (Lesueur 1993). Anadromous brook trout outmigrate from the system as early as age 1+ (Thériault & Dodson 2003).

Habitat use

Two comparative approaches were taken to investigate the habitat use of brook trout in migrant-resident and resident-only streams: (a) comparing fish occupancy (density) in a migrant-resident and resident-only stream using dichotomous surrogates of current velocity (pool and riffle habitats), and (b) describing fish habitat use relative to current velocities available in the habitat across multiple migrant-resident and resident-only streams. All sampled streams are headwater streams and flow directly into the Ste. Marguerite River. All sampling was conducted following the spring (mid-May to mid-June) outmigration period. Apart from young-of-the-year brook trout (YOY), brook trout remaining in streams following this period are mostly 1+ and 2+, with 3+ and older making up about 10% (resident-only stream) to 25% (migrant-resident stream) of the population, and at densities of no more than 2 per 100m^2 and 1 per 100m^2, respectively (Lenormand 2003). Accordingly, the majority of trout remaining in streams are juveniles.

(a) Pool and riffle use of fish in anadromous-resident and resident-only streams

The pool and riffle occupancy of fish from a migrant-resident stream (Édouard) was compared to that of a resident-only stream (Épinette) during the summer of 2003. Édouard contains no barriers to migrant fish in the lower 1 km, and juvenile Atlantic salmon, migrant brook trout and resident brook trout coexist. Longnose dace (*Rhinichthys cataractae*) are also found in the lowest sections but at low densities (<2/100m^2).

Following the spring out-migration, the population of brook trout remaining in the stream comprises an unknown proportion of ‘true’ residents and future migrants. YOY also consist of both future migrants and residents. In contrast, Épinette contains a ‘pure’ resident brook trout population, as fish movement from the Ste. Marguerite River into Épinette has not been possible for the last 40 years due to the presence of a poorly constructed culvert at its mouth. Substrates in both Édouard and Épinette range from sand in the lower 100 m, to fine gravel and pebbles, to gravel and finally to coarse cobble and small boulders in the reaches above an upstream impassable waterfall. Stream gradient ranges from 1.7% in the lower reaches to 8% in the reaches prior to the impassable waterfall in Édouard. In Épinette, stream gradient ranges from 1.7% in the lower reaches to 7% in the upper reaches. Very few deep pools except at higher gradients are found in the streams. In the summer, habitats mostly consist of shallow riffles and pools, and smooth, laminar flow areas. These two streams were selected for comparison since they are the two most accessible and physically similar streams in the Ste. Marguerite watershed, with the main difference being the presence or absence of anadromous fish. Summer water temperatures were also very similar and did not differ during sampling (both were at 18°C).

Habitat sections were selected and identified one day prior to the day of fishing. Streams were ascended beginning at the mouth and pool or riffle sections that were about 20 m^2 in area were selected for sampling. Riffles and pools were chosen so as to be as similar as possible between the two streams and the 20-m^2 criterion minimized the habitat size effect on our sampling efficiency. All habitat-specific sections had similar depths and substrates thus minimizing any intra-habitat differences between streams. Habitat sections were considered pools if current velocities were below 14 cm/s and had depths between 30-45 cm, while riffle sections had current velocities above 22 cm/s and had depths of less than 20 cm. Habitat sections were not contiguous; that is, there was a minimum distance of 10 m between any selected pool and riffle.

All fish (brook trout and Atlantic salmon) were captured, using a backpack electrofisher (Smith-Root, Inc. model 12A), the day following the selection of habitat sections. Field crews consisted of one fisher and two netters. The fisher and netters were the same for both stream samplings. Fishing occurred from downstream to upstream until all selected habitat sections had been crossed. Electrofishing was limited to one pass through each habitat section. All fish collected from each sampled section were identified and enumerated. Fish were then released back into the sampled section. Both streams were fished on sunny days starting mid-morning and ending no later than early afternoon.

The mean number of fish found in each section (number of fish per $20m^2$ section) was calculated for each habitat type and for each stream. The density of fish (YOY brook trout, brook trout and Atlantic salmon) found in pool and riffle habitats were then compared within, and between streams using two-way analyses-of-variance, or standard *t* tests using SYSTAT (Version 10.2).

b) General stream habitat use of fish across migrant-resident and resident-only streams

The stream habitat use of fish relative to that available in the habitat was investigated in reaches from 4 streams open to (migrant-resident) and 3 streams closed to anadromy (resident-only) over a two-month period during the summer of 2002 (Table 3.1). Four migrant-resident streams (Édouard, Morin, and the lower sections of Portage and Allaire that are below a waterfall) were selected and contained Atlantic salmon, brook trout migrants and residents. Longnose dace (*Rhinichthys cataractae*) were also found in both Portage and Morin stream. Morin substrate ranges from coarse cobble and small boulders in the upper reaches, to gravel, to fine gravel and pebbles and finally to sand in the lower 250m. Habitats range from riffles, very few pools, to smooth, shallow, laminar flow areas. Stream gradient is lower in the lower reaches at 1.7%, ranging up to 6.8% in the upper reaches. Stream gradient in Portage ranges from about 2 % in the first 100 m up to 6 % in the reach closest to the first impassable waterfall. The gradient decreases to 2 % in the reaches above the impassable waterfall. The lower reaches consist of sandy substrates, followed by fine gravel and pebbles, to coarse cobble and boulders in the upper reaches. In contrast, Allaire runs over a bed of large boulders of 0.5 m to 1m in diameter, especially in the upper reaches, mixed with large cobble, rubble and coarse gravel. Habitats are typically rapids and riffles, interspersed with pools, and vertical drops can often exceed 0.5 m at summer water levels. Allaire is steep even in its lower reaches (3%) and increasing to around 7% in the reaches below the first impassable waterfall. Stream sections above the waterfall were more similar to those of other streams, with a gradient ranging between 2% and 4% and less coarse substrates.

Sampled reaches ranged between 80 m to 1 km long, with the majority being approximately 200 m in length (Table 3.1). Approximately 1 km of Édouard stream was fished in order to provide an example of an entire stream open to migrant and resident fish. Fish (brook trout and Atlantic salmon) were captured following the same procedure as that outlined above. The same fisher and catchers fished both upstream and downstream reaches of a stream containing a barrier (e.g. sections of Allaire below and above the waterfall). All streams were sampled starting early-morning and ending no later than mid-afternoon.

Current velocities were measured in the mid to upper water column (approximately 0.8 from bottom) in each stream section, using a Pygmy-Gurley current meter (Model D625, Model 1100 digital flow indicator). Current velocities were taken at the beginning and end of each section (every 5 m) at three locations transecting stream flow. The mean of the beginning and end velocities of each section was taken as the section's mean velocity. Each fish captured in each section was then attributed the respective velocity for that section. This method provided a general description of the habitats surrounding the fish, instead of a description of its precise location at the moment of capture.

Current velocities in Édouard and Épinette streams were re-sampled during the summer of 2003 over a two-day period in order to verify that the beginning and end velocity measurements of each section adequately described the mean section velocity. Reaches of 100 m on both streams were marked every 5 m. Velocities were taken at the beginning and end of sections as described above, and at four random positions by creating an imaginary grid over each section and selecting positions generated from a random number table. The mean of the random position velocities was then calculated and compared to the beginning and end of section mean velocities using paired t-tests.

A proportional frequency distribution curve was generated for the habitat use of each fish species for each stream and compared with the available habitats in the stream. Kolmogorov-Smirnov (K-S) tests were used to compare the frequency distribution of habitat velocities to the velocities of Atlantic salmon and brook trout. All statistical analyses were conducted using SYSTAT (Version 10.2).

Results

Habitat use

a) Pool and riffle use of fish in migrant-resident and resident-only streams

The objective of choosing similar habitat-specific sections resulted in a final selection of 18 pools and riffles in the migrant-resident stream (Édouard), and 17 pools and riffles in the resident-only stream (Épinette). In total, 59 young-of-the-year (YOY) brook trout, 85 juvenile brook trout and 34 juvenile Atlantic salmon were captured in the migrant-resident stream. In the resident-only stream, 23 YOY and 95 juvenile brook trout were captured.

Juvenile brook trout and Atlantic salmon

The mean number of juvenile brook trout found in pool sections (20 m^2) of Édouard (migrant-resident) and Épinette (resident-only) stream was 1.9 and 3.5, respectively (Fig. 3.1). In riffles, juvenile brook trout were found at densities of 2.8 and 2.1 per 20-m^2 in Édouard and Épinette, respectively. A two-way ANOVA revealed significant differences in pool and riffle use between Édouard and Épinette (habitat type*stream, $p = 0.002$). As predicted, Épinette had a greater density of juvenile trout in pools than in riffles ($t = 3.4$, $p = 0.002$). In contrast, there was no difference in the pool and riffle use of juvenile brook trout in the migrant-resident stream (Édouard), although there was a tendency towards a higher riffle use ($t =-1.8$, $p = 0.085$). Interestingly, pool densities of the resident-only stream (Épinette) were 1.8 times higher than the migrant-resident stream (Édouard).

In the migrant-resident stream (Édouard), Atlantic salmon occurred at densities of 0.17-1.7 per 20-m^2 pool and riffle section, respectively (Fig. 1). As expected, Atlantic salmon used riffle habitats more than pools ($t = -4.89$, $p < 0.001$). Overall, a greater proportion of fish utlise riffle habitats in the migrant-resident (Édouard), which is in contrast to that observed in the resident-only stream (Épinette) where a greater proportion of fish utilise pool habitats.

<u>YOY brook trout</u>

The mean number of YOY brook trout found in pool sections of Édouard (migrant-resident) and Épinette (resident-only) stream was 2.2 and 1.3 per 20 m^2, respectively (Fig. 3.1). YOY brook trout were found in riffles at densities of 1.0 and 0.06 per 20 m^2 section, in the migrant-resident and resident-only streams, respectively. More YOY brook trout were found in pools than in riffles in both streams (ANOVA: $p = 0.002$), although the relative difference between pool and riffle densities in Édouard was lower than in Épinette. In addition, the migrant-resident stream (Édouard) had a higher density of YOY in riffles (ANOVA: $p = 0.009$). As pool densities were higher than riffle densities in both streams, the occupancy (number of habitat-specific sections with at least 1 YOY/total number of habitat-specific sections) of pools and riffles by YOY was measured. Only 1 (6%) riffle section in the resident-only stream contained YOY, thus YOY were virtually absent from riffle habitats (Fig.

3.2). In contrast, 72% and 56% of pools and riffles, respectively, contained YOY in the migrant-resident stream. YOY thus exploit at a high proportion both types of habitats.

b) General stream habitat use across migrant-resident and resident-only streams

No significant differences were found between the different methods (mean of beginning and end of section versus random velocity measurements within section) for describing mean section velocity in either Édouard (paired t = -0.46, df = 18, p = 0.65) or Épinette (paired t = -1.21, df = 18, p = 0.24). The method of taking velocities at the beginning and end of each section is thus considered adequate for describing mean section velocity.

Mean available habitat velocities varied between 0.20 m/s to 0.27 m/s in migrant-resident streams (Table 3.2). The mean velocities occupied by brook trout and Atlantic salmon varied between 0.17 to 0.22 m/s and 0.21 to 0.30 m/s, respectively.

General stream habitat use by fish in comparison to the habitats available in migrant-resident streams varied depending on the stream (Fig. 3.3). In Édouard, brook trout occupied slower velocities than the average available in the stream (D = 0.20, p < 0.005) and those occupied by Atlantic salmon (D = 0.23, p < 0.005), which exploited velocities more or less in the same proportion to their availability in the stream (D = 0.044, p = 0.96). In Morin, brook trout (D = 0.18, p = 0.47) and Atlantic salmon (D = 0.062, p = 1.0) occupy the same velocities as those available in the habitat. There was also no difference in habitat use between brook trout and Atlantic salmon (D = 0.19, p = 0.17). Brook trout (D = 0.085, p = 0.99) and Atlantic salmon (D = 0.11, p = 0.91) velocities did not differ from those available in the habitats in the lower sections of Allaire. There was also no difference in habitat use between brook trout and Atlantic salmon (D = 0.12, p = 0.54). In the lower section of Portage stream, brook trout (D = 0.25, p = 0.45) and Atlantic salmon (D = 0.10, p = 0.93) also occupy all available habitats, although the sample size for brook trout was very low (N = 18). Atlantic salmon tend to occupy slightly faster velocities than brook trout but the difference is not significant (*D* = 0.32, *p* = 0.062).

When all migrant-residents streams were pooled, other than Édouard which was sampled much more intensively than the others, brook trout (*D* = 0.10, *p* = 0.57) and Atlantic salmon (*D* = 0.094, *p* = 0.40) occupy velocities in the same proportion as to those available in the stream. However, as expected, salmon utilise faster velocities than brook trout (*D* = 0.19, *p* < 0.005).

In resident-only streams, mean habitat velocities ranged between 0.17 and 0.22 $m \cdot s^{-1}$ (Table 3.2). Brook trout had mean velocities that varied between 0.14 and 0.18 m/s.

Brook trout in resident-only streams generally occupy habitats slower than the average velocities available in the streams, although the pattern is not significant in all streams (Fig. 3.4). In Épinette, brook trout occupied slower current velocities than those available in the habitat (*D* = 0.26, *p* = 0.047). Brook trout captured in the upper section of Allaire exploited similar current velocities as those available in the habitat (*D* = 0.20, *p* = 0.24), although 41% of the fish were found between 0 and 0.15 m/s, compared to 24% of habitats exhibiting these velocities. In Portage, 57% of brook trout were found between 0 and 15m/s, compared to 31% of habitats exhibiting these velocities. Although it seems that brook trout occupy slower velocities than those available, the difference is not significant (*D* = 0.25, *p* = 0.53). This is most likely the result of a small sample size since only 75 m of stream was sampled and only 23 trout were captured. When all resident-only streams were pooled, brook trout occupied slower current velocities than those found in the habitat (*D* = 0.21, *p* = 0.009).

Discussion

Habitat use of fish in migrant-resident and resident-only streams

Different patterns of brook trout habitat use in streams open (migrant-resident) and closed to anadromy (resident-only) were revealed using the approaches developed in 2002 and 2003. The results obtained from sampling pool and riffle habitats in 2003 as dichotomous surrogates of current velocity indicate that juvenile brook trout from a resident-only stream (Épinette) occupy slower habitats (pools) than trout found in a migrant-resident stream (Édouard). As migrant-resident streams contain different metabolic phenotypes (future migrants and residents), a wider habitat use distribution was expected, where fish densities would either be the same in pools and riffles, or tending higher in riffles due to the presence of future migrants, depending on the proportion of migratory fish. Indeed, brook trout occupied both habitat types in migrant-resident streams, and riffles tended to have higher densities than pools, albeit not significant. Observations across several migrant-resident streams in 2002 showed that brook trout tended to exploit all velocities in the same proportion as those available in the habitat, but there was a tendency towards slower current velocities in Édouard. As expected, higher densities of Atlantic salmon were found in riffles compared to pools, although they were found to use all habitats, agreeing with previous reports (Gibson 1966, 1973). Atlantic salmon occupied faster current velocities than resident brook trout, in agreement with previous bioenergetic findings that Atlantic salmon have higher total metabolic costs than coexisting resident brook trout from migrant-resident streams (Tucker & Rasmussen 1999).

In contrast, we expected juvenile brook trout from resident-only streams to exploit slow velocities over fast velocities since the population comprises only one metabolic phenotype (only the resident form). Indeed, juvenile brook trout from Épinette were found at higher densities in pools than riffles. This pattern in habitat use differed significantly from that observed in the migrant-resident stream, Édouard. Although there are no other species to compete with in Épinette, trout, on average, exploited faster currents at a lower proportion than slow ones, suggesting a preference for slower flowing water. These results were also supported by the general habitat use patterns observed across resident-only streams where, with all streams pooled, trout exploited slow velocities at a greater proportion than those available in the habitat. Not all individual streams generated significant differences between trout habitat use and available habitats. However, this most likely occurred because the differences between the available habitat and trout were too small to be significantly detected since the power of the analyses was weak due to low within-stream sample sizes. Nevertheless, trout from resident-only streams (mean trout velocity = 0.17 m/s) were found in slower currents than trout from migrant-resident streams (mean trout velocity = 0.20 m/s). This is consistent with previously reported morphological differences where resident trout from resident-only streams are less streamlined than trout from migrant-resident streams (G.R. Morinville & J.B. Rasmussen, Chapter 2).

The observations we report assume that the differences in habitat use persist over time, i.e. habitat switching between pools and riffles is not occurring on a frequent basis. Stable isotope analysis supports this as differences between migrants and residents can be detected (Morinville & Rasmussen 2003, G.R. Morinville & J.B. Rasmussen, Chapter 2). In addition, young salmonids occupying lotic systems are generally sedentary, defending their feeding territory from a central position (Grant, Noakes & Jonas 1989, Keeley & Grant 1995).

Previously reported salmonid densities of streams of the Ste. Marguerite River system range from 0.3-44 fish·100m^{-2} (Tucker 1998, Tucker & Rasmussen 1999, Lenormand 2003) and are typical of the range observed in other salmonid streams (Mills & Tomison 1985, Kennedy 1988, Mills 1989, Gibson et al. 1993). Our densities, extrapolated to an area of 100 m^2 and assuming a 50% capture rate from one pass fishing, are also consistent with previous reports in the system. Densities below 15 fish per 100m^2 are considered marginal to poor. The densities reported for brook trout in Édouard pools (~18 per100m^2) could be considered marginal, and thus not likely contributing to strong intra-specific interactions. In contrast, Épinette trout densities were almost twice as high (~35 per 100m^2) as those in Édouard, and possibly leading to agonistic interactions. This could explain the observation of trout in riffle habitats of Épinette, where dominant fish in pools push weaker fish into faster and less preferred habitats. Indeed, higher trout densities and poorer growth has been consistently reported in Épinette compared to migrant-resident streams (Lenormand 2003).

Interestingly, the differences in habitat use between stream-types could be observed as early as at age 0+. As expected with small fish, densities of YOY were highest in pools compared to riffles in both migrant-resident and resident-only streams, although the migrant-resident stream had higher YOY densities in riffles compared to the resident-only stream. Specifically, pools in Épinette had YOY densities 20 times higher than those in riffles whereas in Édouard, pool densities were only 2 times greater the riffle densities. In addition, YOY occupancy of pool and riffle habitats, that is, the proportion of habitat-specific sections containing at least 1 YOY, revealed that over 50% of the sampled riffle habitat sections were occupied by YOY in the migrant-resident stream, compared to less than 6% (1 section out of 17) of the riffles in the resident-only stream (Épinette). In contrast, 90% of the sampled pools contained YOY in Épinette (migrant-resident). The results thus clearly demonstrate that YOY in resident-only streams prefer pool habitats to riffle habitats, even though pool habitats are more densely populated with juvenile trout than riffle habitats. In addition, the finding that YOY exploit both riffle and pool habitats (wider habitat use distribution) concurs with habitat use expectations of migrant-resident streams as YOY in such streams comprise both resident and migrant phenotypes, with the latter migrating as early as age 1+ (Lenormand 2003, Thériault & Dodson 2003).

Given that migrations occur on a yearly basis, if a large proportion of the population migrates, few migrants will remain in the system, resulting in a higher proportion of slow habitats to be exploited as the population mostly consists of true residents. In contrast, if few fish migrate, the remaining population may consist of a high proportion of future migrants, leading to a wider habitat distribution. This may explain the differences in habitat distribution observed across the migrant-resident streams sampled in 2002. For example in Édouard, a larger proportion of fish were found to exploit slow currents than those available in the habitat. Using a linear discriminant function developed in a parallel study to classify migrant and resident brook trout (G.R. Morinville & J.B. Rasmussen, Chapter 2), 88% of trout captured in Édouard had a resident-type morphology, supporting the habitat use observations. Similarly, trout distributions also tended to skew to slower current velocities on Portage, albeit not significant due to small sample sizes. Portage stream experienced a large migration of brook trout where over 150 migrants were captured in the outmigration trap. Only 11 trout were subsequently captured in the entire stream section up to an impassable waterfall following migration suggesting these to be mostly residents. Indeed, 82% (9 out of 11 trout) of the remaining trout were identified as having a resident-type morphology and the majority were found in slow currents. In contrast, on Morin where a wider distribution of habitats were found to be exploited, earlier sampling for a parallel study indicated that 33% of trout (total N = 403) captured in 2002 following the migration period had migrant-type morphologies, concurring with wider distributions observations. Habitat distributions thus appear to reflect the presence and absence of migrant trout such that in the reduction or absence of migrant trout, slow habitats are exploited at a greater proportion than fast habitats. Importantly, this pattern appears consistent both in migrant-resident streams where the proportion of migrants in a population varies from year to year between migrant-resident streams and in resident-only streams, where only residents are present.

Overall, the data corroborates expected patterns of wider habitat occupancy when a population is comprised of different metabolic forms compared to a population composed of only resident phenotypes. It is accepted that Atlantic salmon use faster, more costly habitats than resident brook trout (Gibson 1966, 1973, Gibson et al. 1993), leading to their higher consumption rates but higher metabolic costs (Tucker & Rasmussen 1999). Similarly, it has also been demonstrated that migrant brook trout have higher consumption rates than resident brook trout stemming from higher metabolic costs (Morinville & Rasmussen 2003). However, unlike the case of the resident brook trout and Atlantic salmon dichotomy, we cannot conclude from the results of this study that the YOY and juvenile trout captured in faster current velocities in migrant-resident streams are indeed future migrants. It may be migrants, possessing higher metabolic rates, that are pushing residents into faster currents, as metabolism has been linked to dominance and aggression behaviours in salmonids (Metcalfe, Taylor & Thorpe 1995, Cutts, Metcalfe & Taylor 1998, 1999). However the alternative hypothesis, that migrants occupy faster velocities than residents is better supported.

Firstly, migrants have higher consumption rates than residents (Morinville & Rasmussen 2003), and food delivery is higher in fast current velocities (Grant & Noakes 1987). In addition, given the general acceptance that fish morphology is tightly linked to habitat use and swimming (Riddell & Leggett 1981, Webb 1984, Bisson, Sullivan & Nielsen 1988), migrant brook trout are more streamlined than resident brook trout of the same stream and thereby possess a low drag morphology (G.R. Morinville & J.B. Rasmussen, Chapter 2). On a similar note, trout from migrant-resident streams are also more streamlined than trout from resident-only streams, supporting the between stream-type habitat use observations. The differences are strong enough that trout can be correctly classified as being either migrant-like or resident-like using a linear discriminant function (G.R. Morinville & J.B. Rasmussen, Chapter 2).

Furthermore, a linear discriminant function applied to YOY from an migrant-resident stream (Morin), classified about 60% of YOY as future migrants over 2 years. A large proportion of YOY in migrant-resident streams thus comprise future migrants and observations in habitat use may thus reflect the ratio of migrants and residents in the system. Importantly, YOY predicted as future migrants have more negative δ^{13}C signatures (indicative of feeding in fast currents) than predicted residents, consistent with previously reported signatures for known migrants and residents captured in the spring (Morinville & Rasmussen 2003, G.R. Morinville & J.B. Rasmussen, Chapter 2). As stable isotopes integrate long term feeding information (Peterson & Fry 1987), the signatures of trout captured in spring reflect the previous summer's feeding. All of this evidence, although circumstantial, favours migrants as exploiting faster currents than residents.

In our migrant-resident streams, in which we observe brook trout to prefer faster currents than resident-only streams, salmon were always present. Gibson et al. (1993) found that when Atlantic salmon were introduced to streams above waterfalls where previously only resident brook trout were present, that brook trout selected slower velocity regimes than prior to the salmon introduction. Atlantic salmon are more aggressive and territorial than brook trout, such that they are normally able to obtain the best feeding sites and defend them, limiting trout to slower velocities (Gibson 1973). This could imply that migratory brook trout prefer even faster velocity regimes than those we report. The difference in the preference of velocities between anadromous and resident brook trout may thus be even greater.

Interestingly, pools in the resident-only stream (Épinette) supported higher densities of brook trout than those of the migrant-resident stream (Édouard). Given the higher consumption rates and maintenance rations (minimum amount of energy required to maintain zero growth) of Atlantic salmon and anadromous brook trout compared to resident brook trout

(Tucker & Rasmussen 1999, Morinville & Rasmussen 2003), in addition to the observation that Édouard migrant-resident) contained more than twice the density of fish in riffles than those found in Épinette (resident-only), invertebrate drift may be depleted more rapidly in riffles of migrant-resident than resident-only streams. Indeed, at equal densities, communities dominated by Atlantic salmon depress invertebrate drift densities much more rapidly than those dominated by resident brook trout (J.B. Rasmussen, unpublished data). It is thus quite possible that the lower pool fish densities observed in Édouard (migrant-resident) is the outcome of reduced levels of invertebrate drift entering pools. This further emphasizes the finding that brook trout from resident-only streams exploit slower habitats than those migrant-resident streams.

Juvenile habitat use, metabolic costs and life-history strategies

This study, for the first time, attempts to link juvenile habitat use to anadromous migrations that occur later in life, and the results are consistent with previously observed bioenergetic differences between migrant and resident brook trout (Morinville & Rasmussen 2003). The study implies that the differences between migrants and residents in both habitat selection (this study) and bioenergetic budgets (Morinville & Rasmussen 2003) are detectable as early as the first year of life and persist throughout the juvenile stages. Therefore, it appears that the life-history variation is expressed very early in life and is not simply adopted in the year in which migration occurs.

Habitat selection involves a trade-off between the costs (swimming and foraging) and benefits (prey availability) acquired by occupying certain velocities (Smith & Li 1983, Fausch 1984). Differential swimming capacities of species (Facey & Grossman 1990, Hansson et al. 1997, Peake, McKinley & Scruton 1997, McDonald, McFarlane & Milligan 1998) can thus be linked to varying patterns of habitat use. It is likely that early variations in morphology (McLaughlin & Grant 1994), developmental rates (Thorpe 1989, Marten 1992) or physiology (standard metabolic rate-aerobic capacity) (Metcalfe & Thorpe 1992, Metcalfe, Taylor & Thorpe

1995) within a species also allows for certain individuals to exploit faster waters than others, and that this may be involved in future life-history strategy decisions.

Taylor & McPhail (1986) demonstrated that in prolonged swimming tests, anadromous threespine sticklebacks fatigued less than freshwater threespine sticklebacks. Anadromous sockeye (*Oncorhynchus nerka*) were also found to attain greater mean critical swimming velocities than non-anadromous kokanee of the same size raised under identical conditions (Taylor & Foote 1991). Interestingly, both studies (Taylor & McPhail 1986, Taylor & Foote 1991) also found morphological differences between the freshwater and anadromous forms, which helped to explain the observed differential swimming capacities. In the wild, variations in body shape and fin size among juvenile coho salmon, steelhead and cutthroat trout concurred with those that would be favoured in different locations of a stream channel (Bisson, Sullivan & Nielsen 1988). Anadromous brook trout also possess a body morphology that is more adapted for exploiting fast currents; they are more streamlined (lower drag morphology) than resident brook trout (G.R. Morinville & J.B. Rasmussen, Chapter 2). Possessing a more deeper-bodied morphology can result in higher theoretical drag, leading to higher metabolic costs (Facey & Grossman 1990, Pettersson & Brönmark 1999). Given that fish tend to position themselves where their net energy budget is maximized (Fausch 1984, Hughes & Dill 1990, Hill & Grossman 1993), fish possessing an energetically inefficient morphology may lead to the avoidance of fast currents. This is not to say that fish will never enter fast water, but rather that they will utilize fast currents only on a limited basis.

In summary, on the basis of this study that shows differences in habitat utilisation between migrant (anadromous) and resident brook trout, and our previous study showing bioenergetic differences, we hypothesise that the “pure” resident brook trout do not have the energetic scope to persist in fast currents but that migrant brook trout do. Migrants express their greater energetic scope both in their use of faster water habitats with greater food supply rates as juveniles, and as adults, in the larger scale over which they complete their life cycle and the larger marine prey types that they are able to access. Thus, while they grow larger and return as more fecund adults, there is a cost to this greater energetic scope. This cost includes low growth efficiency in small streams and when migration is not possible due to fragmentation (waterfalls and impassable culverts), the migrant phenotype will not prosper. We also suggest that river systems containing only residents will tend to express local adaptations only and exhibit poor ability to adapt to large-scale climate variations in time and space.

Importantly, the study indicates that in systems containing both anadromous and resident species, all habitats are exploited, leaving few, if any, unused niches compared to streams only containing resident species where many habitats are left unexploited. This should be of important concern for fishery managers since streams containing many empty niches may be at greater risk of being invaded by exotic species and may create further constraints on native species. In addition, this study indicates that the presence of barriers, such as culverts, not only results in the loss of anadromous forms, but also results in changes in the overall upstream habitat use. Furthermore, it supports the idea that fish will not risk employing energetically costly habitats if benefits, on the long term, are impossible to achieve due to the presence of a barrier. Understanding the specific habitat requirements of fish is thus crucial for species conservation and attaining sustainable management practices.

Acknowledgments

We thank M. Bélanger, S. Bodmer-Roy, A. Boivin, J-F. Bourque, D. Browne, A. DuCap, G. Kramer, A. Parkes and V. Thériault for field assistance and laboratory work. We are grateful to J. Smith for providing some physical characteristics of study streams. We also thank D. Browne for his helpful comments on earlier versions of this manuscript. This study is a contribution to the program of CIRSA (Centre Interuniversitaire sur le

Saumon Atlantique). Funding for this project was provided to J.B.R. by the Natural Sciences and Engineering Research Council of Canada (NSERC; Strategic Grant and Collaborative Special Projects), the Foundation de la Faune du Québec, the Government of Quebec (FAPAQ), the Government of Canada (Economic development), the financial partners of CIRSA Inc., and Graduate Fellowships to G.R.M. from McGill’s Department of Biology and the McConnell Family McGill Major.

Literature Cited

Beamish, F.W.H. (1980) Swimming performance and oxygen consumption of the charrs. *Charrs: Salmonid fishes of the genus Salvelinus* (ed. E.K. Balon), pp. 739-748, W. Junk, The Hague, Netherlands.

Bisson, P.A., Sullivan, K. & Nielsen, J.L. (1988) Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. *American Fisheries Society*, **117**, 262-273.

Bohlin, T., Dellefors, C. & Faremo, U. (1996) Date of smolt migration depends on body-size but not age in wild sea-run brown trout. *Journal of Fish Biology*, **49**, 157-164.

Cutts, C.J., Adams, C.E. & Campbell, A. (2001) Stability of physiological and behavioural determinants of performance in Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 961-968.

Cutts, C.J., Metcalfe, N.B. & Taylor, A.C. (1998) Aggression and growth depression in juvenile Atlantic salmon: the consequences of individual variation in standard metabolic rate. *Journal of Fish Biology*, **52**, 1026-1037.

Cutts, C.J., Metcalfe, N.B. & Taylor, A.C. (1999) Competitive asymmetries in territorial juvenile Atlantic salmon, *Salmo salar*. *Oikos*, **86**, 479-486.

Elliott, J.M. (1990) Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. 3. The role of territorial behavior. *Journal of Animal Ecology*, **59**, 803-818.

Facey, D.E. & Grossman, G.D. (1990) The metabolic cost of maintaining position for four North-American stream fishes - Effects of season and velocity. *Physiological Zoology*, **63**, 757-776.

Fausch, K.D. (1984) Profitable stream positions for salmonids - Relating specific growth rate to net energy gain. *Canadian Journal of Zoology*, **62**, 441-451.

Fausch, K.D. (1993) Experimental analysis of microhabitat selection by juvenile steelhead (*Oncorhynchus mykiss*) and coho salmon (*Oncorhyncus kisutch*) in a British-Columbia stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 1198-1207.

Fausch, K.D. & White, R.J. (1981) Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 1220-1227.

Forseth, T., Naesje, T.F., Jonsson, B. & Harsaker, K. (1999) Juvenile migration in brown trout: a consequence of energetic state. *Journal of Animal Ecology*, **68**, 783-793.

Gibson, R. J. (1966) Some factors influencing the distributions of brook trout and young Atlantic salmon. *Journal of the Fisheries Research Board of Canada*, **23**, 1977-1980.

Gibson, R. J. (1973) Interactions of juvenile Atlantic salmon (*Salmo salar* L.) and brook trout (*Salvelinus fontinalis* (Mitchill)). *International Atlantic Salmon Symposium in St. Andrews, NB*, pp.181-202.

Gibson, R.J., Stansbury, D.E., Whalen, R.R. & Hillier, K.G. (1993) Relative habitat use, and inter-specific competition of brook trout (*Salvelinus fontinalis*) and juvenile Atlantic salmon (*Salmo salar*) in some Newfoundland rivers. *Production of juvenile Atlantic salmon (Salmo salar) in natural waters* (eds R.J. Gibson and Pages 53-69 *in* R. J. Gibson & R. E. Cutting), pp. 53-69. *Canadian Special Publications in Fisheries and Aquatic Sciences* **118**.

Grant, J.W.A. & Noakes, D.L.G. (1987) Movers and stayers: foraging tactics of young-of-the-year brook charr, *Salvelinus fontinalis*. *Journal of Animal Ecology*, **56**, 1001-1013.

Grant, J.W.A., Noakes, D.L.G & Jonas, K.M. (1989) Spatial distribution of defence and foraging in young-of-the-year brook charr, *Salvelinus fontinalis*. *Journal of Animal Ecology*, **58**, 773-789

Griffith, J.S. (1972) Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. *Journal of the Fisheries Research Board of Canada*, **29**, 265-173.

Hansson, S., Hobbie, J.E., Elmgren, R., Larsson, U., Fry, B. & Johansson, S. (1997) The stable nitrogen isotope ratio as a marker of food-web interactions and fish migration. *Ecology*, **78**, 2249-2257.

Heggenes, J., Saltveit, J. & Lingaas, O. (1996) Predicting fish habitat use to changes in water flow: Modelling critical minimum flows for Atlantic salmon, *Salmo salar*, and brown trout, *S. trutta*. *Regulated Rivers-Research & Management*, **12**, 331-344.

Hill, J. & Grossman, G.D. (1993) An energetic model of microhabitat use for rainbow trout and rosyside dace. *Ecology*, **73**, 685-698.

Hughes, N.F. & Dill, L.M. (1990) Position choice by drift feeding salmonids - Model and test for arctic grayling (*Thymallus arcticus*) in sub-arctic mountain streams, interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 2039-2048.

Jonsson, B. (1985) Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. *American Fisheries Society*, **114**, 182-194.

Kennedy, G.J.A. (1988) Stock enhancement of Atlantic salmon (*Salmo salar* L.). *Atlantic salmon: planning for the future* (eds D. Mills and D. Piggins), pp 345-372. Croom Helm, London.

Lenormand, S. (2003) *Évolution de l'anadromie et stratégie de reproduction chez l'omble de fontaine (Salvelinus fontinalis)*. PhD thesis, Université Laval, Québec.

Lesueur, C. (1993) *Compte rendu des résultats obtenus lors de l'étude de l'omble de fontaine anadrome de la rivière Ste-Marguerite (Saguenay) en 1992*. Association de la rivière Ste-Marguerite, Sacré-Coeur, Québec.

Marten, P.S. (1992) Effect of temperature variation on the incubation and development of brook trout eggs. *Progressive Fish-Culturist*, **54**, 1-6.

McCormick, S.D., Naiman, R.J. & Montgomery, E.T. (1985) Physiological smolt characteristics of anadromous and non-anadromous brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, **42,** 529-538.

McDonald, D.G., McFarlane, W.J. & Milligan, C.L. (1998) Anaerobic capacity and swim performance of juvenile salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, **55,** 1198-1207.

McLaughlin, R.L. & Grant, J.W.A (1994) Morphological and behavioural differences among recently-emerged brook charr, *Salvelinus fontinalis*, foraging in slow- vs. fast-running water. *Environmental Biology of Fishes*, **39**, 289-300.

Metcalfe, N.B., Taylor, A. & Thorpe, J.E. (1995) Metabolic rate, social status, and life-history strategies in Atlantic salmon. *Animal Behaviour*, **49**, 431-436.

Metcalfe, N.B. & Thorpe, J.E. (1992) Early predictors of life-history events: The link between first feeding date, dominance and seaward migration in Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology*, **41**, 93-99.

Mills, D.H. (1989) *Ecology and Management of Atlantic Salmon*. Chapman and Hall, London.

Mills, D.H. & Tomison, A.T. (1985) *A Survey of the Salmon and Trout Stocks of the Tweed Basin*. Tweed Foundation, Kelso.

Morinville, G.R. & Rasmussen, J.B. (2003) Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 401-410.

Peake, S., McKinley, R.S. & Scruton, D.A. (1997) Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design. *Journal of Fish Biology*, **51**, 710-723.

Peterson, B.J. & Fry, B. (1987) Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, **18**, 293-320.

Pettersson, L.B. & Brönmark, C. (1999) Energetic consequences of an inducible morphological defence in crucian carp. *Oecologia*, **121**, 12-18.

Power, G. (1980) The brook charr, *Salvelinus fontinalis*. *Charrs, salmonid fishes of the genus Salvelinus* (ed. E.K. Balon), pp 141-203. W. Junk, The Hague, Netherlands.

Riddell, B.E. & Leggett, W.C. (1981) Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Science*, **38**, 308-320.

Smith, J.J. & Li, H.W. (1983) Energetic factors influencing foraging tactics of juvenile steelhead, *Salmo gairdneri*. *Predators and prey in fishes (*eds D.L.G. Noakes, D.G. Lindquist, G.S. Helfman & J.A. Ward), pp. 173-180. W. Junk, The Hague, Netherlands.

Taylor, E.B. & Foote, C.J. (1991) Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). *Journal of Fish Biology*, **38**, 407-419.

Taylor, E.B. & McPhail, J.D. (1986) Prolonged and burst swimming in anadromous and fresh-water threespine stickleback, *Gasterosteus aculeatus*. *Canadian Journal of Zoology*, **64**, 416-420.

Thériault, V. & Dodson, J.J. (2003) Body size and the adoption of a migratory tactic in brook charr. *Journal of Fish Biology*, **63**, 1-16.

Thorpe, J. E. (1989) Developmental variation in salmonid populations. *Journal of Fish Biology*, **35**, 295-303.

Tucker, S. (1998) *Using radiocesium (^{137}Cs) to measure and compare the bioenergetic budgets of Atlantic salmon (Salmo salar) and brook trout (Salvelinus fontinalis) in the field*. Master's thesis, McGill University, Montreal.

Tucker, S. & Rasmussen, J.B. (1999) Using 137Cs to measure and compare bioenergetic budgets of juvenile Atlantic salmon (*Salmo* *salar*) and brook trout (*Salvelinus fontinalis*) in the field. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 875-887.

Webb, P.W. (1984) Body form, locomotion and foraging in aquatic vertebrates. *American Zoology*, **24**,107-120.

Table 3.1 Length, basin area, reach length, mean wetted width (± 1 SD), mean depth (± 1 SD) and mean pool depth (± 1 SD) of reaches in migrant-resident and resident-only streams sampled in 2002.

Stream type	**Stream**	**Basin area (km^2)**	**Reach length (m)**	**Mean wetted width (m)**	**Mean depth (cm)**	**Mean pool depth (cm)**
Migrant-resident	Édouard	~9	1075	2.9 ± 1.1	20.4 ± 10.6	35.6 ± 8.3
	Morin	~18	200	5.3 ± 1.6	23.2 ± 10.1	34.7 ± 6.7
	Allaire below	~28	190	5.8 ± 2.2	26.9 ± 11.3	39.1 ± 7.9
	Portage below	na	160	2.9 ± 1.3	22.1 ± 14.4	29.2 ± 10.4
Resident-only	Épinette	~11	200	3.5 ± 1.7	17.7 ± 11.2	31.1 ± 7.6
	Allaire above	~28	170	5.4 ± 1.7	26.7 ± 9.9	29.5 ± 3.2
	Portage above	na	75	3.1 ± 1.3	23.5 ± 13.9	32.9 ± 14.8

na: not available

Table 3.2 Mean velocity (± 1 SE) and sample size (N) of habitat, juvenile brook trout and Atlantic salmon samples in migrant-resident and resident-only streams.

Stream type	**Stream**		**Mean velocity ($m \cdot s^{-1}$)**	**N**
Migrant-resident	Édouard	Habitat	0.20 ± 0.007	210
		Brook trout	0.17 ± 0.008	252
		Atlantic salmon	0.21 ± 0.006	343
	Morin	Habitat	0.21 ± 0.015	40
		Brook trout	0.18 ± 0.012	44
		Atlantic salmon	0.21 ± 0.007	231
	Allaire below	Habitat	0.24 ± 0.013	38
		Brook trout	0.23 ± 0.008	106
		Atlantic salmon	0.25 ± 0.010	80
	Portage below	Habitat	0.27 ± 0.028	32
		Brook trout	0.22 ± 0.036	18
		Atlantic salmon	0.30 ± 0.011	210
Resident-only	Épinette	Habitat	0.17 ± 0.011	40
		Brook trout	0.14 ± 0.008	90
	Allaire above	Habitat	0.22 ± 0.015	34
		Brook trout	0.18 ± 0.009	96
	Portage above	Habitat	0.21 ± 0.021	16
		Brook trout	0.18 ± 0.018	23

Figure 3.1 The mean number of fish captured per 20m^2 section in pool and riffle habitats of Édouard (migrant-resident, AR; 18 pool and riffle sections) and Épinette (resident-only, RO; 17 pool and riffle sections).

Shaded, open and closed bars indicate YOY brook trout (AR: n = 59; RO: n = 23), juvenile brook trout (AR: n = 85; RO: n = 95) and Atlantic salmon (AR: n = 34), respectively. Error bars represent +1 SE.

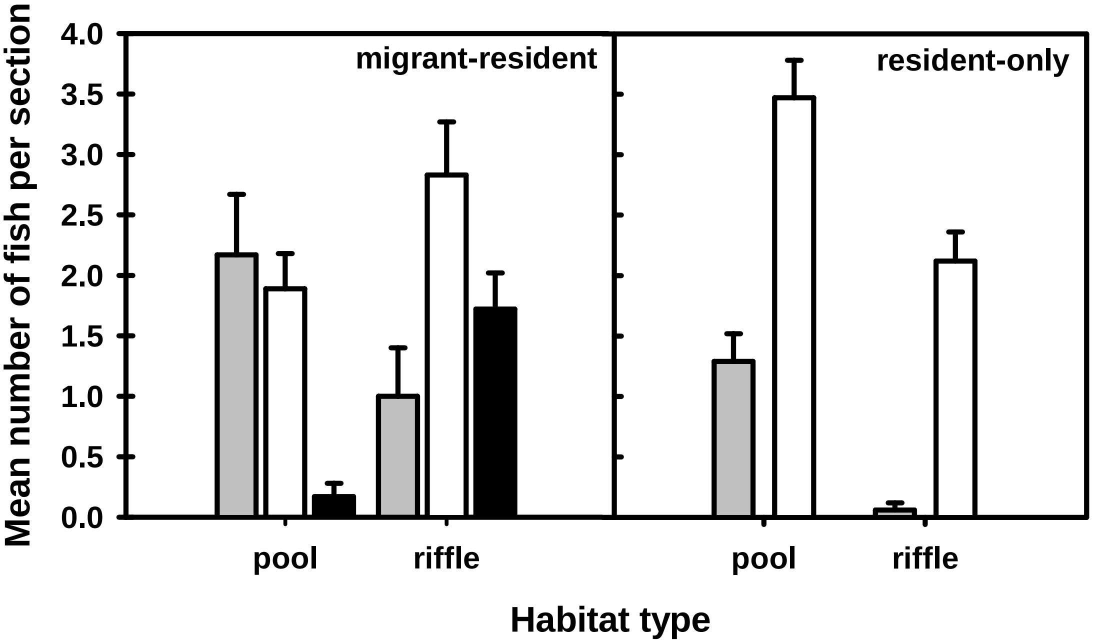

Mean number of fish per section
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
migrant-resident
resident-only
pool
riffle
pool
riffle
Habitat type

Figure 3.2 Young-of-the-year (YOY) brook trout occupancy (ratio of number of habitat-specific sections that contained at least 1 YOY to total number of habitat-specific sections) of pool (closed bars) and riffle habitat sections (open bars) from Édouard (migrant-resident; 18 pool and riffle sections) and Épinette streams (resident-only; 17 pool and riffle sections).

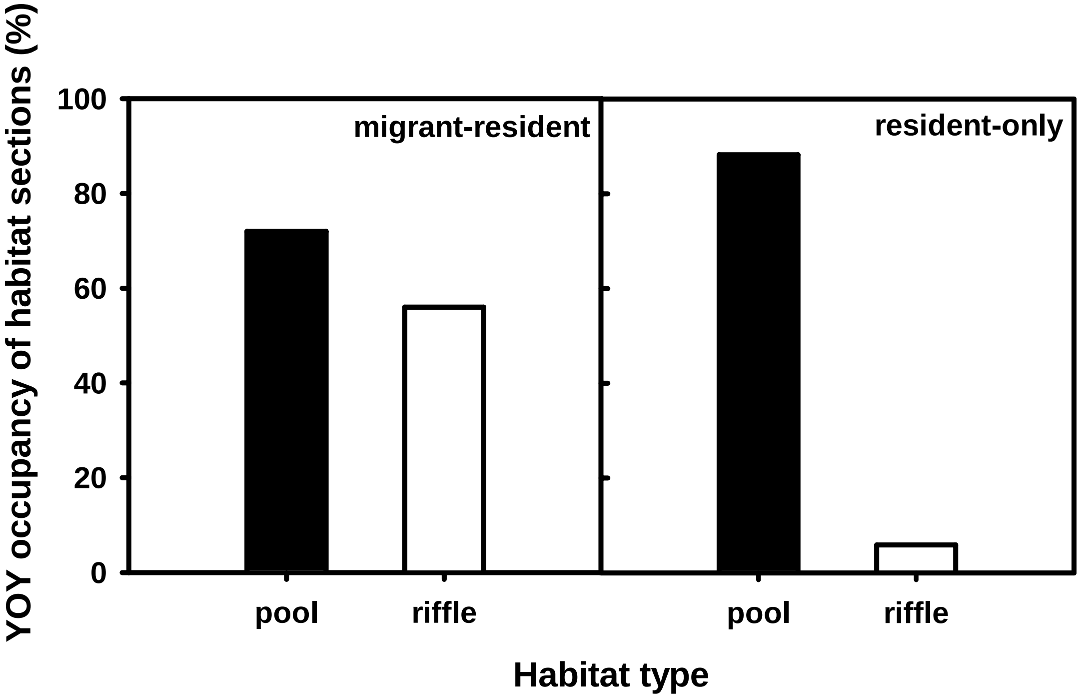

YOY occupancy of habitat sections (%)
100
80
60
40
20
0
migrant-resident
resident-only
pool
riffle
pool
riffle
Habitat type

Figure 3.3 Relative frequency distributions of velocity measurements of habitat (solid line), trout (dashed) and salmon (dotted line) sampled in four migrant-resident streams, (a) Édouard, (b) Morin, (c) Allaire below, and (d) Portage below.

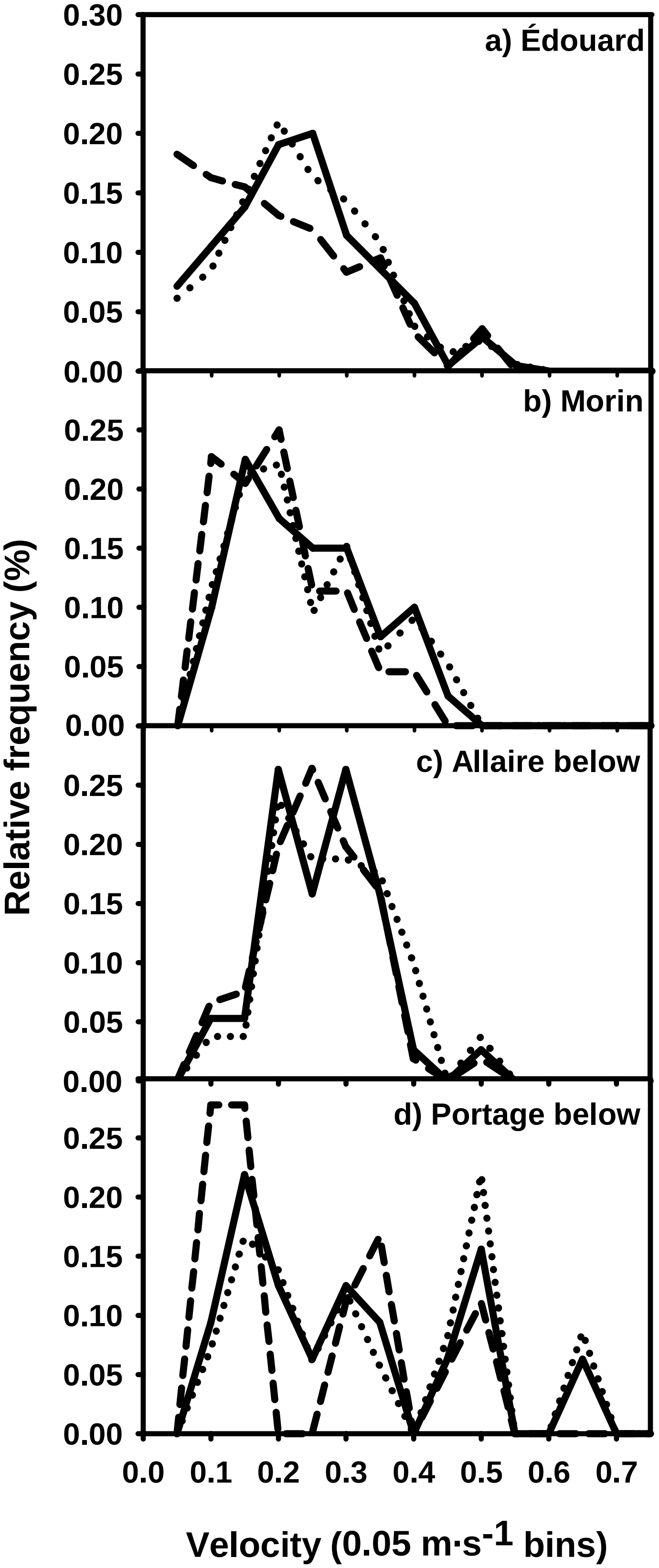
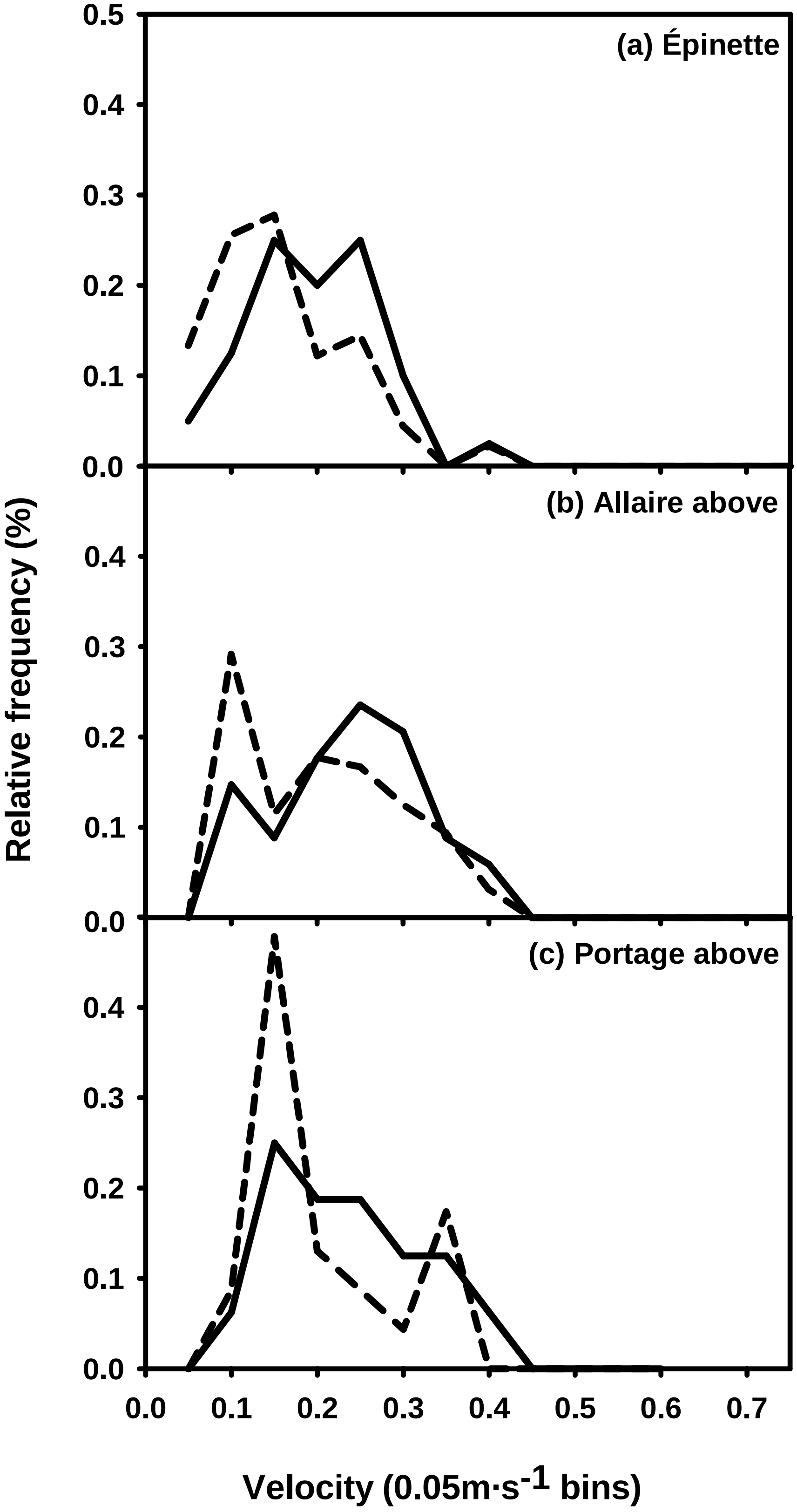

a) Édouard
b) Morin
c) Allaire below
d) Portage below
Relative frequency (%)
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Velocity (0.05 m·s-1 bins)

Figure 3.4 Relative frequency distributions of velocity measurements of habitat (solid line) and trout (dashed line) sampled in three resident-only streams, (a) Épinette, (b) Allaire above, and (c) Portage above.


0.5
0.4
0.3
0.2
0.1
0.0
(a) Épinette
(b) Allaire above
(c) Portage above
Relative frequency (%)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Velocity (0.05m·s-1 bins)

CONNECTING STATEMENT: bridging Chapter 3 and 4

The previous chapters describe differences in bioenergetics, morphology and habitat use detected between coexisting juvenile anadromous and resident brook trout in streams and how differences these link to the adoption of anadromy or residency as life-history strategies.

Together, these chapters demonstrate that anadromous brook trout, prior to migration, are energetically limited in their freshwater habitats due to their costly habitat use and consequent elevated metabolic costs, leading them to undertake a migration in the search for food. This quest for food leads them to the sea, an environment that is likely more productive and/or characterized with larger sized prey than freshwater habitats.

Chapter 4 thus compares food availability between freshwater and the initial site of sea entry, and elucidates the ontogenetic and seasonal feeding patterns of anadromous brook trout throughout the Saguenay River at the onset of sea entry.

CHAPTER 4: Marine feeding patterns of anadromous brook trout (*Salvelinus fontinalis*) inhabiting an estuarine river fjord[1]

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[1] contribution to the program of CIRSA (Centre Interuniversitaire de Recherche sur le Saumon Atlantique)

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fAbstract

Anadromous brook trout, also otherwise known as sea trout, naturally occur in northeastern North America in river systems that have direct access to the sea. They experience a short but seasonally determined sea residence. Sea trout, after life at sea, are significantly larger than residents of the same age class, suggesting good feeding opportunities at sea. This study describes the ontogenetic and seasonal feeding patterns of anadromous brook trout (sea trout) inhabiting the estuarine Saguenay using both stomach content and stable isotope analyses. Sea trout of the Ste-Marguerite River (Quebec) migrate to sea as young as age 1+, entering first through the estuarine Ste. Marguerite Bay (SMB) in early May before venturing into the Saguenay River fjord for the remainder of the summer period. Upon arriving at sea, the 1st year migrants acclimatize to new salinities and temperatures, staying relatively close to river mouths. When first arriving at sea, 1st yr migrants feed on freshwater aquatic invertebrates, but quickly shift to marine prey items such as mysids and amphipods for the remainder of their first summer at sea. These prey items are generally larger than freshwater prey, as the prey spectrum at sea is both larger and wider than that found in freshwater, and this most likely contributes to the trouts' rapid growth experienced at sea. The diet of migrants in subsequent years at sea (2nd year migrants) consists primarily of marine amphipods and mysids, and fish, the latter being most important when feeding in the upper portion of the Saguenay Fjord. Trout were observed to shift to piscivory in all marine sites at a size of 25 cm, regardless of time spent at sea, although the importance of piscivory varied with season and site.

“*Big fish eat little fish*” – Proverb

Introduction

In many populations of salmonids that access the sea, migrant and resident individuals of the same population coexist as juveniles, with the former spending a portion of their life cycle feeding in saline waters, and the latter completing its entire life cycle in freshwater. Those that migrate from freshwater to the sea, returning as large adults to freshwater for spawning, follow an anadromous life cycle. Anadromous brook trout (*Salvelinus fontinalis*), also known as sea trout, naturally occur in northeastern North America in river systems that are open to the sea (White 1940, Wilder 1952, Smith & Saunders 1958, Dutil & Power 1980, Castonguay et al. 1982). They generally experience a short but seasonally determined sea residence, returning to freshwater for winter (Dutil & Power 1980, Power 1980), a response most likely necessitated by their inability to osmoregulate in cold waters (Saunders et al. 1975). In recent years, angling pressure on sea trout has escalated, as the returns of Atlantic salmon to rivers declines. Unfortunately, few studies involving the anadromous phase of the life cycle have been conducted, limiting our understanding and thus ability to implement sustainable management practices.

Juvenile sea trout, prior to their first seaward migration, exhibit high consumption rates but low growth efficiencies (ratio of growth to consumption) in freshwater compared to residents, the consequence of higher metabolic costs (Morinville & Rasmussen 2003). The finding that sea trout (migrant) obtain more food in freshwater compared to residents prior to migration and still migrate suggests that they do not receive enough energy to satisfy their high energy demands. Juvenile sea trout may thus experience growth bottlenecks sooner than residents, leading them to change habitats in the search of an efficient food supply (low cost of capture but high energetic gain). Anadromous fish grow faster in the sea than their resident counterparts of the same age class (Castonguay et al. 1982, Lenormand et al. 2004), suggesting reduced activity costs (swimming, foraging and other behavioural activities) and/or better feeding opportunities at sea. Such feeding opportunities may be in the form of differences in overall productivity or differences in the availability of optimally sized prey (Keeley & Grant 2001). Marine systems are often thought to be more productive for fish than freshwater systems, based on the migratory tendencies of salmonids in north-temperate latitudes (Gross 1987, Gross et al. 1988).

In general, fish need to eat large prey to sustain growth and attain large sizes. Foraging costs, both in terms of the time spent actively searching and the number of feeding attempts, increase as prey sizes become small in relation to the size of the predator (Kerr 1971, Kerr & Ryder 1977). Optimal growth returns can thus be easily achieved when the diet is mostly composed of large prey (Kerr 1971, Wañkowski & Thorpe 1979, Pazzia et al. 2002, Sherwood et al. 2002). As such, fish including salmonids tend to eat larger prey with increasing size, displaying ontogenetic diet shifts from planktivory, to benthivory and ultimately to piscivory (Werner & Gilliam 1984, Mittelbach & Persson 1998, Keeley & Grant 2001). In ocean habitats, salmonids tend to eat large prey (fish) sooner than when inhabiting streams, allowing individuals to attain large sizes more quickly (Keeley & Grant 2001).

Brook trout are commonly considered to be opportunistic feeders, their diet changing with size, season and habitat (Power 1980). However, few studies report in detail the diet of the anadromous form. Of those that exist, most provided only general descriptions of prey items found in stomachs. These studies commonly report the presence of amphipods, mysids and fish including sand lance (*Ammodytes* sp.), sticklebacks (*Gasterosteus*), smelt (*Osmerus* sp.) and hake (*Urophycis* sp.) in the diet (White 1940, White 1942, Wilder 1952, Dutil & Power 1980, Gibson & Whoriskey 1980, Whoriskey et al. 1981, Gaudreault et al. 1982, O'Connell

1982). Only one study has considered the importance of the effect of ontogeny or season on diet (Gaudreault et al. 1982), and no study has attempted to directly link diet to the movement patterns at sea. Such information is necessary for implementing sustainable management plans for sea trout, and thus a better understanding of seasonal diet requirements across marine habitats is necessary to, for example, protect the most important feeding grounds.

Lenormand et al. (2004) recently described the ontogenetic and seasonal movement patterns of sea trout migrating to the estuarine Saguenay River (SR) from the Ste. Marguerite River (SMR) in Quebec, Canada. Sea trout of the SMR migrate in May, as early as age 1+, initially entering the saline waters of the SF by passing through the estuarine Ste-Marguerite Bay (SMB), where they remain for a few weeks acclimatizing to the salinities and temperatures of the new habitat, staying relatively close to freshwater inputs (Lenormand et al. 2004). As summer progresses and water temperatures increase, trout gradually migrate out from the bay, with the largest trout leaving sooner to enter the deeper, colder and more saline waters of the Saguenay River fjord (Lenormand et al. 2004). Unlike most anadromous brook trout populations that seem to remain close to the influence of their natal river (Dutil and Power 1980; White 1940), anadromous populations of the SR fjord are unique in that they migrate large distances, upwards of 100 km, experiencing relatively low salinities and higher temperatures throughout the fjord in comparison to those of the St. Lawrence Gulf (Chassé & Côté 1991, Lenormand et al. 2004).

The present study investigates the diet of anadromous brook trout immediately upon entering the sea through an estuarine bay. The main objectives of this study were to first compare the food availability (feeding opportunities) between freshwater and the initial site of sea entry, and secondly, to describe the feeding patterns of anadromous brook trout both during their first year at sea (hereafter referred as 1st yr migrants) and during their second year at sea and greater (hereafter referred as 2nd year migrants) to better understand the growth patterns experienced at sea. It was predicted that the initial site of sea entry, the estuarine SMB, would have more food available than that found in freshwater, either in total invertebrate biomass and/or mean invertebrate size. Seasonal feeding patterns of anadromous brook trout (sea trout) were described across sites in the SR, including the monthly detailed diet of 1st year migrants captured in the SMB using stomach content and stable isotope analyses. It was expected that, sea trout would initially feed on freshwater derived prey upon sea entry but that they would quickly shift to larger marine derived prey sources leading to rapid growth. It was also expected that tissues of 1st year migrants would become enriched in stable carbon signatures (δ^{13}C) over time due to enriched δ^{13}C values of marine prey items compared to freshwater (Fry and Sherr 1984). Trout were also predicted to shift to higher trophic levels over time as indicated by enriched muscle tissue δ^{15}N signatures.

Study Site and Methods

This study was conducted in the Ste. Marguerite River (SMR) system and in the estuarine Saguenay River (Quebec, Canada; 48º27'N, 69º95'W; Figure 1). The SMR flows into the estuarine Saguenay River, 25 km upstream from the St. Lawrence maritime estuary (Quebec, Canada). The SMR is home to the largest anadromous brook trout population of the Saguenay River basin (Lesueur 1993). Anadromous brook trout can migrate from mid-May to early-June, as early as age 1+, initially passing through the large and shallow Ste. Marguerite Bay before venturing into the Saguenay River (Thériault & Dodson 2003). The Saguenay River is divided into two main sections, (1) the Saguenay fjord defined as the last downstream 100 km of the Saguenay River under tidal influence and characterized as a mixing zone between freshwater upstream sources and salt-water inputs from the St. Lawrence maritime estuary, and (2) the upper Saguenay portion. Freshwater inputs in this sub-arctic fjord are quite variable, with a strong thermo-haline stratification occurring between May and October (Lenormand et al. 2004; Chassé and Côté 1991 and references therein). During this period, the water column is divided into a thin mixed layer (5-10 m) of warm (5-15ºC), brackish (0-18 PSU (practical salinity units)) water and a thick (up to 275 m), underlying layer of cold and saline water (<0.5ºC, >26 PSU at 15 m). The thermo-haline stratification regresses in the fall as exchanges between the two layers increase and salinity at the surface rises with decreasing surface temperatures. The ice-cover period occurring between December and April is characterized by having surface temperatures around 0ºC and salinity around 7 PSU at the surface. Increasing inputs of freshwater and surface water temperatures during the ice melt period (mid-March to early May) re-establishes the stratified water column.

Food availability at sea entry

Food availability for both May and August 1998 was compared between freshwater sites located in 3 tributaries of the SMR (Morin, Allaire and Épinette; for location see Lenormand 2003) and 6-7 randomly selected sites located along 30-km of the SMR, and multiple randomly selected marine sampling locations (~20 sites) in the Ste. Marguerite Bay (SMB), the initial site of sea entry. Sampling was conducted using 1.0 mm mesh kicknets. Sampling in the SMB occurred at tide edges both at high and low tide, depending on location. Some sites were only accessible at low tide. In flowing water sites (river, stream and some bay sites) rocks were kicked around in an area corresponding to the width (0.45 m) of the kicknet squared (0.20 m^2) for approximately 30 seconds, displacing any invertebrates into the kicknet. An average of ten samples were taken at each site and all captured invertebrates were pooled for subsequent estimates. In marine sites with no current, the kicker displaced rocks and moved the kicknet in a circle with a radius equivalent to the width (0.45 m) of the kicknet (area sampled = 0.64 m^2). This created current and allowed for invertebrates to be captured in the kicknet. The same kicker (G.R. Morinville) performed all sampling.

Food availability was estimated by measuring the mean biomass of pooled invertebrates, expressed as the amount of dry weight of invertebrate prey in grams of dry weight per m^2 (g dw·m^{-2}; Boisclair & Leggett 1985) and was compared between freshwater and marine sites. Mean invertebrate size (mg dw·ind^{-1}) was also estimated and compared between freshwater and marine sites. All comparisons were performed using *t*-tests.

Ontogenetic and seasonal feeding patterns

A dual approach using both stomach content analysis (SCA) and stable isotope analysis (SIA) was employed to describe the feeding patterns of anadromous brook trout inhabiting the Saguenay River.

Fish collection

Fish stomachs were obtained from trout captured from anglers, from trout obtained for a parallel study (Lenormand 2003, Lenormand et al. 2004) and additional sampling throughout the Ste. Marguerite River (SMR), the Ste. Marguerite Bay (SMB) and multiple Saguenay River sites (Figure 4.1). At the time of the study, fishing for anadromous brook trout was permitted in the Saguenay River, including the Ste. Marguerite Bay, all year round and in the St. Marguerite River from mid-June to the end of October allowing for samples from anglers across seasons and sites. Stomachs obtained from anglers throughout the years 1998 to 2001 were available due to a parallel mark-recapture program occurring in the Ste. Marguerite River and Bay. Anglers received compensation when they returned tagged fish (Lenormand et al. 2004). Stomachs obtained from trout captured in the SMR during the winter were also made available through this parallel study (Lenormand et al. 2004). Stomachs were either analyzed the day of capture or frozen for future analysis. Both the fork length (to the nearest mm) and weight (to the nearest 0.01g) of sampled trout were measured, although in some cases, this was not possible for trout captured by anglers.

Trout were also sampled in 2000 to 2002 using a 40-m beach seine (0.5-cm mesh, 1.5-m deep) at the onset of sea entry in the Ste. Marguerite bay in May, and every 2 to 4 weeks thereafter until October. In certain years, it was more difficult to catch trout during July and August in the SMB because trout tend to leave the SMB for more saline, colder and deeper areas of the SR with increasing temperatures (Lenormand et al. 2004). Sampling in July and early August was conducted in Anse-de-Sable (AS) and Anse-de-Pierres (AP) (Figure 1). Approximately 20 trout ranging in size were sacrificed at each sampling interval. Both stomach contents and muscle tissue biopsies were obtained from trout for subsequent diet analyses.

Stomach content analysis (SCA)

The percentage of empty stomachs (%ES; number of empty stomachs to the total number of sampled stomachs) was estimated and used as a measure of feeding activity. Filled stomachs consisted of predominantly whole undigested prey items with the exception of freshwater aquatic invertebrate larvae that were sometimes partially digested. Prey items were identified to order or genus for both freshwater aquatic invertebrate and marine prey. Excess moisture was removed from prey items and similar items of each stomach were weighed (to the nearest 1 mg wet weight).

In Saguenay River sites (including Ste. Marguerite Bay, upper Saguenay River and Saguenay fjord sites) prey items were subsequently assigned to 10 prey categories: freshwater aquatic larvae, terrestrial insects excluding beetles (coleopteran), beetles, amphipods (mostly *Gammarus* sp.), striped *Gammarus* (*Gammarus tigrinus*), polychaetes, mysid, penaeid shrimp, fishes and other including unidentified prey, plant matter, winged insects including newly-emerged flies and miscellaneous prey items. In the Ste. Marguerite River prey items were assigned to 9 prey categories: freshwater aquatic larvae, terrestrial insects excluding beetles, beetles, small mammals, salmonid eggs, winged insects including newly-emerged flies, plant matter, fishes and other including all unidentified prey.

Two stomach content analysis methods (occurrence and gravimetric) were applied to describe the diet composition of anadromous brook trout (Hyslop 1980). The estimates were generated using only trout with filled stomachs. The relative importance of individual prey types were assessed in terms of percentage of occurrence (%O) and percentage by weight (%W) where the total wet weight of each prey category was expressed as a percentage of the overall weight of stomach contents, termed ‘prey wet weight contribution’ (Clark 1985).

To describe the ontogenetic and seasonal marine feeding patterns of brook trout, samples were first grouped according to trout type, either 1st year migrants (trout in their first year at sea) or 2nd year migrants (trout in their second or more year at sea). For trout captured in the Ste. Marguerite Bay, stomach contents were pooled by month for years 1998 to 2002, as large samples were available. Monthly means for %ES, %O and %W were subsequently generated using pooled years. In contrast, due to limited available captures of brook trout in the Saguenay River for any given year and at any given site, monthly % ES, %O and %W estimates were obtained by pooling all stomachs obtained across years at a given site for a given month. These site-specific monthly estimates were further pooled according to their location of capture in the Saguenay River, either Saguenay River fjord sites or upper Saguenay River sites, generating mean monthly estimates. Stomachs obtained from trout captured in the Ste. Marguerite River were first pooled by month for years 1998 to 2000, and monthly means for %ES, %O and %W were calculated using pooled years.

Stable isotope analysis (SIA)

Carbon ($\delta^{13}C$) and nitrogen stable isotopes ($\delta^{15}N$) were employed to describe the long-term feeding patterns of 1st year migrant brook trout beginning from their arrival at sea into the Ste. Marguerite Bay and throughout the summer in relation to the Ste. Marguerite Bay (SMB) food web. Muscle biopsies were taken from 1st year migrant trout captured in the BSM in years 2000 to 2002. Changes in both $\delta^{13}C$ and $\delta^{15}N$ were followed according to the size of migrants and time of capture. The muscle tissue of resident brook trout captured in a tributary of the Ste. Marguerite River (Morin tributary) during June and July 1999 were also analysed for stable isotopes, which allowed comparisons between the different regressions with those of sea trout using analyses-of-covariance (ANCOVA).

To describe the food web leading to sea trout, all potential invertebrate prey items found in the BSM and neighbouring sites downstream to the BSM including Anse-de-Sable (AS) and Anse-de-Pierres (AP) during the years of study were analysed for stable isotopes. These included amphipods (*Gammarus* sp. and striped *Gammarus*), polychaetes, mysids and freshwater aquatic larvae and were captured by the use of a kicknet. Penaeid shrimp were also analysed and captured during seine hauls targeting trout. Fish including threespine sticklebacks (*Gasterosteus aculeatus*) and banded killifish (*Fundulus diaphanous*) were sampled using minnow traps baited with white bread. In addition, muscle biopsies were taken from larger prey fish including smelt (*Osmerus mordax*) and sand lance found in the stomachs of certain trout.

Stable carbon and nitrogen isotope analyses were performed using a continuous flow Finnigan MAT Delta plus mass spectrometer (G.G. Hatch Isotope Laboratory, University of Ottawa, Ottawa, ON, Canada). Stable isotope ratios are expressed in delta (δ) notation, defined as the parts per thousand (‰) deviation from a standard material; $\delta^{13}C$ or $\delta^{15}N = ([R_{sample}/R_{standard}]-1) \times 1000$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The standard material is Pee Dee belemnite (PDB) limestone for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$.

Results

Food availability at sea entry

No significant differences were found between river and stream sites for both mean invertebrate biomass estimates or mean invertebrate sizes in either May or August 1998. River and tributaries were thus pooled for all subsequent analyses.

Mean biomass estimates in May 1998 ranged between 0.069-0.30 g $dw \cdot m^{-2}$ and between 0.030-0.71g $dw \cdot m^{-2}$ for river and bay sites, respectively (Figure 4.2). In August, biomass ranged between 0.041-0.43 g $dw \cdot m^{-2}$ and between 0.020-0.50 g $dw \cdot m^{-2}$ for river and bay sites, respectively. No significant differences in mean biomass were found between river and bay sites in either May ($t = -0.89$, $df = 25$, $p = 0.38$) or August ($t = -0.22$, $df = 25$, $p = 0.83$).

In May 1998, mean invertebrate size ranged between 0.36-1.9 mg dw and between 0.60-4.2 mg dw for river and bay sites, respectively (Figure 4.3). Invertebrate sizes varied in August between 0.23-2.0 mg and between 0.40-3.4 mg for river and bay sites, respectively. Invertebrates from river sites were smaller on average than bay sites for both May ($t = -3.5$, $df = 28$, $p = 0.001$) and August ($t = -2.7$, $df = 25$, $p = 0.013$)

Ontogenetic and seasonal feeding patterns

Stomach content analysis (SCA)

i) Ste. Marguerite Bay

In the Ste. Marguerite Bay (SMB), 972 and 492 stomachs of 1st year and 2nd year migrants, respectively, were analysed (Table 4.1). The mean percentage of empty stomachs (%ES) across months ranged from 8.8% to 20.1% for 1st year migrants, and from 14.7% to 76.2% for 2nd year migrants. This amounted to a total of 808 1st year migrants with filled stomachs, captured between May and October and ranging in size from

114 mm to 231 mm (Table 4.2). 2nd year migrants containing filled stomachs were larger (total n = 363), ranging in size from 220 mm to 337 mm.

In May, stomachs of 1st year migrants frequently contained freshwater aquatic invertebrate larvae; they were found in over 60% of stomachs (Table 4.3). Although they were relatively frequently found in June (over 25%), the pattern did not persist for the later months, dropping to less than 12%. The percentage frequency of occurrence (%O) for polychaetes was also high (over 30% of stomachs) in May, but remained below 22% for the remaining months. Amphipods (*Gammarus* sp.) were found in 28% of stomachs in May, and were consistently found in over 45% of stomachs for the remaining months, reaching a maximum PO of 72% in September. Mysids, also frequently found in stomachs from August to October, had a maximum %O of almost 50% in August.

The percentage by weight, or individual prey wet weight contributions (%W) of the stomachs of 1st year migrants agreed well with the %O results (Figure 4.4). Freshwater aquatic invertebrate larvae and polychaetes contributed the most to the overall wet weight of stomach contents in May. From June to October, over 50% of the overall wet weight of stomachs consisted of amphipods (*Gammarus* sp.). In July, terrestrial insects made up an important proportion of the diet, totalling almost 40% of contents. In addition to amphipods, mysids and polychaetes also contributed relatively highly to the diet of 1st year migrants from August to October. Prey fish were found in only a fraction of stomachs (less than 5%) and contributed only minimally to the overall weight of the contents (less than 5%). If prey fish were to be found in stomachs, they were mostly in trout reaching sizes of 25 cm or larger (Figure 4.5). Overall, amphipods consistently contributed the most to the diet of 1st year migrants in the SMB across months.

As in 1st year migrants, freshwater aquatic invertebrate larvae (over 60%) and polychaetes (over 30%) were frequently observed in stomachs of 2nd year migrants in May (Table 4.3). Amphipods, both *Gammarus* sp. and striped *Gammarus* were also frequently observed in stomachs. In June, amphipods (*Gammarus* sp.; 60%) were found most frequently in stomachs, followed by the presence of freshwater aquatic invertebrate larvae (24%). For the remaining months, amphipods (*Gammarus* sp.) had the highest %O, reaching a maximum of 64% in August. Striped *Gammarus* were also found in over 20% of analysed stomachs. Penaeid shrimp also contributed highly to the diet of 2nd year migrants in July, being found in 17% of the stomachs. Mysids appeared less important in the diet of 2nd year migrants compared to that of 1st year migrants, occurring in less than 20% of stomachs from May to August, excluding September where over 30% of stomachs contained mysids. Contrary to 1st year migrants, prey fishes (all species combined including sticklebacks, banded killifish, sand lance and smelt) were found in stomachs of 2nd year migrants during all months of study, reaching frequencies of 14% and 15% in July and September, respectively.

The %W of 2nd year migrants concurred relatively well with %O estimates (Figure 4.4). In May, freshwater invertebrate larvae, polychaetes and amphipods (*Gammarus sp.)* contributed the most to the overall wet weight of contents. In June, the diet of 2nd year migrants was mostly comprised of amphipods (40%) and polychaetes (20%). For the remaining months, fish constituted a large portion of the diet but were mostly found in trout larger than 25 cm (Figure 4.5), with %W estimates ranging from 17% to 33%. The contribution of amphipods to the diet remained relatively high from July to September, with %W estimates ranging from 23% to 59%. Mysids contributed mostly to the diet of 2nd year migrants in the month of September, with a %W of almost 30%.

ii) Saguenay River

Brook trout samples were obtained throughout the Saguenay River, including sites located in the fjord and its upper section. A total of 181 and 166 stomachs of 1st year and 2nd year migrants were analysed across sites, respectively (Table 4.1). Of these, 4.2% to 46.5% of 1st year migrants were empty, whereas 5.0% to 50% of 2nd year migrants were empty. As observed in the Ste. Marguerite Bay, the %ES of both 1st year and 2nd year migrants was low during the summer months. Of the trout with filled stomachs, 160 were 1st year migrants and these had mean sizes ranging from 135 mm to 273 mm (Table 4.4). 2nd year migrants (n = 138) were larger, ranging from 254 mm to 481 mm in fork length.

Amphipods were the most abundant prey item of 1st year migrants captured throughout the Saguenay River fjord between June and September, with percentage frequencies of occurrence (%O) ranging from 54% to 75% (Table 4.5). Terrestrial insects were also observed frequently throughout the year (excluding the month of August). In August, mysids had the second highest frequency of occurrence at 38%. Interestingly, stomachs of trout captured in the upper sections of the Saguenay River in November frequently contained freshwater aquatic invertebrate larvae (75%) and terrestrial insects (75%), although other prey such as polychaetes, amphipods and fish made up the diet. This diet differs from that observed in the winter months (December to February), where 66% of trout stomachs contained fish, with 32% and 29% of stomachs also containing freshwater invertebrate larvae and amphipods, respectively. As in the SMB, prey fish were mostly found in stomachs of trout larger than 25 cm (Figure 5).

As %O estimates indicated for the diet of 1st year migrants, amphipods contributed the most to the percent wet weight of contents (%W), ranging from 50% to 70% between June and September (Figure 6). Only in June did terrestrial insects contribute strongly to the diet of 1st year migrants, comprising 36% of the total wet weight of contents. Amphipods were clearly the most dominant prey item of 1st year migrants captured in the Saguenay River fjord. In contrast, freshwater aquatic invertebrates, terrestrial insects and fish contributed most to the diet of trout captured in the upper Saguenay sections in November. In winter, prey fish were the dominant item, comprising over 75% of the total content wet weight.

Amphipods, terrestrial insects and fish were most frequently observed in the stomachs of 2nd year migrants captured in the Saguenay River fjord during the month of May and June (Table 4.5). Thereafter, amphipods, terrestrial insects and mysids were most frequently observed in stomachs from trout captured from July to September. Prey fish were found more frequently in stomachs of 2nd year migrants compared to those of 1st year migrants, ranging from 4.8% in August to a maximum of 40% in June. In the upper Saguenay sections, prey fish, appearing mostly in fish larger than 25 cm, were found in over 95% of stomachs, although some stomachs were still found to contain freshwater aquatic larvae. The relative frequency of prey fish found in stomachs of 2nd year migrants increases significantly with size of 2nd year migrants (Figure 4.5; $F_{1,16} = 91.2$, $p < 0.001$, $r^2 = 0.85$).

In the fjord, amphipods and fish contributed the most to the overall wet weight of contents across months, ranging from 26% to 50% and from 16% to 65%, respectively (Figure 4.6). In August, mysids contributed to 34% of the overall wet weight of contents. In contrast, prey fish clearly contributed the most to the overall weight of stomach contents of 2nd year migrants captured in the upper Saguenay River, as prey fish %W ranged from 60% to 99% throughout the year. Freshwater aquatic invertebrate larvae were important in November, contributing to 38% of the overall wet weight of contents.

iii) Ste. Marguerite River

Stomachs of trout from the Ste. Marguerite River were mostly obtained in September and October, with the exception of one sampling year where trout were also sampled in February (Table 4.1). A total of 379 stomachs were obtained from 1st year migrants in September and October, whereas 426 stomachs of 2nd year migrants were analysed, including those in February. For the months of September and October, 44.7% to 56.7% of 1st year migrant stomachs were empty. Similarly, the %ES of 2nd year migrants ranged from 48.6% to 55.0% for September and October, with 90% of stomachs being empty in February. 1st year migrants captured in the Ste. Marguerite River and containing food in their stomachs (n = 156) ranged in size from 241 mm to 262 mm (Table 4.6). From the 2nd year migrants captured in the river, 196 had stomach contents, and they ranged in size from 304 mm to 351 mm.

Freshwater aquatic invertebrates, terrestrial insects and plant material were the most frequently observed items in stomachs of both 1st year and 2nd year migrants captured in September and October (Table 4.7). Salmonid eggs were found in a fraction of 1st year and 2nd year migrants, with the latter showing the highest %O. Although at a small frequency, both fish and small mammal remains were found in the stomachs of trout. By wet weight, terrestrial insects made up the largest portion of the diet of 1st year migrants captured in September, whereas in October, the diet was mostly freshwater aquatic invertebrate larvae and salmonid eggs (Figure 4.7). The %W of 2nd year migrants captured in September was highest for terrestrial insects, small mammal and prey fish remains. In October, both freshwater aquatic invertebrate larvae and salmonid eggs make up a large proportion of the diet.

Stable isotope analysis (SIA)

A significant positive relationship exists between stable carbon signatures ($\delta^{13}C$) and fork length (FL) of 1st year migrants (sea trout) captured in the Ste. Marguerite Bay (SMB) ($\delta^{13}C = 0.064FL - 29.4$; $F_{1,74} = 135.9$, $p < 0.0001$, $r^2 = 0.65$; Figure 4.8). Similarly, a relationship also exists between $\delta^{13}C$ and fork length for resident brook trout ($\delta^{13}C = 0.0062FL - 25.4$; $F_{1,38} = 6.1$, $p = 0.02$, $r^2 = 0.14$). The regressions between $\delta^{13}C$ and fork length differ significantly between sea trout and resident brook trout both in slope (ANCOVA: $F_{1,110} = 26.5$, $p < 0.005$) and elevation (ANCOVA: $F_{1,110} = 6.6$, $p = 0.012$).

Significant relationships also exist between stable nitrogen signatures (δ^{15}N) and FL for sea trout ($\delta^{15}N = 5.2 + 0.036FL – 0.0001FL^2$; $F_{2,74} = 18.9$, $p < 0.001$, $r^2 = 0.34$) and for resident brook trout ($\delta^{15}N = 6.0 + 0.0051FL$; $F_{1,35} = 4.8$, $p = 0.04$, $r^2 = 0.10$). A significant difference in intercept exists between BSM trout up to 20 cm and resident brook trout (ANCOVA: $F_{1,108} = 176.5$, $p < 0.005$).

Marine invertebrate prey items captured in the SMB had signatures ranging between –17.8‰ and –15.6‰ for carbon, and between 5.1‰ and 8.5‰ for nitrogen (Figure 4.9). Signatures of prey fish, including sticklebacks, banded killifish and smelt were enriched in nitrogen compared to the marine invertebrate prey items, ranging between 10.5‰ and 14.0‰. Carbon was slightly depleted in comparison with the invertebrate prey. Freshwater insect larvae had typical signatures observed in freshwater systems. Amphipods obtained from Anse-de-Pierre (AP), a more saline site located downstream of the SMB had enriched carbon signatures but depleted nitrogen signatures compared to those of the SMB.

Upon sea entry, 1st year migrants captured in the SMB in May had mean δ^{13}C and δ^{15}N signatures of –25.1‰ and 7.7‰, respectively. By October, trout mean δ^{13}C and δ^{15}N signatures rose to –14.5‰ and 9.1‰, respectively and as expected, nitrogen signatures are 3.3‰ above marine invertebrate prey items including amphipods and mysids. Sea age 1 fish had mean δ^{13}C and δ^{15}N signatures of –14.7‰ and 9.8‰, respectively while 2nd year migrants (both adult SMR system spawners and non-spawners) have signatures of about –17.8‰ for carbon and about 12.3‰ for nitrogen.

Discussion

Anadromous brook trout following their migration from the Ste. Marguerite River (SMR) to the Saguenay River more than double their size over the course of a single summer spent at sea (Lenormand et al.

2004). It is expected that in order for trout to experience such rapid growth rates, the sea must provide better feeding opportunities than what is available in freshwater. Such opportunities may come in the form of overall higher productivity and/or a higher occurrence of large prey (Keeley & Grant 2001), which also includes the increased accessibility to such prey. Our results confirms this prediction, as the Ste. Marguerite Bay (SMB), the trouts' initial site of sea entry, exhibits higher food availability than the SMR. Mean invertebrate biomass estimates did not differ between the river and the SMB in either May or August. However, invertebrates in the SMB were 2.4 times and 2.2 times larger than those found in the river in both May and August, respectively. Potentially having immediate access to more energetically profitable prey (larger prey) permits an efficient growth return, since fewer items need to be consumed (and thus captured) to acquire the same amount of energy (Pazzia et al. 2002, Sherwood et al. 2002). Moreover, growth benefits are materialized more rapidly since the migration, and thus shift to larger prey, follows soon after a period of starvation.

Interestingly, a wider range of prey sizes was also observed in the bay in comparison with that found in the river indicating, that newly arrived fish are presented with a broad range of feeding opportunities. The presence of a larger available prey spectrum is also important as it can serve the needs of a wider predator size range, and consequently reduce intraspecific competition between individuals for similarly sized prey, because fish generally consume larger prey sizes with increasing body size when available (Werner & Gilliam 1984, Keeley & Grant 1997, Keeley & Grant 2001).

Anadromous brook trout migrating to sea for the first time (1st year migrants) appear to capitalize almost immediately on the better feeding opportunities available in the SMB. Less than 15% of trout sampled in the bay contained an empty stomach, suggesting high feeding activity. Their initial food at sea reflects the transition to a saline habitat from a freshwater habitat. Upon sea entry in May, 1st year migrants initially consume freshwater derived prey, a conclusion based upon the frequency of occurrence and percent wet weight contribution of aquatic insect larvae. High occurrences of aquatic invertebrate larvae in stomachs of brook trout outmigrating from Newfoundland rivers has also been observed, with *Gammarus* sp. being the most important consumed crustacean (O'Connell 1982). Other studies have also reported a higher aquatic invertebrate contribution to the diet in the spring, but the trout rapidly shift to marine prey items (like amphipods) almost immediately (Gaudreault et al. 1982). This initial high occurrence of freshwater derived prey in addition to polychaetes, located mostly in the sand and clay flats surrounding the main river channel outflow (G.R. Morinville, personal observation), agrees with their need to remain under the influence of the natal river to minimize the costs associated with osmoregulation prior to their acclimatization to the salinities and temperatures of the new habitat (McCormick et al. 1985, Lenormand et al. 2004).

By June, 1st year migrants inhabiting the SMB quickly shift to a diet composed of larger prey, obtaining over 60% of their energy from amphipods and polychaetes within a few weeks of sea entry, consistent with previous reports of feeding behaviours (White 1940). This feeding pattern is observed in trout exploiting the bay throughout the remaining summer months and early fall, where at least 50% of the energy is derived from amphipods, in addition to prey items such as mysids and polychaetes. Amphipods, in addition to sand lance were the dominant prey items in trout sampled between late August and early October in the Matamek River estuary (Whoriskey et al. 1981). The frequent ingestion of mysids may also suggests feeding near the surface (Montgomery et al. 1990). Other than a few occurrences of sticklebacks and sand lance in the spring and fall, fish are infrequently encountered in stomachs of 1st year migrants captured in the Ste. Marguerite Bay. Similarly, 2nd year migrants, having spent at least one previous summer at sea, return to the deeper waters of the Saguenay fjord passing through the SMB during the month of May. Like 1st year migrants, they initially feed on polychaetes and aquatic invertebrate larvae during their descent into the bay although by June, their diet is composed mostly of marine crustaceans (amphipods).

1st year migrants that venture into the Saguenay fjord also have a diet composed mainly of amphipods, contributing over 50% to their diet, in addition to terrestrial insects and mysids. These trout will acquire an orange pink flesh over the course of the summer, confirming a diet composed of carotenoid-rich marine crustaceans (Peterson et al. 1966). No piscivorous 1st year migrants feeding in the fjord during the summer were ever encountered in the 5 years of study. This contrasts the diet of 2nd year migrants inhabiting the fjord and upstream regions where piscivory strongly contributes to the diet of 2nd year migrants. Similarly, fish makes up only a minor component of the diet of 1st year Arctic charr and St. John brook trout migrants whereas veteran migrants (2nd year migrants) feed more heavily on fish (Gaudreault et al. 1982, Rikardsen 2000).

The rapid shift to marine prey items in 1st year migrants is clearly observed with stable isotope signatures of trout muscle tissues. Between May and October, the $\delta^{13}C$ signature of 1st year migrants increased by more than 10‰ from a freshwater signature of –25‰ to a more marine signature of –14.5‰. This change was detected with increasing trout size. As expected, such abrupt changes in $\delta^{13}C$ are not observed in resident brook trout with increasing size. The diet of trout remaining in freshwater streams, as revealed by stomach content analyses, indicates no important change of diet with ontogeny since trout continue to feed mostly upon freshwater aquatic invertebrates and some terrestrial insects (G.R. Morinville, unpublished data).

$\delta^{15}N$ signatures of 1st year migrants also change with size, increasing from 7.7‰ to 9.1‰ by October. Slight increases are also observed in resident brook trout, possibly reflecting a shift to larger and slightly higher level prey items, such as predatory caddisflies. In the SMB, amphipods have δ^{13}C and δ^{15}N signatures averaging –16‰ and 5.8‰, respectively while mysids have signatures averaging –16.6‰ and 6.1‰. Given the expected fractionation between prey and predator of about 0-1‰ for carbon and of about 3-4‰ for nitrogen (DeNiro & Epstein 1978, Minagawa & Wada 1984, Peterson & Fry 1987) and the information obtained from stomach content analyses, amphipods and mysids appear to be the main prey items from which 1st year migrants obtain their energy.

Trout (1st year migrants) that migrate to the upstream sections of the Saguenay River to overwinter in freshwater have a diet consisting primarily of fish and freshwater aquatic invertebrate larvae in late fall followed by a diet made up almost entirely of fish (mostly smelt) in the winter months. This diet shift to piscivory occurs when sea trout reach sizes of 20 cm, with a relative frequency of piscivory of 50% occurring at 25 cm. Similarly, prey fish were also found to be predominant in stomachs of trout, larger than 30 cm in length, captured in coastal waters of Newfoundland, Richmond Gulf, Quebec and the St. Jean River, Quebec (Castonguay et al. 1982, Dutil & Power 1980, O'Connell 1982). Trout migrating to the upper Saguenay instead of returning to their natal river remain actively feeding (less than 20% empty stomachs), obtaining high-energy returns throughout the winter months and allowing them to maintain their condition. In contrast, those returning to their natal river during fall decrease their feeding activity (50% empty stomachs), feeding mainly on small, low energy prey including terrestrial insects and aquatic invertebrate larvae. Traces of fish (either trout or salmon) and small mammals can be noted in a fraction of stomachs, in addition to salmonid eggs supporting their opportunistic feeding behaviour (Power 1980), although sea trout still tend to be of poor condition upon their return to sea following winter (Lenormand et al. 2004).

Interestingly, trout having spent the previous summer at sea and captured the following spring have a similar δ^{13}C signature as those captured at the end of October, indicating no change in feeding habits or habitats over winter. The enriched δ^{15}N signature in comparison with the October trout may reflect a starvation effect leading to enrichment (Vander Zanden & Rasmussen 2001), inferred from the observation that trout descending the river in spring are of lower condition than those that overwintered in and continued to feed in the upper Saguenay (Lenormand et al. 2004). The effect of starvation may also explain the 1‰ difference in δ^{15}N observed between 1st year migrants and residents at small sizes as differences in diet during their coexistence in streams are unlikely.

Although δ^{15}N of 1st year migrants increases with size during the course of the summer, the change is not linear. It follows a curvilinear pattern with increasing size, reaching a high at around 20cm in length and decreasing slightly thereafter. This non-linear pattern most likely reflects changes in their feeding location rather than a change in trophic level. As mentioned previously, trout during the summer exit the SMB and migrate to neighbouring sites across the Saguenay including the downstream Anse de Pierre (AP) and Anse de Roche (AR) sites. 1st year migrants initially captured in the SMR have been frequently recaptured in these locations (Lenormand et al. 2004). As indicated by SIA, migrants continue to feed heavily on marine amphipods at these sites and throughout the Saguenay fjord. Marine amphipods collected in AP were found to be more enriched in δ^{13}C but lighter in δ^{15}N compared to those in the SMB. It is thus quite likely that trout, when feeding outside of the SMB and in the fjord, acquire the signature of amphipods found in sites such as AP prior to their return to the SMB in the fall, leading to the observed curvilinear pattern with increasing size. This is likely as trout (not necessarily originating from the SMR system) captured in August in AP had lower δ^{15}N signatures than those captured in the SMB in July.

It is important to mention that 2nd year migrants captured in the SMB from July to September most likely did not remain in the bay for the entire summer, but rather are returning from migrations to the greater Saguenay River. These trout are possibly future spawners (Lenormand et al. 2004) and may have started reducing their energy intake upon return to the bay, although they may continue to eat amphipods and some fish. This has been previously reported in sea trout populations of the Moser River, Nova Scotia where over 50% had empty stomachs and of those with contents, 27% were almost empty (Wilder 1952). Indeed, the percentage of empty stomachs of 2nd year migrants is highest in the bay during the months of August and September, reaching levels of almost 40%. Those that continue upstream into the SMR presumably continue to reduce their feeding activity even further, as over 50% of captured trout had empty stomachs in the fall. Over 80% of sea trout likely to spawn and captured on the spawning grounds also had empty stomachs (G.R. Morinville and J.B. Rasmussen, unpublished data). Similarly, White (1940) also reported no food in the stomachs of ascending trout. In winter, over 75% of 2nd year migrants captured in the SMB or SMR had empty stomachs, suggesting older migrants in winter virtually cease feeding until the following spring. This reduced feeding behaviour may explain the low condition factor of trout descending the river in early spring (Lenormand et al. 2004).

Anadromous brook trout have previously been considered as being largely piscivorous (Power 1980), although these conclusions were based on earlier reports of feeding which failed to take into consideration the size at which piscivory begins or whether fish eating occurred on a seasonal basis. We were able to show that for all sampled habitats including the Ste. Marguerite Bay and the Saguenay River, the occurrence of piscivory arose only when a fish surpassed a length of 20 cm, with the majority of occurrences arising at 25 cm, which is consistent with other salmonid populations (Keeley & Grant 2001). This threshold of piscivory was consistent regardless of whether trout were in their first year at sea or greater. Moreover, high occurrences of piscivory generally occurred in specific locations of the Saguenay River, notably the upper Saguenay River (CHIC and VDLB sites) and during specific seasons, winter and spring, with rainbow smelt being the dominant fish species in stomachs of trout (G.R. Morinville, personal observation). In winter, smelt may be more susceptible to predation by trout as the activity of smelt is lowered under ice cover (Vinni et al. 2005) whereas in the spring, smelt migrate upstream towards their spawning grounds in streams and rivers providing another opportunity for sea trout feeding (Pigeon et al. 1998).

Stable isotope signatures of SMR adult migrant spawners and non-spawners indicate that the sea trout never fully become piscivorous on smelt. This can be inferred from the dual isotope approach where migrants have lighter δ^{13}C (difference of 2.5‰) but similar δ^{15}N signatures to upper Saguenay River smelt. If smelt had contributed fully to the diet of sea trout, we would expect trout to attain a δ^{15}N signature of about 3.4‰ above the smelt signature given the fractionation between predator and prey (Minagawa & Wada 1984, Vander Zanden & Rasmussen 2001), but this is not observed. Muscle tissue δ^{15}N signatures of sea trout from the SMR system seldom go beyond 14‰ (G.R. Morinville and J.B. Rasmussen, unpublished data). Such signatures are largely supported by SIA as 2nd year migrants continue to feed on amphipods and mysids during the summer across the SMB and fjord. Sea trout of the St. Jean River (Quebec) have also been reported in feed heavily on amphipods throughout the year, even at large sizes, although fish made up a larger part of the diet during the summer (Gaudreault et al. 1982). Alternatively, migrants may also be feeding heavily upon sand lance, since δ^{15}N signatures of sand lance are approximately 2.8‰ lower than that of adult migrants.

Of interest, few competitors to brook trout are present at their initial site of sea entry. Both sticklebacks and banded killifish can be found in the SMB, with sticklebacks being the most abundant permanent resident species of the bay (Mousseau & Dodson 1996). However, threespine sticklebacks in the bay are relatively small, with sizes ranging between 5 cm and 8 cm (M. Bélanger and J.B. Rasmussen, unpublished data). Both SCA and SIA indicate that sticklebacks captured in the SMB between May and July consume mostly marine amphipods and freshwater aquatic invertebrate larvae, depending on their proximity to freshwater influxes (M. Bélanger and J.B. Rasmussen, unpublished data). 1st year migrants were also found to eat such prey items, although migrants entering the SMB are, on average, larger than sticklebacks, ranging in size from 7 to 17 cm (Lenormand et al. 2004). Given their larger size and the wider prey spectrum available in the bay, it is unlikely that trout strongly compete with sticklebacks for the same prey size categories. However, stronger competitive interactions could develop over time if trout were to migrate at increasingly smaller sizes, a situation that could arise following increasingly poor growth conditions in freshwater prior to migration.

In conclusion, marine crustaceans, mostly amphipods, are the most important prey item in the diet of 1st year migrants, allowing them to experience rapid growth rates during their first summer spent at sea. During their ontogeny, migrants, whether they are in their first year at sea or greater, gradually shift their dependence to prey fish at the threshold size of 25 cm. 1st year migrants will generally reach these sizes after their first summer of growth, allowing them to benefit from energy rich fish (mostly smelt) in the first winter provided they migrate to the upper Saguenay River for winter. The highest levels of piscivory occurred in the upper Saguenay River sites, signifying this region as an essential feeding ground for sea trout allowing for continual growth. Of concern, the agglomeration of sea trout in these feeding grounds during winter and early spring makes sea trout especially vulnerable to overfishing and habitat destruction. As a consequence, strict regulations need to be implemented, including both the protection of feeding grounds and limits to fishing during these months. Additional regulations protecting the prey base of sea trout also need to be implemented if we are to preserve the anadromous form.

Acknowledgements

We thank S. Bodmer-Roy, A. Boivin, A. DuCap, M. Dunn, S. Lenormand, K. Lunn, S. Marshal, A. Ménard, C. Mimeault, V. Thériault for their field assistance and/or laboratory help. We are also grateful to S. Lenormand for providing us the ages of most trout captured in this study. This work would not have been possible without the help of the Saguenay region brook trout anglers who repeatedly contributed to the mark-recapture program, providing us many samples. This study is a contribution to the program of CIRSA (Centre Interuniversitaire sur le Saumon Atlantique). Funding for this project was provided to J.B.R. by the Natural Sciences and Engineering Research Council of Canada (NSERC; Strategic Grant and Collaborative Special Projects), the Foundation de la Faune du Québec, the Government of Quebec (FAPAQ), the Government of Canada (Economic development), the financial partners of CIRSA Inc., and graduate fellowships to G.R.M. (Vineberg McGill Major, McConnell Family McGill Major, and McGill's Department of Biology graduate fellowship).

References Cited

Boisclair, D. & W.C. Leggett. 1985. Rates of food exploitation by littoral fishes in a mesotrophic north-temperate lake. Canadian Journal of Fisheries and Aquatic Sciences 42: 556-566.

Castonguay, M., G.J. Fitzgerald & Y. Cote. 1982. Life-history and movements of anadromous brook charr, *Salvelinus fontinalis*, in the St-Jean River, Gaspé, Québec. Canadian Journal of Zoology 60: 3084-3091.

Chassé, R. & R. Côté. 1991. Aspect of winter primary production in the upstream section of the Saguenay Fjord. Hydrobiologia 215: 251-260.

Clark, M.R. 1985. The food and feeding of seven fish species from the Campbell Plateau, New Zealand. New Zealand Journal of Marine and Freshwater Research 19: 339-363.

DeNiro, M.J. & S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42: 495-506.

Dutil, J.D. & G. Power. 1980. Coastal populations of brook trout, *Salvelinus fontinalis*, in Lac Guilaume-Delisle (Richmond Gulf) Quebec. Canadian Journal of Zoology 58: 1828-1835.

Gaudreault, A., M. Castonguay & G.J. Fitzgerald. 1982. Répartition des ressources et changements saisonniers de l'alimentation d'ombles de fontaine anadromes, *Salvelinus fontinalis*. Canadian Journal of Zoology 60: 3068-3070.

Gibson, R.J. & F.G. Whoriskey. 1980. An experiment to induce anadromy in wild brook trout in a Quebec river on the north shore of the Gulf of St. Lawrence. Le Naturaliste Canadien 107: 101-110.

Gross, M.R. 1987. Evolution of Diadromy in Fishes. American Fisheries Society Symposium 1: 14-25.

Gross, M.R., R.M. Coleman & R.M. McDowall. 1988. Aquatic Productivity and the Evolution of Diadromous Fish Migration. Science 239: 1291-1293.

Hyslop, E.J. 1980. Stomach contents analysis-a review of methods and their application. Journal of Fish Biology 17: 411-429.

Keeley, E.R. & J.W.A. Grant. 1997. Allometry of diet selectivity in juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 54.

Keeley, E.R. & J.W.A. Grant. 2001. Prey size of salmonid fishes in streams, lakes, and oceans. Canadian Journal of Fisheries and Aquatic Sciences 58: 1122-1132.

Kerr, S.R. 1971. Prediction of growth efficiency in nature. Journal of the Fisheries Research Board of Canada 28: 809-814.

Kerr, S.R. & R.A. Ryder. 1977. Niche theory and percid community structure. Journal of the Fisheries Research Board of Canada 34: 1952-1958.

Lenormand, S. 2003. Évolution de l'anadromie et stratégie de reproduction chez l'omble de fontaine (*Salvelinus fontinalis*). Doctoral thesis, Université Laval, Québec. 122 pp.

Lenormand, S., J.J. Dodson & A. Ménard. 2004. Seasonal and ontogenetic patterns in the migration of anadromous brook charr (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 61: 54-67.

Lesueur, C. 1993. Compte rendu des résultats obtenus lors de l'étude de l'omble de fontaine anadrome de la rivière Ste-Marguerite (Saguenay) en 1992, Association de la rivière Ste-Marguerite, Sacré-Coeur, Québec.

McCormick, S.D., R.J. Naiman & E.T. Montgomery. 1985. Physiological smolt characteristics of anadromous and non-anadromous brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 42: 529-538.

Minagawa, M. & E. Wada. 1984. Stepwise enrichment of N-15 along food chains - Further Evidence and the relation between delta-N-15 and animal age. Geochimica et Cosmochimica Acta 48: 1135-1140.

Mittelbach, G.G. & L. Persson. 1998. The ontogeny of piscivory and its ecological consequences. Canadian Journal of Fisheries and Aquatic Sciences 55: 1454-1465.

Montgomery, W.L., S.D. McCormick, R.J. Naiman, F.G. Whoriskey & G. Black. 1990. Anadromous behaviour of brook charr (*Salvelinus fontinalis*). Polski Archiwum Hydriobiologii 37: 43-61.

Morinville, G.R. & J.B. Rasmussen. 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 60: 401-410.

Mousseau, L. & J.J. Dodson. 1996. Caractérisation de la biodiversité animale dans la Baie Ste-Marguerite, Saguenay. pp. 1-36, Centre Interuniversitaire de Recherche sur le Saumon atlantique, Ste-Foy.

O'Connell, M.F. 1982. The biology of anadromous *Salvelinus fontinalis* (Mitchill, 1815) and *Salmo trutta* (Linnaeus, 1758) in river systems flowing into Placentia Bay and St. Mary's Bay, Newfoundland. M.Sc., Memorial University of Newfoundland, St. John's. 253 pp.

Pazzia, I., M. Trudel, M. Ridgway & J.B. Rasmussen. 2002. Influence of food web structure on the growth and bioenergetics of lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 59: 1593-1605.

Peterson, B.J. & B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18: 293-320.

Peterson, D.H., H.K. Jager & G.M. Savage. 1966. Natural colouration of salmonids using xanthophylls. Transactions of the American Fisheries Society 35: 408-415.

Pigeon, D., J.J. Dodson & L. Bernatchez. 1998. A mtDNA analysis of spatiotemporal distribution of two sympatric larval populations of smelt (*Osmerus mordax*) in the Ste. Lawrence River estuary, Quebec, Canada. Canadian Journal of Fisheries and Aquatic Sciences 55: 1739-1747.

Power, G. 1980. The brook charr, *Salvelinus fontinalis*. pp. 141-203. *In:* E.K. Balon (ed.) Charrs, salmonid fishes of the genus *Salvelinus*. W. Junk, The Hague, Netherlands.

Rikardsen, A.H., and Elliott, J.M. 2000. Variations in juvenile growth, energy allocation and life-history strategies of two populations of Arctic charr in North Norway. Journal of Fish Biology 56: 328-346.

Saunders, R.L., B.C. Muise & E.B. Hendersen. 1975. Mortality of salmonids cultured at low temperature in sea water. Aquaculture 5: 243-252.

Sherwood, G.D., I. Pazzia, A. Moeser, A. Hontela & J.B. Rasmussen. 2002. Shifting Gears: Enzymatic Evidence for the energetic advantage of switching diet in wild-living fish. Canadian Journal of Fisheries and Aquatic Sciences 59: 229-241.

Smith, M.W. & J.W. Saunders. 1958. Movements of brook trout, *Salvelinus fontinalis* (Mitchill) between and within fresh and salt water. Journal of the Fisheries Research Board of Canada 15: 1403-1449.

Thériault, V. & J.J. Dodson. 2003. Body size and the adoption of a migratory tactic in brook charr. Journal of Fish Biology 63: 1-16.

Vander Zanden, M.J. & J.B. Rasmussen. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: Implications for aquatic food web studies. Limnology and Oceanography 46: 2061-2066.

Vinni, M., J. Lappalainen & J. Horppila. 2005. Temporal and size-related changes in the frequency of empty stomachs in smelt. Journal of Fish Biology 66: 578-582.

Wañkowski, J.W.J. & J.E. Thorpe. 1979. The role of food particle size in the growth of juvenile Atlantic salmon (*Salmo salar* L.). Journal of Fish Biology 14: 351-370.

Werner, E.E. & J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15: 393-425.

White, H.C. 1940. Life history of sea-running brook trout (*Salvelinus fontinalis*) of Moser River, N.S. Journal of Fisheries Research Board of Canada 5: 176-186.

White, H.C. 1942. Sea life of the brook trout (*Salvelinus fontinalis*). Journal of Fisheries Research Board of Canada 5: 471-473.

Whoriskey, F.G., R.J. Naiman & W.L. Montgomery. 1981. Experimental sea ranching of brook trout, *Salvelinus fontinalis* Mitchill. Journal of Fish Biology 19: 637-651.

Wilder, D.G. 1952. A comparative study of anadromous and freshwater populations of brook trout (*Salvelinus fontinalis*). Journal of the Fisheries Research Board of Canada 9: 169-203.

Table 4.1 Number of analysed stomachs (N) and percentage of empty stomachs (% ES; ± 1 SE) from 1st year and 2nd year migrant brook trout captured in the Ste. Marguerite Bay (SMB), the upper Saguenay (Upper) and fjord (Fjord), and the Ste. Marguerite River (SMR) in years 1998 to 2002.

1st year migrants				**2nd year migrants**			
Month	**Site**	**N**	**% Empty**	**Month**	**Site**	**N**	**% Empty**
	---	---	---	Mar-May	Upper	17	15.2 (8.8)
	---	---	---	Apr	SMB	5	40
May	SMB	153	13.4 (4.6)	May	SMB	263	19.1 (2.5)
	---	---	---		Fjord	14	5.0 (5.0)
Jun	SMB	235	20.1 (6.2)	Jun	SMB	106	14.7 (8.0)
	Fjord	14	4.2 (2.9)		Fjord	57	22.9 (15.5)
	Upper	---	---	Jun-Jul	Upper	5	12.5 (12.5)
Jul	SMB	72	18.4 (8.5)	Jul	SMB	27	15.9 (8.3)
	Fjord	66	9.8 (6.1)		Fjord	32	8.3 (5.3)
Aug	SMB	60	8.8 (2.5)	Aug	SMB	19	39.2 (14.2)
	Fjord	53	22.1 (19.4)		Fjord	13	11.1 (11.1)
Sept	SMB	283	20.1 (5.8)	Sept	SMB	54	38.7 (9.8)
	Fjord	18	6.7 (6.7)		Fjord	6	16.7 (16.7)
	SMR	170	44.7 (10.3)		SMR	204	55.0 (4.2)
Oct	SMB	169	15.0 (7.8)	Oct	SMB	5	20
Oct-Nov	Upper	11	46.5 (3.6)		---	---	---
Oct	SMR	209	56.7 (9.6)	Oct	SMR	212	48.6 (2.9)
	---	---	---	Nov	Upper	4	50
Dec-Feb	Upper	19	19.4 (10.0)	Dec-Feb	Upper	18	26.9 (10.9)
	---	---	---	Jan-Feb	SMB	13	76.2 (9.6)
	---	---	---	Feb	SMR	10	90

Table 4.2 Sample size (N) and mean size (± 1 SD) of 1st year and 2nd year brook trout migrants captured in the Ste. Marguerite Bay (SMB) in May to October in years 1998 to 2002 and containing food in stomach.

		1st year migrants		**2nd year migrants**	
Year	**Month**	**N**	**Mean size (mm)**	**N**	**Mean size (mm)**
1998	May	6	148 (14.9)	23	220 (44.5)
1999		12	114 (29.2)	76	240 (44.0)
2000		14	117 (24.2)	31	337 (86.7)
2001		86	118 (25.5)	71	248 (61.9)
2002		6	160 (16.1)	15	229 (32.9)
1998	June	23	177 (25.8)	10	224 (35.7)
1999		33	149 (34.1)	16	231 (40.3)
2000		49	122 (35.5)	47	247 (43.1)
2001		62	118 (28.2)	19	235 (57.6)
2002		19	121 (29.7)	---	---
1998	July	---	---	---	---
1999		9	147 (21.1)	---	234 (18.9)
2000		12	155 (33.0)	15	264 (35.4)
2001		17	122 (20.8)	4	256 (71.9)
2002		22	135 (28.6)	---	---
1998	Aug	15	212 (13.8)	---	---
1999		25	196 (25.9)	---	266 (24.4)
2000		14	177 (63.6)	4	274 (22.0)
2001		---	---	---	---
2002		---	---	---	---
1998	Sep	80	231 (32.6)	4	303 (10.6)
1999		78	221 (28.7)	11	275 (30.6)
2000		47	228 (32.1)	18	312 (26.6)
2001		11	201 (21.2)	3	304 (18.0)
2002		22	204 (33.8)	---	---
1998	Oct	56	228 (22.3)	---	---
1999		39	226 (22.5)	---	---
2000		14	211 (24.2)	---	---
2001		11	191 (25.7)	---	---
2002		26	226 (29.6)	---	---

Table 4.3 Number (N) of stomachs filled with contents and percent occurrence (%O) of prey types found in stomachs (± 1 SE) from May to October (number of pooled years) of 1st year and 2nd year brook trout migrants captured in the Ste. Marguerite Bay (SMB) in years 1998 to 2002.
The two highest prey occurrences for each month are shown in bold.

	Month	N	FW	Co	Ter	Am	SAm	Po	My	Pa	Fish	Other
1st	May (5)	124	**63.6**	2.4	3.2	27.8	13.8	**31.7**	9.5	0	0.23	11.8
year			(12.7)	(1.6)	(3.2)	(11.8)	(6.0)	(13.4)	(3.2)	(0)	(0.23)	(5.2)
	Jun (5)	186	**26.4**	9.0	9.0	**44.7**	4.6	19.4	4.1	0.87	2.4	7.3
			(8.8)	(2.6)	(3.3)	(6.9)	(1.8)	(7.1)	(1.5)	(0.87)	(1.0)	(2.9)
	Jul (4)	60	4.1	7.6	**49.2**	**59.8**	0	12.2	5.8	2.8	0	1.5
			(2.8)	(4.4)	(17.1)	(15.0)	(0)	(8.3)	(2.1)	(2.8)	(0)	(1.5)
	Aug (3)	54	9.8	0	6.1	**66.4**	6.1	8.5	**48.8**	(1.3	0	5.8
			(3.1)	(0)	(4.3)	(7.8)	(3.5)	(6.6)	(4.7)	(1.3)	(0)	(0.94)
	Sept (5)	237	10.4	0	11.4	**71.8**	9.8	17.3	**28.7**	3.2	3.6	6.5
			(3.0)	(0)	(8.6)	(7.5)	(3.7)	(4.9)	(9.3)	(1.6)	(1.8)	(3.2)
	Oct (5)	146	11.3	1.8	25.4	**68.3**	19.8	21.2	**28.7**	0	2.3	8.1
			(2.6)	(1.8)	(16.3)	(7.1)	(5.9)	(6.2)	(9.4)	(0)	(1.5)	(3.0)
2nd	May (5)	216	**55.7**	0.81	5.9	26.3	28.5	**45.1**	8.1	0.26	4.4	4.3
year			(14.4)	(0.53)	(2.7)	(8.1)	(6.3)	(11.3)	(3.2)	(0.26)	(2.4)	(3.0)
	Jun (4)	91	**24.4**	4.6	9.0	**60.0**	6.8	13.5	19.6	1.6	4.4	9.2
			(8.7)	(2.2)	(3.1)	(8.6)	(4.2)	(4.8)	(5.4)	(1.6)	(2.2)	(2.3)
	Jul (3)	21	13.5	5.1	13.5	**56.4**	2.6	10.9	13.5	**16.7**	13.5	0.38
			(7.3)	(5.1)	(7.3)	(6.4)	(2.6)	(7.4)	(7.3)	(16.7)	(7.3)	(0.36)
	Aug (2)	11	7.1	0	16.7	**64.3**	**21.4**	0	0	0	7.1	0.25
			(7.1)	(0)	(16.7)	(35.7)	(21.4)	(0)	(0)	0)	(7.1)	(0.025)
	Sept (4)	36	30.9	0	22.2	**36.7**	11.3	12.0	**31.5**	0	15.0	2.3
			(15.4)	(0)	(11.8)	(15.7)	(5.2)	(7.4)	(5.2)	(0)	(5.3)	(2.3)

FW: freshwater aquatic invertebrate larvae; Co: coleopteran; Ter: terrestrial insects excluding coleopteran; Am: amphipod; SAm: striped amphipod; Po: polychaete; My: Mysid; Pa: penaeid shrimp; Fish: includes sticklebacks, sand lance, smelt and killifish; Other: includes plant matter, winged insects (newly emerged) and all other miscellaneous items.

Table 4.4 Number of stomachs filled with contents (N) and mean size (± 1 SD) of 1st year and 2nd year brook trout migrants captured from spring to winter in various sites located throughout the Saguenay River fjord and upstream Saguenay River in pooled years 1998 to 2002.

	1st year migrants			**2nd year migrants**		
Month	**Site**	**N**	**Mean size (mm)**	**Site**	**N**	**Mean size (mm)**
Mar	---	---	---	CHIC	2	Na
Apr	---	---	---	CHIC	1	283
May	---	---	---	AR	9	346 (107.8)
	---	---	---	AP	4	274 (93.3)
	---	---	---	VDLB	2	388 (46.7)
	---	---	---	CHIC	8	382 (68.9)
June	AR	11	173 (17.3)	AR	17	303 (98.8)
	AP	2	155 (1.4)	AS	10	254 (43.5)
	---	---	---	AP	7	271 (30.3)
	---	---	---	PS	4	Na
	---	---	---	ASE	9	432 (64.9)
	---	---	---	CHIC	3	408 (106.5)
				SRN	2	454 (18.5)
July	ASE	3	180 (16.7)	ASE	8	334 (65.1)
	AI	11	142 (23.9)	AR	7	283 (24.5)
	AR	24	177 (43.9)	AS	8	269 (52.4)
	AS	23	159 (30.1)	AP	6	282 (25.2)
	---	---	---	VDLB	1	481
Aug	AP	18	164 (29.6)	AS	7	274 (48.7)
	AS	8	198 (29.6)	AP	3	268 (10.0)
	AI	2	214 (20.5)	ASE	2	308 (21.2)
	AL	6	188 (64.9)	---	---	---
	AG	13	135 (9.2)	---	---	---
Sep	AS	4	201 (29.5)	APOR	2	287 (24.8)
	AI	2	234 (31.8)	AS	2	285 (20.5)
	APOR	11	229 (12.2)	---	---	---
Oct	CHIC	4	219 (32.1)	---	---	---
Nov	CHIC	2	191 (27.6)	CHIC	2	356 (5.7)
Dec	CHIC	3	na	VDLB	1	345
	---	---	---	CHIC	5	365 (27.6)
Jan	CHIC	9	247 (25.9)	CHIC	2	389 (102.5)
Feb	CHIC	4	273 (23.2)	CHIC	4	390 (38.4)

Table 4.5 Number (N) of stomachs filled with contents and percent occurrence (%O) of prey types found in stomachs (± 1 SE) from spring to winter (number of pooled sites) of 1st year and 2nd year brook trout migrants captured in sites located in the Saguenay River fjord and upper Saguenay River in years 1998 to 2002.
The two highest prey occurrences for each month are in bold.

	Site	Month	N	FW	Co	Ter	Am	SAm	Po	My	Pa	Fish	Other
1st year	Saguenay fjord	Jun (2)	13	12.5 (8.8)	8.3 (5.9)	**62.5** (26.5)	**54.2** (2.9)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.0 (0.73)
	Saguenay fjord	July (4)	61	6.3 (4.3)	9.2 (8.1)	**16.4** (7.2)	**75.0** (6.3)	0 (0)	12.9 (8.1)	9.6 (3.9)	0 (0)	0 (0)	3.9 (2.4)
	Saguenay fjord	Aug (5)	47	2.2 (2.2)	3.8 (2.4)	7.0 (3.1)	**61.9** (12.0)	2.6 (2.6)	16.3 (11.8)	**37.8** (8.4)	0.87 (0.87)	0 (0)	4.8 (3.0)
	Saguenay fjord	Sep (3)	17	16.7 (16.7)	0 (0)	**23.3** (14.5)	**57.9** (4.1)	0 (0)	19.7 (15.4)	12.1 (12.1)	9.7 (5.8)	0 (0)	4.1 (4.1)
	Upper Saguenay	Oct/Nov (2)*	6	**75.0** (25.0)	0 (0)	**75.0** (25.0)	12.5 (12.5)	0 (0)	12.5 (12.5)	0.50 (0.50)	0 (0)	12.5 (12.5)	0 (0)
	Upper Saguenay	Dec/Jan/ Feb (3)*	16	**31.5** (11.3)	11.1 (11.1)	11.1 (11.1)	28.7 (23.4)	20.4 (15.2)	0 (0)	14.8 (9.8)	0 (0)	**65.7** (16.7)	18.5 (9.8)
2nd year	Saguenay fjord	May (2)	13	17.5 (7.5)	0 (0)	10.0 (10.0)	**52.5** (22.5)	0 (0)	17.5 (7.5)	0 (0)	0 (0)	**37.5** (12.5)	0 (0)
	Saguenay fjord	June (6)	49	5.0 (2.2)	11.4 (7.9)	**30.6** (13.0)	27.4 (9.6)	0 (0)	7.9 (5.0)	14.1 (7.5)	0.79 (0.79)	**40.1** (18.4)	11.4 (5.0)
	Saguenay fjord	July (4)	29	9.0 (5.9)	5.9 (3.4)	**43.8** (7.7)	**41.7** (15.3)	0 (0)	13.5 (8.9)	19.8 (7.9)	0 (0)	14.2 (10.5)	5.9 (3.4)
	Saguenay fjord	Aug (3)	12	0 (0)	0 (0)	9.5 (9.5)	**57.1** (29.7)	0 (0)	0 (0)	**38.1** (31.2)	11.1 (11.1)	4.8 (4.8)	0 (0)
	Saguenay fjord	Sep (2)	4	0 (0)	0 (0)	0 (0)	**50** (50)	0 (0)	0 (0)	**25** (25)	0 (0)	**25** (25)	0 (0)
	Upper Saguenay	Mar/Apr/ May (4) **	13	**21.9** **(12.9)**	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	**96.9** (3.1)	0.083 (0.083)
	Upper Saguenay	Jun/Jul (2) **	4	**33.3** (33.3)	0 (0)	0 (0)	16.7 (16.7)	0 (0)	0 (0)	16.7 (16.7)	0 (0)	**100** (0)	2.1 (2.1)

	Upper Saguenay	Nov (1) **	2	**50**	**50**	0	0	0	0	0	0	**50**	0
	Upper Saguenay	Dec/Jan/ Feb (4)**	10	**21.3** (14.2)	0 (0)	0	5.0 (5.0)	0 (0)	2.1 (2.1)	0 (0)	0 (0)	**78.8** (14.2)	2.3 (2.3)

*Only includes Chicoutimi site

** Includes both Chicoutimi and La Baie sites

FW: freshwater aquatic invertebrate larvae; Co: coleopteran; Ter: terrestrial insects excluding coleopteran; Am: amphipod; SAm: striped amphipod; Po: polychaete; My: Mysid; Pa: penaeid shrimp; Fish: includes sand lance and smelt; Other: includes plant matter, winged insects (newly emerged) and all other miscellaneous items. Other: includes plant matter, winged insects (newly emerged), and all other miscellaneous items.

Table 4.6 Number of stomachs filled with contents (N) and mean size (± 1 SD) of 1st year and 2nd year brook trout migrants captured in the Ste. Marguerite River following seaward migration from September to October in years 1998 to 2000 and containing food in stomach.

		1st year migrants		2nd year migrants	
Year	**Month**	**N**	**Mean size (mm)**	**N**	**Mean size (mm)**
1998	Sep	62	256 (26.9)	39	320 (31.2)
1999		16	249 (27.5)	34	326 (28.6)
2000		6	256 (19.2)	13	304 (37.9)
1998	Oct	44	256 (19.5)	40	330 (44.0)
1999		23	262 (26.0)	53	341 (44.1)
2000		5	241 (18.8)	17	353 (60.2)

Table 4.7 Total number (N) and percent occurrence (%O) of prey types found in stomachs (± 1 SE) from September to October (number of pooled years) of 1st year and 2nd year brook trout migrants captured in the Ste. Marguerite River (SMR) in years 1998 to 2002.
The two highest prey occurrences for each month are in bold.

	Month	N	FW	Co	Ter	Wing	Ma	Egg	Plant	Fish	Other
1st year	Sept (3)	84	**42.0**	0	**60.3**	3.6	0.54	0	10.6	6.3	1.6
			(13.4)	(0)	(24.0)	(0.6)	(0.54)	(0)	(5.5)	(6.3)	(1.6)
	Oct (3)	72	**68.7**	7.4	12.3	13.0	6.7	8.1	**16.9**	2.3	1.4
			(8.4)	(6.3)	(4.9)	(12.8)	(6.7)	(5.1)	(10.1)	(2.3)	(1.4)
2nd year	Sept (3)	86	**59.9**	5.1	**23.1**	11.0	7.5	0	11.4	9.4	9.6
			(6.7)	(5.1)	(8.3)	(5.5)	(5.3)	(0)	(2.0)	(7.0)	(2.9)
	Oct (3)	110	**52.4**	1.3	**23.6**	7.9	3.3	17.9	14.8	5.3	3.4
			(11.7)	(1.3)	(8.9)	(3.0)	(2.2)	(6.0)	(4.0)	(2.9)	(1.2)

FW: freshwater aquatic invertebrate larvae; Co: coleopteran; Ter: all terrestrial insects excluding coleopteran; Wing: includes newly-emerged flies and adult flies; Ma: Small mammals Eggs: includes eggs of either brook trout or Atlantic salmon; Po: polychaete; Plant: includes all plant matter; Fish: includes short-nose dace and Atlantic salmon; Other: includes all unidentifiable prey and miscellaneous items.

Figure 4.1 Map of Saguenay River (Quebec, Canada) sampling sites located in the ‘Saguenay fjord’ and the ‘Upper Saguenay’, as separated by ‘End of fjord’.

CHIC refers to City of Saguenay (Chicoutimi), VDLB refers to Ville de la Baie (now City of Saguenay), SRN refers to Ste-Rose-du-Nord, BE refers to Sainte Eternité Bay, ASJ refers to Anse St-Jean, APOR refers to Anse du Portage, SMB refers to Sainte Marguerite Bay, ASE refers to Anse-St-Étienne, AS refers to Anse au Sable, AP refers to Anse-à-Pierre, AR refers to Anse de Roche, PP refers to Pointe à Passe-Pierre , AI refers to Anse aux Petites Iles, AG refers to Anse à Gagnon and AL refers to Anse à l’île.

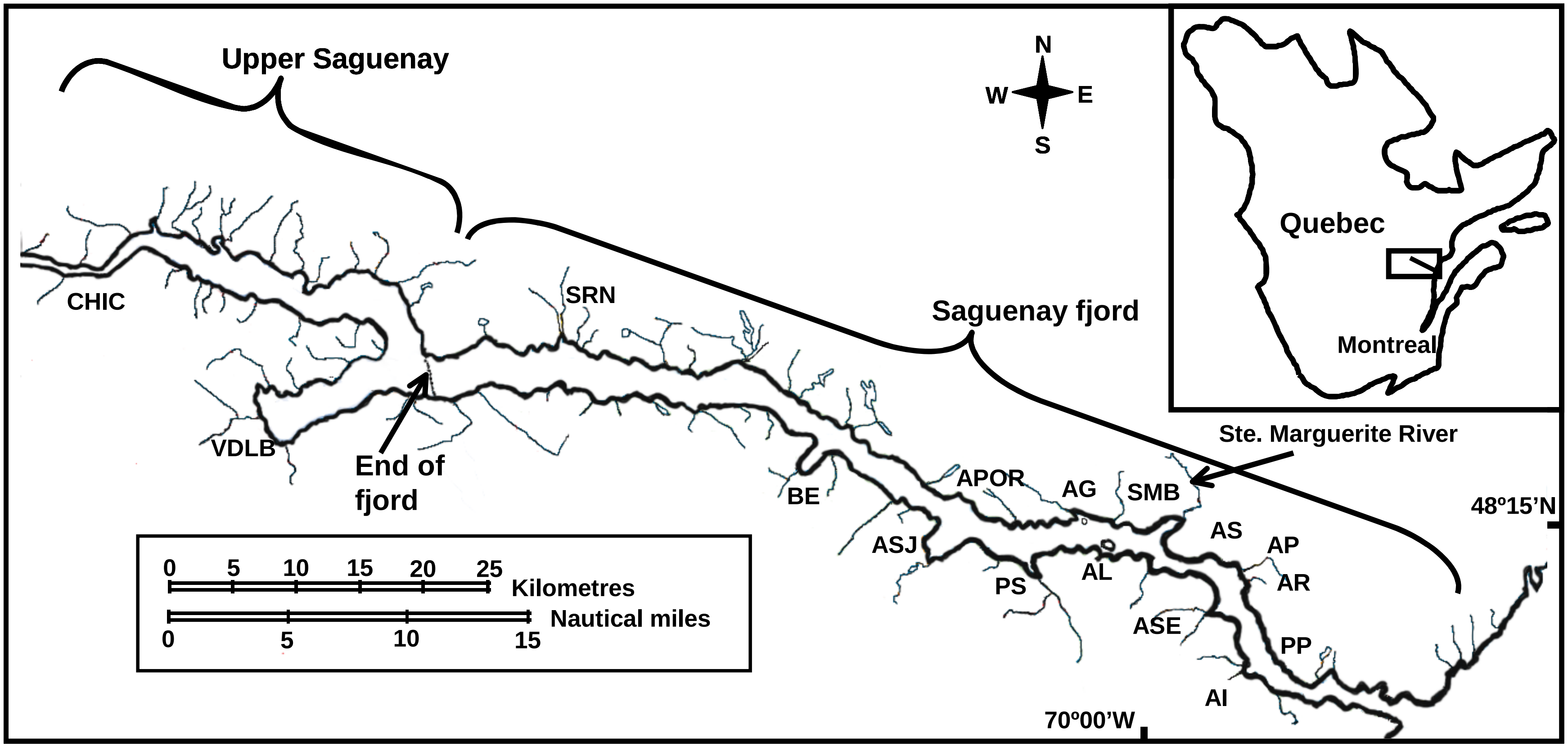
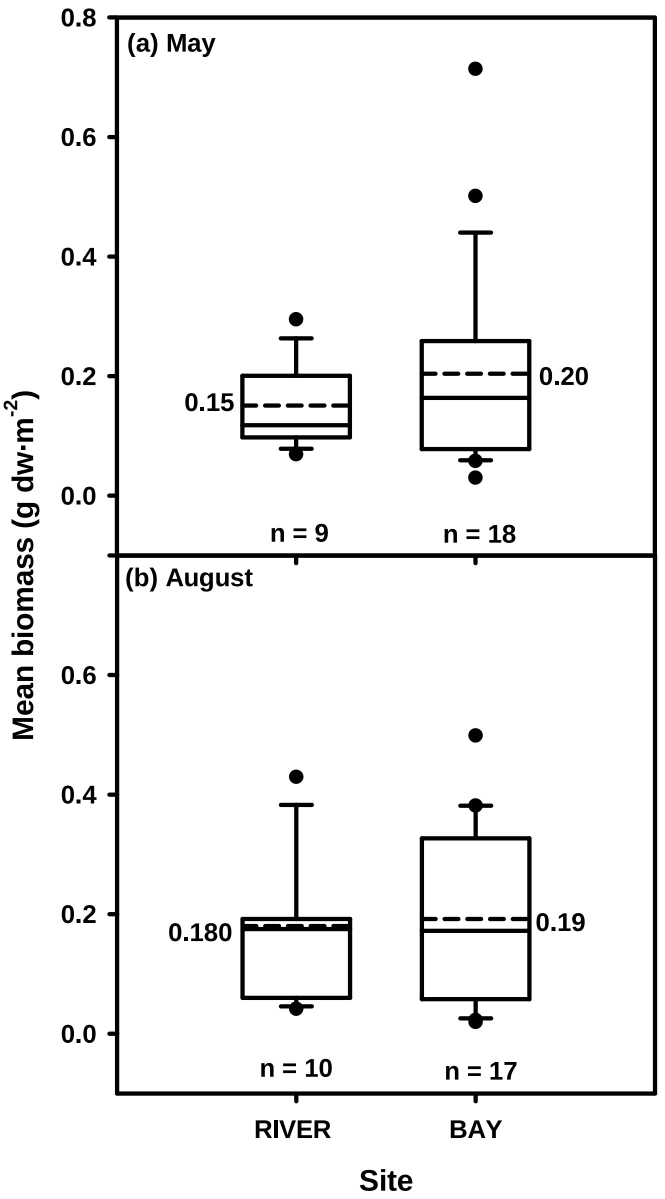

Upper Saguenay
N
W
E
S
Quebec
Montreal
CHIC
SRN
Saguenay fjord
VDLB
End of fjord
Ste. Marguerite River
APOR
AG
SMB
BE
48º15'N
AS
ASJ
AP
AL
AR
PS
ASE
PP
AI
70º00'W
0 5 10 15 20 25 Kilometres
0 5 10 15 Nautical miles

Figure 4.2 Mean invertebrate biomass (g dw·m^{-2}) for sites located in the Ste. Marguerite River and Bay in (a) May and (b) August.

No significant differences in invertebrate biomass exist between river and bay sites in either May (t = -0.89, df = 25, p = 0.38) or August (t = -0.22, df = 25, p = 0.83). The boundary of the box closest to zero indicates the 25th percentile, the solid line within the box marks the median, the dashed line indicates the mean (and number), and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers above and below the box indicate the 90th and 10th percentiles. Dots indicate outliers.



(a) May
(b) August
0.8
0.6
0.4
0.2
0.0
0.6
0.4
0.2
0.0
Mean biomass (g dw·m^{-2})
0.15
0.20
0.180
0.19
n = 9
n = 18
n = 10
n = 17
RIVER
BAY
Site

Figure 4.3 Mean invertebrate size (mg dw·ind^{-1}) for sites located in the Ste. Marguerite River and Bay in (a) May and (b) August.

River sites have smaller invertebrates than bay sites in both May (t = -3.5, df = 28, p = 0.001) and August (t = -2.7, df = 25, p = 0.013). The boundary of the box closest to zero indicates the 25th percentile, the solid line within the box marks the median, the dashed line indicates the mean (and number), and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers above and below the box indicate the 90th and 10th percentiles. Dots indicate outliers.

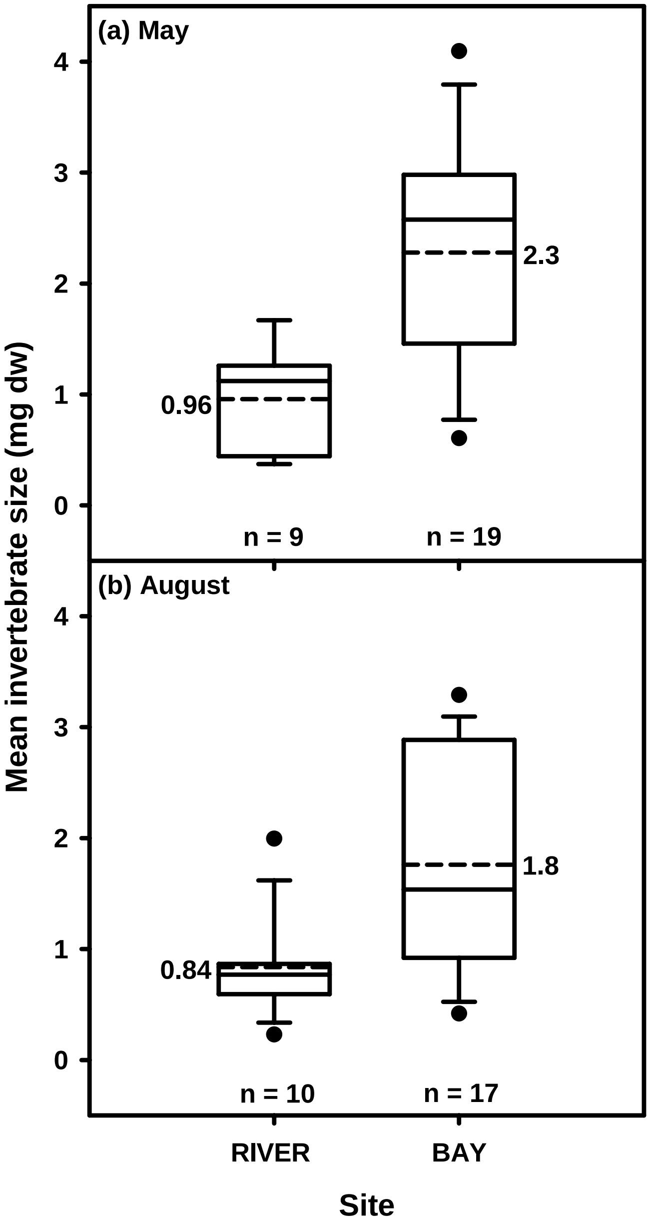

(a) May
4
3
2
1
0
0.96
2.3
n = 9
n = 19
(b) August
4
3
2
1
0
0.84
1.8
n = 10
n = 17
Mean invertebrate size (mg dw)
RIVER
BAY
Site

Figure 4.4 Prey wet weight contribution to overall diet of (a) 1st year and (b) 2nd year migrant brook trout captured in the estuarine Ste. Marguerite Bay (SMB) in 1998 to 2002 from May to October.

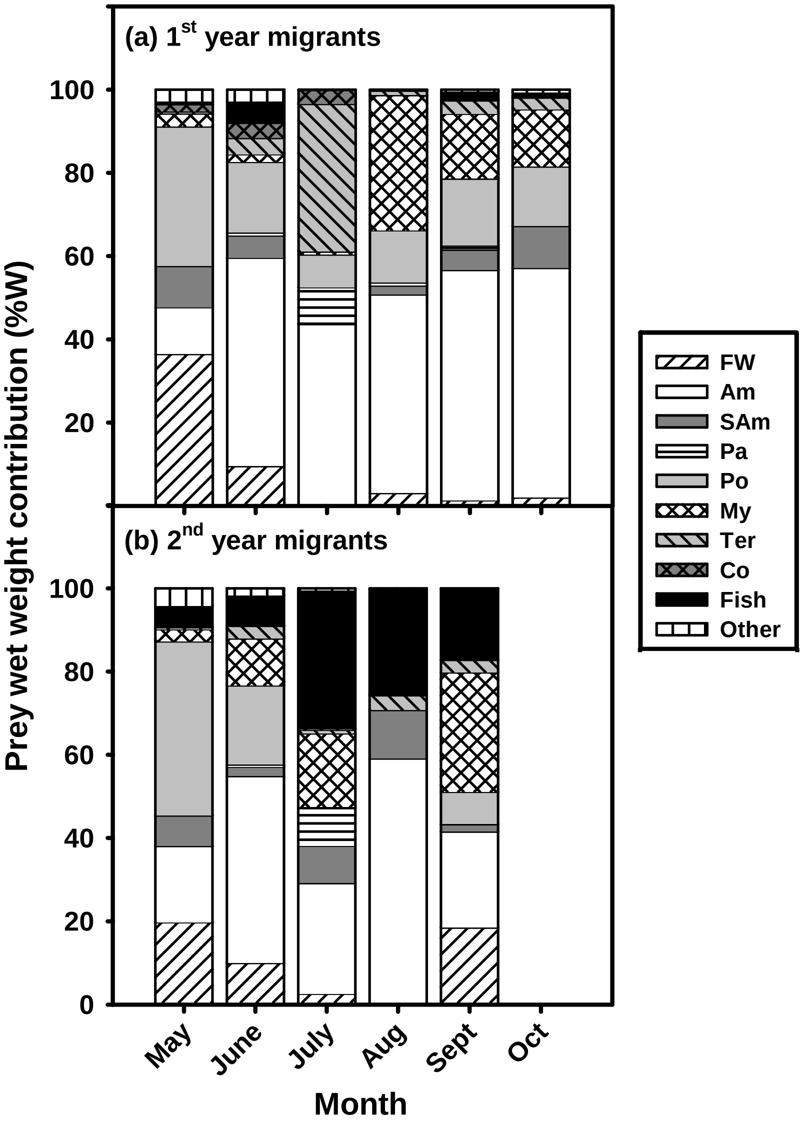

(a) 1st year migrants
(b) 2nd year migrants
Prey wet weight contribution (%W)
0
20
40
60
80
100
May
June
July
Aug
Sept
Oct
Month
FW
Am
SAm
Pa
Po
My
Ter
Co
Fish
Other

Figure 4.5 Relative frequency of piscivory in migrants separated according to size (a, b) and the relative size frequency of piscivorous trout (c,d) captured in the Ste. Marguerite Bay and the Saguenay River, respectively.

Black circles (and bars) and grey circles (and bars) refer to 1st year and 2nd year migrants, respectively. The dotted line separates trout above and below the threshold of 25 cm.

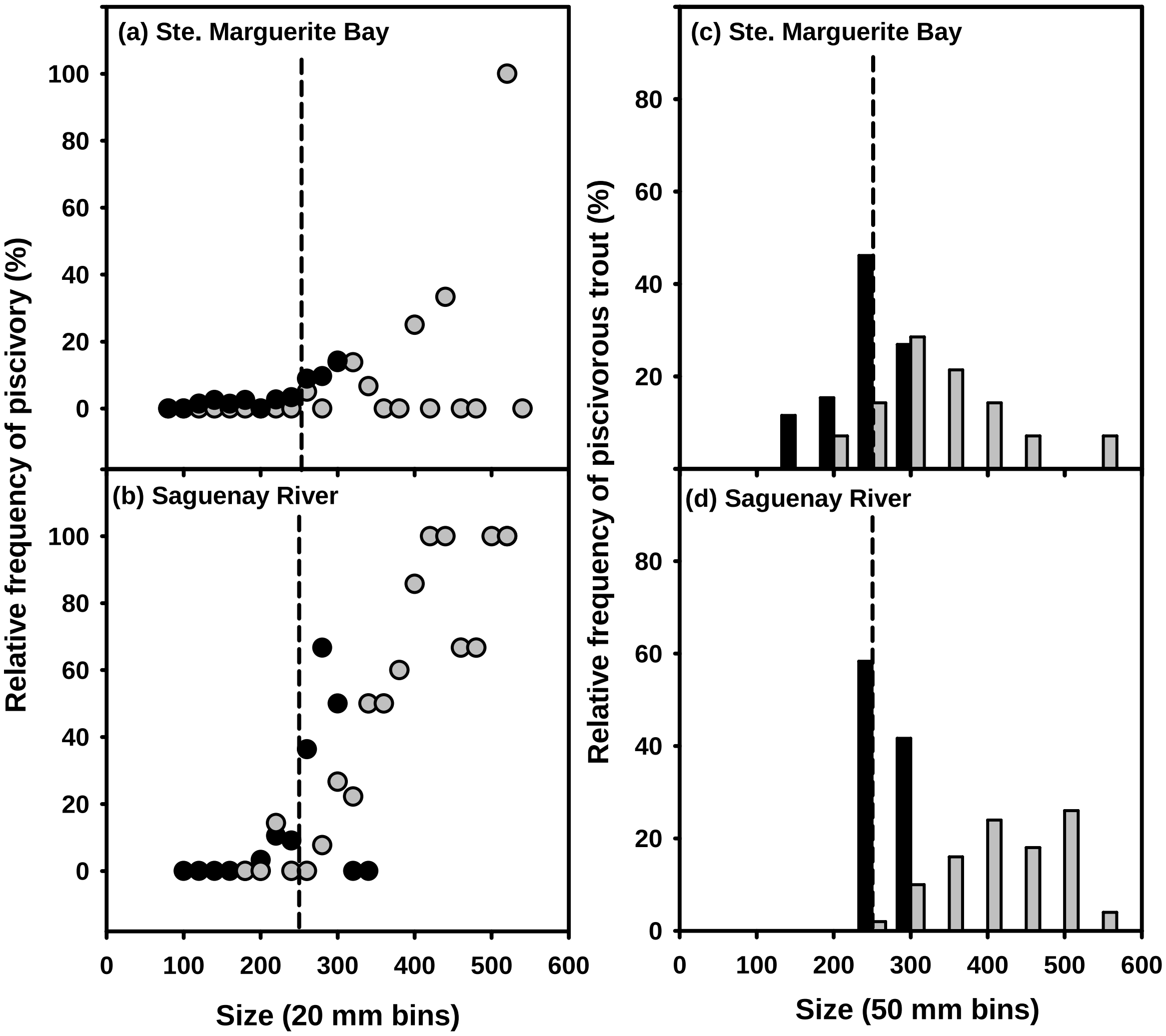

(a) Ste. Marguerite Bay
(b) Saguenay River
(c) Ste. Marguerite Bay
(d) Saguenay River
Relative frequency of piscivory (%)
Relative frequency of piscivorous trout (%)
Size (20 mm bins)
Size (50 mm bins)
0
20
40
60
80
100
0
100
200
300
400
500
600

Figure 4.6 Prey wet weight contribution to overall diet of (a) 1st year and (b) 2nd year migrant brook trout captured in the estuarine Saguenay River (Saguenay fjord and Upper Saguenay) from 1998 to 2002 across months.

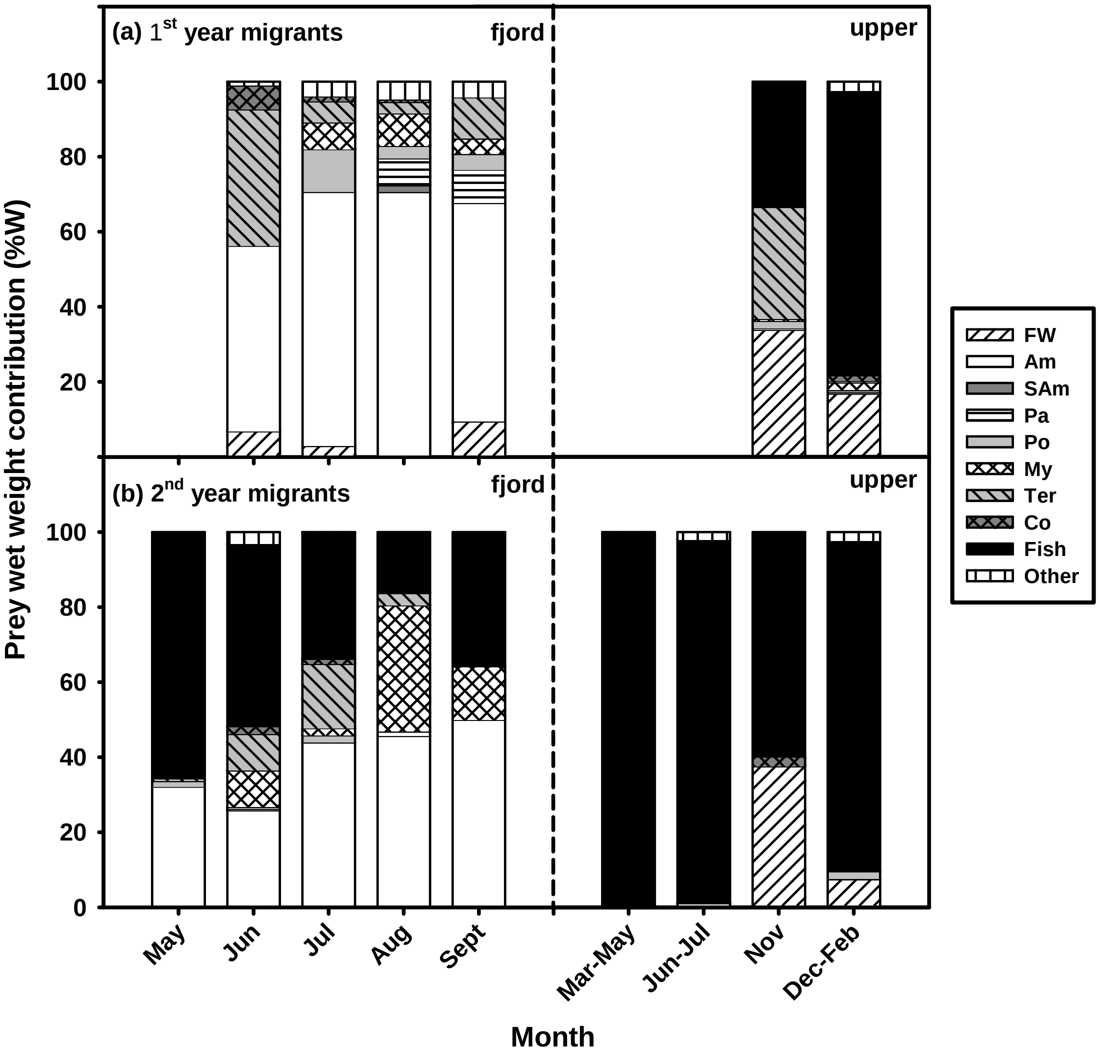

(a) 1st year migrants
fjord
upper
(b) 2nd year migrants
fjord
upper
Prey wet weight contribution (%W)
0
20
40
60
80
100
May
Jun
Jul
Aug
Sept
Mar-May
Jun-Jul
Nov
Dec-Feb
Month
FW
Am
SAm
Pa
Po
My
Ter
Co
Fish
Other

Figure 4.7 Prey wet weight contribution to overall diet of (a) 1st year and (b) 2nd year migrant brook trout captured in the Ste. Marguerite River from 1998 to 2000 in September and October.

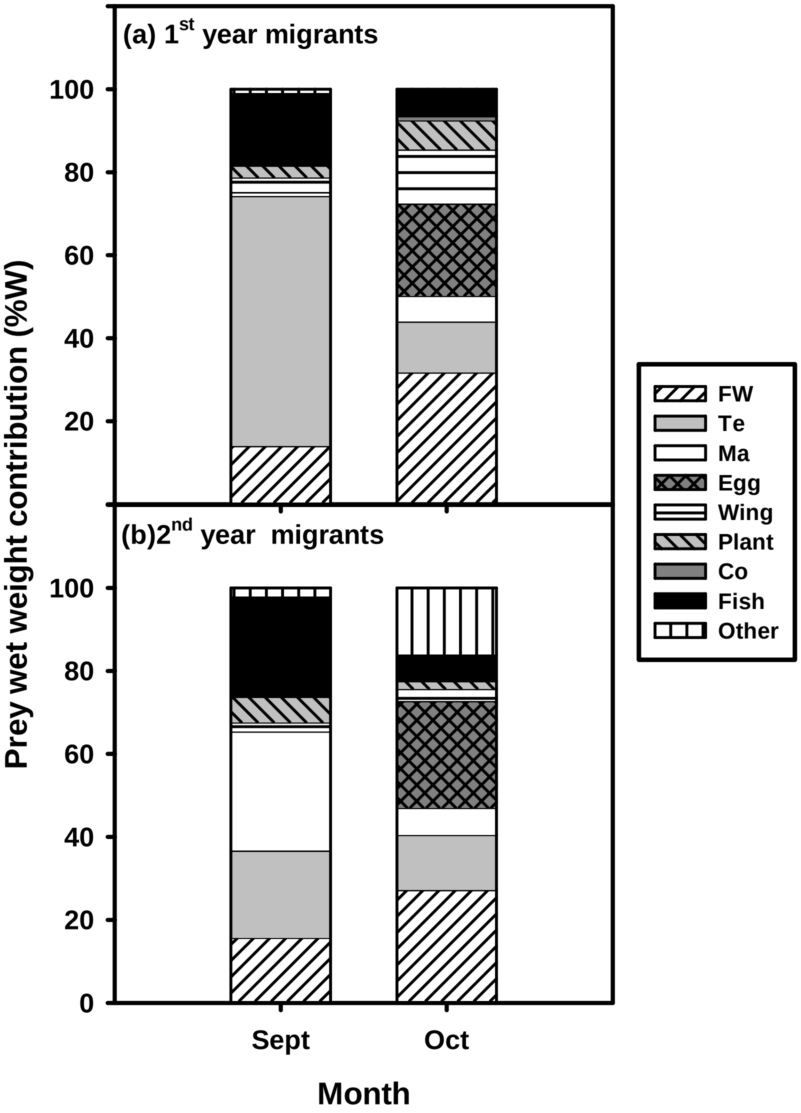

(a) 1st year migrants
(b)2nd year migrants
Prey wet weight contribution (%W)
0
20
40
60
80
100
Sept
Oct
Month
FW
Te
Ma
Egg
Wing
Plant
Co
Fish
Other

Figure 4.8 Stable carbon ($\delta^{13}C$) and nitrogen signatures ($\delta^{15}N$) as a function of fish length for sea trout (anadromous brook trout; closed circles) captured in the Ste. Marguerite Bay ($\delta^{13}C = 0.064FL – 29.4$, $p < 0.0001$, $r^2 = 0.65$; $\delta^{15}N = 5.2 + 0.036FL – 0.0001FL^2$, $p < 0.001$, $r^2 = 0.34$) and for resident brook trout (open circles) captured in Morin stream, a tributary of the Ste. Marguerite River ($\delta^{13}C = 0.0062FL – 25.4$, $p = 0.02$, r2 = 0.14; $\delta^{15}N = 6.0 + 0.0051FL$, $p = 0.04$, $r^2 = 0.10$).

Sea trout were captured from May to September. Resident trout were captured in June and July.

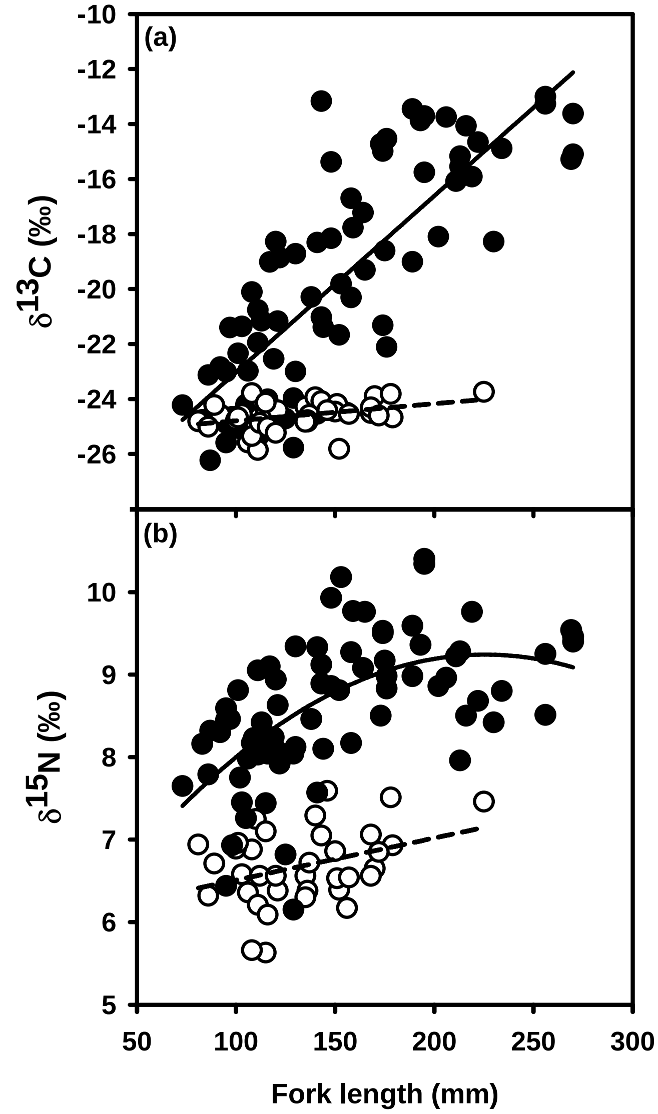
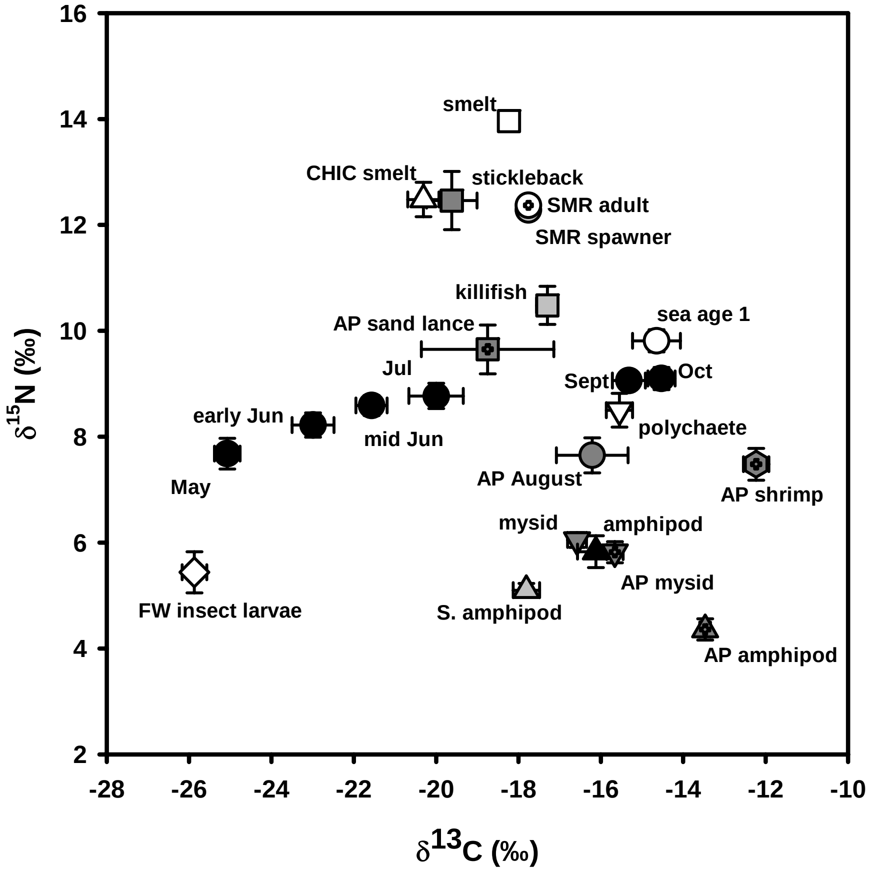

(a)
-10
-12
-14
-16
-18
-20
-22
-24
-26
$\delta^{13}C$ (‰)
(b)
10
9
8
7
6
5
$\delta^{15}N$ (‰)
50
100
150
200
250
300
Fork length (mm)

Figure 4.9 δ^{15}N and δ^{13}C of anadromous brook trout (sea trout) from the Ste. Marguerite River system, Quebec.

May, early and late June (Jun), July (Jul), September (Sept) and October (Oct) indicates the mean signature of first-time sea trout captured in the Ste. Marguerite Bay (SMB) during those months. “AP” August and “AP” prey items refer to isotope signatures of first-time migrants and prey items captured in Anse à Pierre (Saguenay River), respectively, and is located downstream of the SMB. Sea age 1 refers to sea trout captured in the SMB in early May who are beginning their second summer at sea. FW indicates freshwater and S indicates striped. SMR spawner and adult refers to an anadromous brook trout spawner and non-spawner captured in the Ste. Marguerite River. “CHIC” smelt refers to smelt found in the stomach of a trout captured in CHIC (upper Saguenay River site).



16
14
12
10
8
6
4
2
-28
-26
-24
-22
-20
-18
-16
-14
-12
-10
δ15N (‰)
δ13C (‰)
smelt
CHIC smelt
stickleback
SMR adult
SMR spawner
killifish
AP sand lance
sea age 1
Jul
Sept
Oct
early Jun
mid Jun
polychaete
May
AP August
AP shrimp
mysid
amphipod
AP mysid
FW insect larvae
S. amphipod
AP amphipod

GENERAL CONCLUSIONS AND SUMMARY

This thesis elucidates some potential mechanisms leading to the adoption of anadromy in populations of brook trout using a bioenergetics approach. This study, by focussing on the early life stages of brook trout, provides support to the idea that variation in energy allocation leads to the adoption of migration or residency as life-history strategies. More specifically, juvenile anadromous brook trout (migrant), in the year(s) prior to migration, were shown to have higher metabolic costs than resident brook trout. These metabolic costs appear to be the result of differential habitat use whereby migrants exploit faster (more costly) habitats than residents, corroborated with differences in $\delta^{13}C$ (migrants have more negative $\delta^{13}C$ compared to residents; Chapter 1) and morphology (migrants are more streamlined than residents; Chapter 2), in addition to field observations conducted in ‘pure’ resident and migrant-resident streams (brook trout inhabiting migrant-resident streams exploit a wider range of habitats than those inhabiting ‘pure’ resident streams; Chapter 3). There thus appears to be a link between metabolic costs, morphology, habitat use and the adoption of life-history strategies.

Interestingly, the results demonstrate that although migrants obtain more food compared to residents in their local environment, the fact that they still migrate to a new habitat suggests that they do not obtain enough energy to satisfy their metabolic demands. Their new habitat, immediately upon entry, appears to have better feeding opportunities, as the prey spectrum at sea is both larger and wider than that found in freshwater (Chapter 4). This permits them to undergo diet shifts to larger prey, reducing their costs related to foraging and most likely increases their growth efficiency leading to high growth rates at sea. However, future studies are still needed to elucidate the energy allocation patterns (consumption rates and growth efficiency) of anadromous brook trout during their marine life.

Our results therefore suggest that fish migrate as a response to energetic limitations. Such a finding is not surprising, although previous attempts using simple growth and body size comparisons have not been able to show how this arises (for more detail see introduction of Chapter 1). This stems from the limits associated with simply measuring growth outputs (body size) as it cannot provide a complete picture of fish energetic status. Both the inputs (consumption) and outputs (growth) are needed to assess a fish's condition, leading to information regarding metabolic costs.

Importantly, the results demonstrate that although the migrant strategy is more costly (the use of faster habitats) than the resident strategy, there are also compensating benefits, because, in the long run the migration permits them to achieve larger sizes than if they had remained in streams, and thus become more fecund. Their energetic scope permits them to capitalize on better feeding opportunities and are thus better adapted to profit from large-scale environmental heterogeneity as they are able to achieve high growth in new habitats. In contrast, residents are better adapted to living in streams, exhibiting an efficient life-history strategy (higher growth efficiency), and are thus winners in their local environment. Since both strategies coexist and persist in the same system, these results indicate the presence of a trade-off between local adaptability and the ability to exploit large-scale environmental heterogeneity.

Our ability to study fish at early stages may provide some insight into some of these issues. The model we have developed distinguishing migrants and residents in the field using morphology (Chapter 2) may thus contribute to the further elucidation of bioenergetic mechanisms leading to anadromy, but an important limitation first needs to be addressed. Although we were able to differentiate migrants from residents using a discriminant function, the model has not been applied on individuals prior to migration with subsequent verifications. A field study needs to be conducted in order to validate the predictive ability of the model. This would involve catching and measuring the morphological traits of young-of-the-year and 1+ brook trout in the fall, prior to the spring migration. All captured fish would be tagged and their strategy would be predicted based on their morphology. During the following spring outmigration and subsequent stream samplings for the trout remaining in the system, a success rate of accurately predicted migrants and residents would be calculated based on earlier predictions.

A high prediction success rate would allow for future studies to be conducted comparing the two forms during their coexistence in streams as juveniles. Future studies could include comparing the habitat preferences, aggressive behaviours, foraging modes and territory size of migrant and resident forms. In addition, it could permit an investigation of the differences in standard metabolic rates and activity between the two forms. For example, the use of enzymatic markers (Smith and Chong 1982; Lind 1992; Sullivan and Somero 1980; Sherwood et al. 2002) could help to determine the relative metabolic differences (standard metabolic rates and activity) between coexisting juvenile anadromous and resident brook trout in the field.

The results presented in this study cannot establish whether there is a genetic basis for anadromy, although field observations on salmonid life-history variability would tend to suggest that there is some kind of genetic basis for it. For example, fish located above a waterfall do not exhibit outmigrations. In addition, stream habitats that become fragmented following the construction of roads and the installation of poorly constructed culverts impeding upstream movements also result over time in the loss of anadromous forms in the stream sections upstream of these obstructions.

Mechanisms leading to the loss of the anadromous phenotype may involve, for example, an increasing shift to more resident-like traits due to the lack of contribution to the gene pool since migrants would no longer be attaining spawning grounds. A potential life scenario could be for example, that early morphological or standard metabolic rate (SMRa) variations of recently emerged young-of-the-year (YOY) from a mixed population of migrant and resident brook trout would determine their initial positioning in a stream. This would lead to the observed bioenergetic variability and subsequent life-history strategies. In a situation with no barriers to migration, assortative mating between migrant and resident forms would serve to maintain this life-history variability. Then, assuming that morphological and SMRa variability has a genetic basis, a reduction in this variability following the loss of anadromous genes would be expected to lead to a predominance of resident-like phenotypes. This could originate from a physical barier reducing the access of the stream to anadromous spawners. Such losses in morphological or SMRa variation could over time, result in fewer fish having sufficient metabolic scope to occupy fast and more costly habitats. In such a scenario, it would be expected that eventually, fish inhabiting such streams would primarily utilise the slower habitats.

Indeed, earlier studies suggest a genetic basis to variations in morphology and SMRa, including swimming capacities within fish species (Proulx and Magnan 2004; Taylor and Foote 1991; Taylor and McPhail 1985). However, studies have also shown that morphological variations can be induced under differential current regimes (Imre et al. 2002; Pakaasma and Piironen 2001). It thus remains to be determined whether it is streamlined fish with a higher aerobic capacity (higher SMRa) that ‘choose’ faster currents leading to higher metabolic costs, or alternatively, that fish utilize fast currents minimize their costs by becoming more streamlined and adapt by increasing their aerobic capacity to improve their swimming ability. Thus for the time being, it appears to be a “what came first, a chicken or the egg?” situation.

A recent initiative by colleagues is attempting to answer some of these very questions (A. Carrier and J.J. Dodson, Laval University, Ste.

Foy, Quebec, personal communication). Under laboratory conditions, the morphology, habitat use and metabolic rates are being compared between first-generation offspring at YOY stages of pure resident crosses, between resident-migrant crosses and between migrant-migrant crosses. The detection of differences at such young stages would suggest a genetic basis to the results obtained in the field. Another parallel study is also attempting to examine the heritability of anadromy in brook trout (V. Thériault and J.J. Dodson, Laval University, Ste. Foy, Quebec, personal communication). Parents are being assigned using mitochondrial DNA (mtDNA) to juveniles captured during the downstream outmigration and trout remaining in streams following outmigration to determine whether migrant parents produce more migrant offspring than resident offspring. A link may also be made between genetic variations and morphology since the individuals (from Morin tributary) used in this parallel study are the same as those employed in Chapter 2.

Before I conclude, I would like to mention that the research set forth in this thesis contributed to a larger collaborative effort, beginning in the summer of 1998. This larger project, entitled ‘Projet truite de mer’, involved multiple partners including research academics, the Ste. Marguerite River Association and the Government of Quebec. The project was initiated and carried out by researchers with diverse expertises from various universities including Université de Montréal (in its early stages), Université Laval, Université du Québec à Rimouski (in its later stages) and McGill University. Its initial overall goal was to acquire a better understanding of brook trout populations containing anadromous and resident forms and to study their interaction with coexisting Atlantic salmon populations in the Ste. Marguerite River, Quebec, Canada. As such, most of the effort largely focused towards determining the potential mechanisms leading to the anadromy of brook trout in addition to the basic life-history differences of anadromous and resident forms. This thesis thus contributes some important information regarding the potential bioenergetic mechanisms leading to anadromy.

In conclusion, I would like to end this thesis with the following excerpt from “Trout streams I’ve known” by Jimmy D. Moore:

"*All of us search for that perfect trout stream. Those who find it treasure it the rest of their lives. Those who don't keep on searching*."

I’m happy to say that after all of these years, I have found it…

References

Imre, I., R. L. McLaughlin & D. L. G. Noakes. 2002. Phenotypic plasticity in brook charr: changes in caudal fin induced by water flow. Journal of Fish Biology 61:1171-1181.

Lind, Y. 1992. Summertime and early autumn activity of some enzymes in the carbohydrate and fatty acid metabolism of the crucian carp. Physiology and Biochemistry 9: 409-415.

Pakkasmaa, S. & J. Piironen. 2001. Water velocity shapes juvenile salmonids. Evolutionary Ecology 14:721-730.

Petterson, L.B., and C. Brönmark. 1999. Energetic consequences of an inducible morphological defence in crucian carp. Oecologia 121:12-18

Proulx, R. and P. Magnan. 2004. Contribution of phenotypic plasticity and heredity to the trophic polymorphism of lacustrine brook charr (*Salvelinus fontinalis* M.). Evolutionary Ecology Research 6: 503-522

Sherwood, G.D., I. Pazzia, A. Moeser, A. Hontela, and J.B. Rasmussen. 2002. Shifting gears: Enzymatic evidence for the energetic advantage of switching diet in wild-living fish. Canadian Journal of Fisheries and Aquatic Sciences 59: 229-241

Smith, J.C., and C.K. Chong. 1982. Body weight, activities of cytochrome oxidase and electron transport system in the liver of the American plaice *Hippoglossoides platessoides*. Can these activities serve as indicators of metabolism? Marine Ecology-Progress Series 9: 171-179

Sullivan, K.M., and G.N. Somero. 1980. Enzyme activities of fish skeletal muscle and brain as influenced by depth of occurrence and habits of feeding and locomotion. Marine Biology 60: 91-99

Taylor, E.B. and C.J. Foote. 1991. Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). Journal of Fish Biology 38: 407-419

Taylor, E. B. & J. D. McPhail. 1985. Burst swimming and size-related predation of newly emerged Coho salmon, *Oncorhynchus Kisutch*. American Fisheries Society 114:546-551.

APPENDICES

Appendix A: Copy of scientific permits allowing fish handling and sacrificing issued to researchers of the sea trout project (Projet ‘truite de mer’) from years 1999-2004

Appendix B: Reprint of scientific article by Morinville and Rasmussen 2003