ENVIRONMENTAL INFLUENCES ON THE MARINE MIGRATION OF ARCTIC CHAR AND BROOK TROUT (*SALVELINUS* SPP.)

by

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DEDICATION PAGE

I dedicate this thesis to my first-born child. May he embrace life as if it were a fleeting blink in time, and understand that all life is linked.

"Love life my child. Every connection I've made, I've done for love of you."

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ABSTRACT

Environmental influences on the marine migration of Arctic char *Salvelinus alpinus* and brook trout *Salvelinus fontinalis* were determined by correlating movements, habitat use and diving behaviours to distance traveled from freshwater inputs, salinity, temperature, tides and prey availability. Using acoustic tracking, *S. alpinus* were detected either continuously (maximum 34 days) or intermittently in estuarine zones, on average residing approximately ⅓ of time tracked and returning once every 9 days. Low travel rates during flood tide suggested individuals staged before accessing intertidal flats. A portion of tagged individuals (19%) used two main estuaries situated 22 km apart. Extra-estuarine travel was within 3 km of shore ranging < 30 km straight line distance of either estuary. Higher estuarine residency prior to freshwater re-entry suggested a marine-fresh water transition phase.

Tracking revealed *S. alpinus* spent the most of their time in surface waters (0 to 3 m). Inter/sub-tidal movements and consecutive repetitive dives (maximum 52.8 m) resulted in extreme body temperature shifts (-0.2 to18.1^{o}C). Stomach contents analysis and diving suggested inter- and sub-tidal feeding. Although *Salvelinus fontinalis* continued to feed while overwintering within an estuary, near-zero body temperatures may have stopped gastric evacuation. *Salvelinus alpinus* mostly occupied warmer estuaries and surface waters, limiting time spent in colder environments, as part of thermoregulatory behaviours which enhanced feeding/digestion physiology. Both *Salvelinus* spp increased body condition by marine feeding in near-zero temperatures.

Salmoninae adaptability to the marine environment was evaluated based on the following criteria: (1) extent, and (2) duration of migration; (3) horizontal and (4) vertical habitats; and (5) minimum and (6) maximum thermohaline limits experienced. The most-to-least marine adapted genera were *Oncorhynchus*, *Salmo* and *Salvelinus*. The lowest and highest thermohaline limits were reached by *O. keta, S. salar, S. alpinus* and *S. malma;* and *O. kisutch, O. keta* and *O. nerka*, respectively. Our top three ranked species, *O. keta, O. nerka* and *O. gorbuscha*, suggested recently evolved salmonids are more marine adapted. The plasticity of *Salvelinus* spp. marine migration strategies, demonstrated by wider thermal/habitat zone niches described within this thesis, may have allowed exploitation of extreme environments, offering a survival advantage when faced with rapid climate change.

LIST OF ABBREVIATIONS USED

ADS	Aaron Drew Spares
ANOVA	analysis of variance
AR	Armshow River
ATPase	adenosine triphosphatase
bl.s^{-1}	body lengths per second
BR	Bay of Two Rivers estuary
C_{24}	daily ration, consumption rate, mg prey g M^{-1}
C_t	consumption over the feeding interval considered
df	degrees of freedom
DFO	Department of Fisheries and Oceans Canada
D-S-C-F	Dwass-Steel-Chritchlow-Fligner pairwise comparison statistical test
% ES	percentage of empty stomachs
F	ANOVA test statistic value
FB	Frobisher Bay
FL	fork-length
FUBAR	F*@%ed Up Beyond All Recognition
FW	fresh water
H	Kruskal-Wallis test statistic
H'	Shannon-Weiner diversity index
HTA	Hunters and Trappers Association
i	taxon being considered
iFB	inner Frobisher Bay
IQ	interquartile range
I_R	stomach fullness = Hureau’s index
I_{RO}	mean stomach fullness index at the beginning of the interval
I_{RT}	mean stomach fullness index at the end of the interval
I_{RI}	index of relative importance
I_S	Schoener’s overlap index
IT	intertidal
K	Fulton’s condition factor
K^+	potassium
L.	Linnaeus
LDO	liquid dissolved oxygen
L_F	fork-length
L_T	total-length
ln	natural logarithm of a number to the base e, where $e = 2.718281828$
$\%M$	percent by mass
M	body mass
Ma	million years ago
MJWS	Michael J. W. Stokesbury
M_P	mass of prey
MR##	Floy ID tagged fish only
MS-222	tricaine mesylate or tricaine methanesulfonate
$\%N$	percent by number

N	north or sample size (i.e. N = 3).
n	sample size or number of
Na$^+$	sodium (salt)
nr	not reviewed
NSERC	Natural Sciences and Engineering Research Council of Canada
NW	northwest
%O	frequency of occurrence
OTN	Ocean Tracking Network
P	*p*-value, probability of obtaining the observed sample results
PGS-D	post-graduate scholarship-doctorate
pH	measure of the acidity or basicity of an aqueous solution
p_i	mean *% M* x 0.01 of taxon *i*
pm	post meridiem, after noon
p_{xi}	mean *% M* of prey taxon *i* for season *x*
p_{yi}	mean *% M* of prey taxon *i* for season *y*
R	instantaneous gastric evacuation rate (h^{-1})
RA	Rounsefell's (1958) anadromy rank
RV	Quinn & Myers (2004) revised anadromy rank
R^2	regression analysis statistic value
r^2	regression analysis statistic value
S	salinity
SCA	stomach content analysis
SD	standard deviation
S.D.	standard deviation
SG	Sylvia Grinnell River estuary
SGR	Sylvia Grinnell River
SLD	straight line distance
SST	sea surface temperature
ST	subtidal
SW	southwest
SW	salt water
T	Mann U Whitney test statistic value
t	interval duration (h)
t	Kruskal-Wallis or Mann U Whitney test statistic value
TAD	Terry A. Dick
T_b	body temperature (°C)
T_{low}	species' lower incipient lethal temperature (°C)
T_{max}	maximum preferred marine temperature (°C)
T_{min}	minimum preferred marine temperature (°C)
T_{upp}	species' upper incipient lethal temperature (°C)
TP	temperature/pressure (depth) sensor acoustic transmitter
T test	statistical comparison of two sample means
t-Test	statistical comparison of two sample means
T##	acoustically & ID tagged fish
UTC	Coordinated Universal Time
VR100	Vemco active tracking acoustic monitoring receiver

VR2	Vemco acoustic monitoring receiver (69 kHz), discontinued model
VR2W	Vemco acoustic monitoring receiver (69 & 180 kHz)
VR3-UWM	Vemco underwater modem receiver (69/180 kHz), discontinued model
V6	6 mm diameter coded acoustic transmitter (180 kHz)
V7	7mm diameter coded acoustic transmitter (69 kHz)
V9	9 mm diameter coded acoustic transmitter (69 kHz)
V13	13 mm diameter coded acoustic transmitter (69 kHz)
%*W*	percentage of wet weight of contents
W	west
yr	year(s)
Z	depth
Z_{max}	maximum depth
2x	twice, two times

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CHAPTER 1
INTRODUCTION

1.1 BACKGROUND

Salvelinus spp. is one of the most highly studied anadromous salmonid genera (Klemetsen *et al*., 2003). Relatively few studies, however, document the marine migration of Arctic char *Salvelinus alpinus* (L. 1758) (Moore, 1975; Dempson & Kristofferson, 1987; Bégout Anras *et al*., 1999; Rikardsen & Amundsen, 2005; Rikardsen *et al*., 2007; Jensen & Rikardsen, 2008) and brook trout *Salvelinus fontinalis* Mitchill 1814 (Lenormand *et al*., 2004; Curry *et al*., 2006; Morinville & Rasmussen, 2006; MacMillan & Madden, unpublished data), limiting understanding (Dadswell, 2009) and the ability to implement sustainable management practices (Morinville & Rasmussen, 2006). Aspects of marine entry transition, summer migration and overwintering phases relative to freshwater inputs, salinity, temperature and tidal phase have been described by archival and acoustic tracking, but only for a select few populations (Bégout Anras *et al*., 1999; Curry *et al*., 2006; Rikardsen *et al*., 2007; Jensen & Rikardsen, 2008).

Due to extreme variation in anadromous *Salvelinus* spp. life histories, regional knowledge of marine migration timing and behaviours are needed to enhance fisheries management and conservation efforts (Brenkman *et al*., 2007; Swanson & Kidd, 2009), especially in populations potentially isolated from outside recruitment and subjected to increasing human demands (Klemetsen *et al*., 2003; Morinville & Rasmussen, 2006). Considering this, I chose to examine two increasingly exploited *Salvelinus* populations: *S. alpinus* from inner Frobisher Bay, NU (Gallagher & Dick, 2010), and *S. fontinalis* from Antigonish Harbour, NS (MacMillan & Madden, 2007). Due to increasing anthropogenic pressures on Salmoninae and the marine environment being affected by rapid climate change, new marine migration information on *S. alpinus* and *S. fontinalis* was used to answer the questions: How adapted are *Salvelinus* spp. to the marine environment, and how do *S. alpinus* and *S. fontinalis* compare to other Salmoninae species?

1.2 MARINE MIGRATION OF *S. ALPINUS* AND *S. FONTINALIS*

For the majority of *S. alpinus* and *S. fontinalis* populations, seaward emigration occurs in spring (Moore, 1975; Gulseth & Nilssen, 2000; Klemetsen *et al*., 2003; Curry *et al*., 2006; MacMillan & Madden, 2007). Migrants remain in relatively warm, estuarine waters near freshwater inputs during a marine transition phase (Bégout Anras *et al*., 1999; Morinville & Rasmussen, 2006). Both species undertake a short duration migrations (Klemetsen *et al*., 2003; Morinville & Rasmussen, 2006) spending the most of their time in surface waters ($Z < 3$m) within 5 km of shore, with shoreline movements linked to tide phases (Moore, 1975; Dempson & Kristofferson, 1987; Rikardsen & Amundsen, 2005; Curry *et al*., 2006). Some individuals show a marked preference for their origin estuary (Curry *et al*., 2006) while other migrants venture farther (Dempson & Kristofferson, 1987; Morinville & Rasmussen, 2006) with maximum distances from origin estuary within one season recorded as 940 and 100 km for *S. alpinus* and *S. fontinalis*, respectively (Dempson & Kristofferson, 1987; Bégout Anras *et al*., 1999; Klemetsen *et al*., 2003; Lenormand *et al*., 2004). Travel rates for *S. alpinus* average 0.6 km.h^{-1} (13.8 km.d^{-1}; Bégout Anras *et al*., 1999) with considerable mixing occurring between populations within 80 km of each other (Moore, 1975; Dempson & Kristofferson, 1987). These iteroparous species return to fresh water for autumn spawning and overwintering, with migrants often decreasing or ceasing feeding within fresh water (Dempson & Kristofferson, 1987; Klemetsen *et al*., 2003; Curry *et al*., 2006; Morinville & Rasmussen, 2006). Depending on local conditions, a few populations remain or return to the estuary or sea post-spawning to over winter (Bigelow & Welsh, 1925; Smith & Saunders, 1958; Gaudreault *et al*., 1982; Curry *et al*., 2002; Morinville & Rasmussen, 2006; pers. comm. MacMillian & Madden, 2009; Jensen & Rikardsen 2008, 2012).

1.3 FACTORS SHAPING MARINE MIGRATION

Marine migration duration, stock mixing and movements of *Salvelinus* spp are influenced by local abiotic (ie. depth, light, salinity, temperature) and biotic (ie. prey availability) environmental conditions; migrant size, sex and state of maturation; and proximity to other river systems (Dempson & Kristofferson, 1987; Dadswell *et al*., 2010).

1.3.1 TEMPERATURE

Ambient temperature controls life process of ectothermic fishes, ultimately determining success and survival (McCormick *et al*., 1997). In anadromous salmonids, cold temperatures encountered by parr and smolts may not only delay smoltification and emigration to sea, but also decrease movement, growth, organ development and osmoregulation rates at sea, thus increasing both juvenile mortality and marine migration duration. Warmer temperatures may cause earlier spring freshets resulting in plankton blooms which may benefit early sea-run emigration or disadvantage later emigrants (Chittenden *et al*., 2009). At sea, warmer water may enhance feeding and maintenance, but temperatures >21°C may increase respiration and lack of appetite (Straty & Jaenike, 1980), resulting in lower energy stores of returning migrants (Chittenden *et al*., 2009). In response to ambient temperatures, behavioural thermoregulation may occur, whereas migrants move to alter physiological processes such as digestion (Bégout Anras *et al*., 1999).

Both *S.alpinus* and *S. fontinalis* are eurythermal (Larsson *et al*., 2005; Curry *et al*., 2006; MacMillan & Madden, 2007) surviving water temperatures from -1.7 to 23.2°C (Larsson *et al*., 2005). Selected marine temperatures range from 5-18°C (Bégout Anras *et al*., 1999; Curry *et al*., 2006; MacMillan & Madden, 2007; Rikardsen *et al*., 2007)). Landlocked *S. alpinus* have selected water temperatures of 5.1 to 9.2°C during summer (Peterson *et al*., 1979; Dick *et al*., 2009), while laboratory experiments revealed a preferred temperature of 10.9°C from spring to autumn optimized food conversion efficiency (Larsson, 2005; Mortensen *et al*., 2007).

Although both species have been deemed poor osmoregulators in cold water (Saunders *et al*., 1975; Finstad *et al*., 1989; Claireaux & Audet, 1999; Klemetsen *et al*., 2003) with temperatures < 3°C inhibiting osmoregulation (Claireaux & Audet, 1999), *S. alpinus* has been recorded in full strength saltwater at temperatures below -1°C (Klemetsen *et al*., 2003; Bystriansky *et al*., 2007). In near-freezing temperatures, the majority of salmonids remain inactive to keep oxygen demand low (DeVries & Cheng, 2005). Yet cold adapted *S. alpinus* increase essential fatty acids within cellular membrances to enhance flexibility (Metusalach *et al*., 1995), facilitate enzyme function (i.e. Na^+/K^+-ATPase) and decrease ion leakage by decreasing activity or density of ion channels (Schwarzbaum *et al*., 1991, 1992; Wu & Fletcher, 2000).

1.3.2 SALINITY

Salinity tolerance increases with fish size (Bystriansky *et al*., 2007). Small *S. alpinus* (L_F <12 cm) can tolerate salinities of < 21 for up to four days in temperatures ranging from -1.1 to 12.0°C, whereas in salinities > 30 and temperatures < 0°C, survival depends on access to fresh or brackish water (Dempson, 1993). Adult *S. alpinus* (L_F = 38-50 cm) overwintering in an estuary have been exposed to a salinity of 33 at 0°C (Jensen & Rikardsen, 2008) while larger individuals (mean 3.8 ± 0.56 kg) have been caught during summer in salinities of 25 to 32 with SSTs ranging from -1.5 to 1°C (Bystriansky *et al*., 2007). The majority of *S. alpinus* populations overwinter in fresh water (Moore, 1975) avoiding saltwater temperatures below 0°C (Dempson & Kristofferson, 1987). Ambient salinity is not just a factor to be tolerated by fishes, it may also be used as a navigational aid to river mouths or the open ocean (Quinn, 2005; Bos &Thiel, 2006; Dadswell *et al*., 2010; Thorstad *et al*., 2011; Lefèvre *et al*., 2012).

1.3.3 PREY AVAILABILITY

Both species are opportunistic feeders within the marine environment, feeding on clams, crustaceans, fishes, and polychaete worms (Moore, 1975; Hunter, 1976; Grønvik & Klemetsen, 1987; Isinguzo *et al*., 2002; Klemetsen *et al*., 2003; Rikardsen & Amundsen, 2005; Morinville & Rasmussen, 2006). First-time migrants initially feed on freshwater prey close to river mouths, but later shift to marine crustaceans. Veteran migrants prey upon crustaceans and fish, with an ontogeny shift to piscivory noted in larger *S. fontinalis* (L_F>25 cm; Morinville & Rasmussen, 2006).

Limited time of acceptable temperatures during marine migrations means *Salvelinus* spp feeding is voracious, with individual *S. alpinus* estimated to consume 7.5% of their body weight per day (Klemetsen *et al*., 2003). From marine diet and movement pattern data of an anadromous *S. fontinalis* population from the Ste. Marguerite River, Quebec, Morinville and Rasmussen (2006) determined spring and fall feeding were similar in habits and habitats. Winter estuarine feeding within a SST of 0°C and salinity of 7 was documented (Morinville & Rasmussen, 2006), yet no study on *S. alpinus or S. fontinalis* has documented year-round marine feeding behaviour using concurrent acoustic tracking, diet and environmental monitoring (Bégout Anras *et al*., 1999). Seasonal feeding migration information is necessary to understand diet requirements across marine habitats and to protect critical feeding grounds and access routes (Morinville & Rasmussen, 2006).

1.4 MARINE ADAPTABILITY

1.4.1 ANADROMY

Rounsefell (1958) defined 'anadromy' as the degree to which freshwater species establish residency at sea and assigned a taxa hierarchy based on the following criteria: marine migration (1) extent and (2) duration, (3) state of gonad maturation obtained at sea, (4) fresh water or marine spawning, (5) post-spawning mortality, and (6) occurrence of fresh water resident populations. Rounsefell's (1958) hierarchy from most to least anadromous Salmoninae genera were *Oncorhynchus*, *Salmo* and *Salvelinus*. At the species level, pink salmon *Oncorhynchus gorbuscha* (Walbaum 1792) ranked highest with *S. alpinus* and *S. fontinalis* the lowest (Rounsefell, 1958). Quinn & Myers (2004) revised the ranking based on new information, suggesting chum *Oncorhynchus keta* (Walbaum 1792) and sockeye *Oncorhynchus nerka* (Walbaum 1792) salmon ranked higher than *O. gorbuscha* due to a more extensive range and longer duration at sea. Chinook *Oncorhynchus tshawytscha* (Walbaum 1792) was less anadromous than coho *Oncorhynchus kisutch* (Walbaum 1792) salmon due to the existence of mature male parr, and iteroparity under experimental conditions. Upon discovering steelhead trout *Oncorhynchus mykiss* (Walbaum 1792) undertook more extensive open-ocean migrations, the species ranked higher than *O. tshawytscha* (Quinn & Myers, 2004). Dolly varden char *Salvelinus malma* (Walbaum 1792) ranked higher than bull trout *Salvelinus confluentus* Suckley, 1859, *S. alpinus* and *S. fontinalis* (Goetz *et al*., 2004). Due to lack of marine migration information, amago *Oncorhynchus rhodurus* Jordan & McGregor 1925 and masu *Oncorhynchus masou* (Brevoort 1856) salmon, and white-spotted char *Salvelinus leucomaenis* (Pallas 1814) have not been reviewed (Quinn & Myers, 2004).

1.4.2 MARINE ADAPTABILITY CRITERIA

Rounsefell (1958) was not assessing Salmoninae marine adaptability, yet criteria 1 to 3 did infer degrees of marine adaptability. Criterion 4 dealt with marine spawning, however only a select few *O. gorbuscha* and *O. keta* populations spawn in intertidal zones (Rounsefell, 1958), thus this criterion was not included. McCormick (1994) gauged marine adaptability on preparatory physiology/morphology and saltwater acclimation upon marine exposure, thus salinity tolerance was considered. For Chapter 5, the degree of a species' marine adaptability was inferred based on the following criteria: (1) extent, and (2) duration of migration; (3) horizontal, (4) vertical and (5) preferred minimum and (6) maximum thermohaline niche; and (7) condition factor (*K*) of migrants returning to fresh water.

1.5 THESIS OBJECTIVES

The main objectives of this thesis are (*i*) to describe marine movements (spatial patterns, migration range and travel rates) and residency of *S. alpinus* relative to environmental influences (temperature, salinity, tide phase and freshwater inputs) using acoustic tracking and concurrent environmental monitoring (**Chapter 2**), (ii) to document concurrent marine feeding behaviours of *S. alpinus* and *S. fontinalis* relative to habitat (inter-/sub-tidal), season (autumn to spring) and temperature using stomach content and feeding intensity (% empty stomachs, stomach fullness, consumption rates & body condition) analyses with concurrent acoustic temperature/depth sensor tracking (**Chapters 3 & 4**), and (iii) to include results into a critical literature review of marine migration strategies within the family Salmoninae to infer relative inter-specific marine adaptability, based on horizontal and vertical niches, and thermohaline limits experienced (**Chapter 5**).

It is hypothesized marine migrating *S. alpinus* will be limited to <40 km maximum straight line distance (SLD) from river mouths due to availability of freshwater inputs, and that movement patterns and travel rates will be influenced by daily tide phase (Moore, 1975). Based on previous depth preferences (Bégout Anras *et al*., 1999; Rikardsen *et al*., 2007), it was hypothesized *S.alpinus* migrants would occupy intertidal/upper water column habitats due to warmer temperatures. Intertidal foraging in macrotidal estuaries has been documented in other anadromous fishes, such as Atlantic sturgeon *Acipenser oxyrhynchus* Mitchill, 1815 in the Bay of Fundy (Dadswell, 2006), thus *S. alpinus* movements into the intertidal zone of inner Frobisher Bay were predicted to be influenced by prey availability. Feeding by *S. fontinalis* would vary with seasonal prey availability, with piscivory occurring in migrants >250 mm L_F (Morinville & Rasmussen, 2006), and rainbow smelt *Osmerus sp*. Steindachner & Kner, 1870 being the dominant prey from December to January. Feeding intensity was expected to decrease with colder temperatures, with percentage of empty stomachs being the highest, and stomach fullness and consumption rates being the lowest. Body condition was expected to increase from an autumn post-spawning low to the highest in late spring.

1.5.1 LIST OF ORIGINAL PAPERS

This thesis is based on the following original papers, which are referred to in the text by

Chapter #:

2 Spares, A.D., Stokesbury, M.J.W., Dadswell, M.J., O'Dor, R.K. & Dick, T.A. (2015). Residency and movement patterns of Arctic char, *Salvelinus alpinus*, relative to major estuaries. *Journal of Fish Biology* **86**, 1754-1780. doi:10.1111/jfb.12683

3 Spares, A.D., Stokesbury, M.J.W., O'Dor, R.K. & Dick, T.A. (2012). Temperature, salinity and prey availability shape the marine migration of Arctic char, *Salvelinus alpinus*, in a macrotidal estuary. *Marine Biology* **159,** 1633-1646.

4 Spares, A.D., Dadswell, M.J., MacMillan, J., Madden, R., O'Dor, R.K. & Stokesbury, M.J.W. (2014). To fast or feed: an alternative life history for anadromous brook trout *Salvelinus fontinalis* overwintering within a harbour. *Journal of Fish Biology* **85,** 621-644. doi:10.1111/jfb.12447

5 Spares, A.D., Dadswell, M.J., Dickinson, M.P. & Stokesbury, M.J.W. (2015). A critical review of marine adaptability within the anadromous Salmoninae. *Reviews in Fish Biology and Fisheries* **25**, 503-519. doi:10.1007/s11160-015-9392-z

CHAPTER 2

RESIDENCY AND MOVEMENT PATTERNS OF ARCTIC CHAR, *Salvelinus alpinus*, RELATIVE TO MAJOR ESTUARIES.

2.1 ABSTRACT

Estuarine residency and marine movements of forty-three anadromous Arctic char *Salvelinus alpinus* (mean ± S.D. fork length = 523 ± 97 mm) were examined using acoustic tracking in inner Frobisher Bay (63^{o} N 68^{o} W), Canada, from July to September 2008 and 2009. Recaptures occurred from July to August over a mean ± S.D. migration duration of 63 ± 7 days. Detected *S. alpinus* were either continuously (maximum 34 days) or intermittently present in estuarine zones, on average residing approximately ⅓ of time tracked and returning once every 9 days. Significantly higher estuarine residency during the final 15 migration days suggested a transition phase may occur prior to freshwater re-entry. Low travel rates during flood tide suggested individuals staged before accessing intertidal/estuarine zones. Although the two main estuaries were approximately 22 km apart, a portion of tagged individuals used both (19%). Individuals remained relatively close to freshwater overwintering systems, although late-migration inter-estuarine movements may have indicated natal homing. Approximately half of individuals exhibited extra-estuarine travel, mostly during mid-migration, but remained within 3 km of shore ranging < 30 km straight line distance of either estuary. It was concluded inner Frobisher Bay *S. alpinus* (1) spent a significant portion of their migration within or adjacent to the estuaries, and (2) had a restricted marine distribution within 30 km SLD of the river mouths.

2.2 INTRODUCTION

Anadromous *S. alpinus* undertake a short, seasonally determined, summer sea residency of one to four months (Sprules, 1952; Dempson & Kristofferson, 1987; Bégout Anras *et al*., 1999; Gulseth *et al*., 2000; Klemetsen *et al*., 2003; Morris & Green, 2012). Migration to the sea occurs in early spring as soon as rivers are ice-free (Moore, 1975; Gulseth & Nilssen, 2000; Klemetsen *et al*., 2003) and individuals remain in relatively warm, estuarine waters up to ten days during a marine transition phase (Bégout Anras *et al*., 1999). Marine migrations significantly increase or restore *S. alpinus* somatic growth, lipid reserves and fecundity (Dutil, 1986; Dempson & Kristofferson, 1987; Jobling *et al*., 1998). The majority of anadromous populations overwinter in fresh water leaving the sea before water temperatures drop to 0^{o}C (Moore, 1975; Dempson & Kristofferson, 1987), however, some Norwegian populations have been shown to overwinter at 2^{o}C in full-strength salt water (Jensen & Rikardsen, 2012).

Summer marine migrants travel along shorelines (Moore, 1975; Chapter 3), although some, mainly males (Dempson & Kristofferson, 1987), have been caught up to five km offshore (Rikardsen & Amundsen, 2005). Large, non-ripening fish travel the greatest distances (Dempson & Kristofferson, 1987), whereas smaller fish ($L_F < 200$ mm) remain close to natal river mouths. Marked fish have been recaptured 25 to 940 km away from origin river mouths within one season (Dempson & Kristofferson, 1987; Bégout Anras *et al*., 1999; Klemetsen *et al*., 2003), moving at rates up to 0.6 km.h^{-1} (13.8 km.d^{-1}; Bégout Anras *et al*., 1999). Considerable mixing of individuals occurs for populations within 80 km of each other (Moore, 1975; Dempson & Kristofferson, 1987). Marine migrants have been observed moving into intertidal zones and up rivers with flooding tides (Moore, 1975; Chapter 3).

Marine migration duration, stock mixing and movements of *S. alpinus* are influenced by local environmental conditions; availability of food resources; fish size, sex and state of maturation; and proximity to other river systems (Dempson & Kristofferson, 1987). Relatively few details of marine distribution and movements, however, have been documented due to difficulties of tracking fishes underwater (Dadswell, 2009). Rikardsen *et al*. (2007) described the summer temperature and depth preferences of *S. alpinus* using archival tags, and suggested the need for concurrent spatial information. Acoustic tracking has illuminated aspects of marine entry transition, summer migration and overwintering phases (Bégout Anras *et al*., 1999; Jensen and Rikardsen, 2008; Jensen *et al*., 2014), but as of yet, no study has described spatial and temporal summer marine movements relative to freshwater inputs and tidal phase.

Environmental niche studies are important for predicting species-specific responses to climate change (Rikardsen *et al*., 2007). Due to extreme variation in anadromous *S. alpinus* life histories, regional knowledge of marine migration timing and behaviours are needed to enhance fisheries management and conservation efforts (Brenkman *et al*., 2007; Swanson & Kidd, 2009; Jensen *et al*., 2014), especially in populations potentially isolated from outside recruitment (ie. straying) and subjected to increasing human demands. This study describes the summer marine movements and residency of *S. alpinus* relative to freshwater inputs and tide phase. The aims were to (1) determine the degree of site fidelity adult *S. alpinus* have to river mouths and their immediate estuaries and (2) characterize the marine movements (spatial patterns, migration range and travel rates) of individuals relative to two main estuaries, Bay of Two Rivers (BR) and Sylvia Grinnell (SG); migration period (early, mid & late) and tidal phase (high, ebb, low & flood). It was hypothesized that individuals will be limited to <40 km maximum straight line distance (SLD) from river mouths due to availability of freshwater input, and that movement patterns and travel rates will be influenced by daily tide phase (Moore, 1975).

2.3 MATERIALS AND METHODS

2.3.1 STUDY AREA

Frobisher Bay is a semi-enclosed, macrotidal bay located in southeast Baffin Island, Nunavut, Canada. Its length is divided by islands into a larger outer and a smaller inner bay. Inner Frobisher Bay (iFB; 63°N 68°W) is approximately 25 by 70 km (Fig. 2.1a) with depths < 250 m. Maximum tidal amplitudes of 11 m move approximately 17 km^3 of water at a mean velocity of 1 m s^{-1} (3.6 km h^{-1}) through the bay during a tidal cycle. Sea-ice cover occurs from November to June, with break-up around mid-June, leaving the bay relatively ice free from July to October (Chapter 3).

Two major river systems within iFB, the Sylvia Grinnell (SGR; 63°44'N 68°34'W) and Armshow (AR; 63°36'N 68°50'W; Fig. 2.1a), contain anadromous populations of *S. alpinus*. Riverine temperatures from August to September range from 6.6 to 15.9°C. At its mouth, the SGR forms three branches, each with its own waterfall. Two of these waterfalls are adjacent to each other and their plunge pools form the innermost extent of the estuary. High tide rises to all three falls, reducing flow to rapids during spring tides. At low tide, approximately 2 km of intertidal zone is exposed, yet shallow runoff still continues to the low tide mark. The Armshow River (AR) consists of the Northwest and Southwest branches, with both emptying into the same cove approximately 450 m apart at the head of Bay of Two Rivers (BR) estuary. The cove floods at high tide and offers a lagoon with a surface freshwater lens over top a saline bottom layer at low tide. The lagoon empties over the intertidal flats, yet run-off is too shallow for passage of large fish. Run-off funnels into a 2 m deep tidal channel which begins at the BR tag site and runs approximately 2 km, tide dependent, to the low tide mark. Approximately 12 km^2 of intertidal flats are exposed at low tide (Chapter 3).

The two estuaries offer significantly warmer (mean 6.4^{o}C) and brackish (mean 15.5 salinity) water in the top 3 m. This upper layer decreases in thickness with increasing distance from river mouths, often occurring over 4 km from freshwater inputs depending on river discharge. Outside the estuarine zone, water below the surface layer becomes significantly colder (< 3^{o}C) and increasingly saline (> 30; Chapter 3).

2.3.2 ACOUSTIC TRACKING

Marine migrating *S. alpinus* to be tagged and released were captured intertidally with a 4.5” gill net or by spin casting at BR during 21 to 25 July and 9 to 11 August, 2008 (*n* = 41); and 17 to 21 July plus 14 August, 2009 (*n* = 16). In 2009, *S. alpinus* (*n* = 4) were also captured by rod, tagged and released at the Sylvia Grinnell (SG) estuary 7 to 9 July (Table 2.1). Individuals were surgically implanted with one of four models of acoustic transmitters (V6 [180 kHz frequency], V7, V9TP, V13TP [69.9 kHz frequency]; length 18, 23, 39, 36 mm; diameter 6, 7, 9, 13 mm; weight in water 0.6, 1.0, 2.2, 6.0 g; battery life 113,140, 205/510, 1030 d.; respectively; Vemco, 2009), according to procedures outlined by Spares *et al*. (2012). In 2009, nineteen additional individuals captured at BR were Floy ID tagged only and released for recapture information. Fishers were requested to release tagged individuals if unharmed; or if deceased, to be delivered to the Nunavut Research Institute. Upon receipt, a reward was offered.

A passive acoustic receiver array (VR2W, Amirix/Vemco Ltd., Nova Scotia, Canada) was used to track tagged *S. alpinus* from 2 August to 30 September 2008 (Fig. 2.1a), and 24 June to 26 September 2009 (Fig. 2.1b). Thirty receivers were deployed from 2 to 8 August 2008, covering BR, its adjacent coastlines extending approximately 15 km northwest and southeast, and 1 km upstream the Southwest AR. Three receivers were subsequently relocated to the SG on 21 and 22 August. Receiver recovery occurred from 20 to 30 September. Twenty-eight receivers (VR2/VR2W) were deployed 24 June to 23 July and recovered 9 to 26 September, 2009. The 2009 array again monitored the two estuaries and their respective rivers, but extended to include the coastline between them and along iFB's north and south coastlines ending near the Channel Islands (Fig. 2.1b). Five receivers were lost during the two tracking periods.

Receivers were deployed according to procedures outlined by Spares *et al*. (2012). Detection range was tested 13 August to 29 September, 2008, at the BR tag site in a 2 m deep tidal channel with a V13TP transmitter tied 0.5 m off the bottom to a vertical riser with a clear line of sight to a VR2W receiver anchored just off the bottom 47 m away. Detection efficiencies were calculated for the V13TP transmitter during *S. alpinus* tracking (13-29 August) and range test period. To determine any effects of tide phase on detection efficiency, detection efficiencies were calculated for each tide phase (high, ebb, low and flood) from 13 to 29 August. In 2009, a V7 was moored <10 m below a surface float for a minimum of one tidal cycle at stations 200 to 800 m from an intertidal VR2W receiver located at the mouth of the BR tidal channel corresponding to the low tide mark.

2.3.3 MARINE MIGRATION

2.3.3.1 Duration

The beginning of the marine migration 2009 occurred during ice-out in the SGR and was confirmed by the first catches of *S. alpinus* in the estuary below the falls at the river mouth.

Duration was calculated as the period between saltwater entry and freshwater re-entry. Freshwater re-entry was considered the last saltwater detection by receivers closest to head of tide. If no marine detection was recorded near the head of tide, the first detection by a freshwater receiver in either the AR or SGR was considered the re-entry date. Freshwater receivers were placed < 5 km upstream in the first available stretch of water > 1 m deep with no rapids. Individuals were unlikely to overwinter downstream of these receiver locations considering the water freezes solid to the bottom (pers. obs.). Freshwater entry sites were considered to be natal rivers, and fidelity was assessed during the two seasons of tracking. Tagging locations were considered as potential natal rivers since these sites were < 3 km from river mouths, however, since considerable mixing of individuals occurs for populations within 80 km of each other (Moore, 1975; Dempson & Kristofferson, 1987) and the fact the majority of tagging occurred during mid migration, migrants could have easily moved between the BR and SG estuaries.

2.3.3.2 Estuarine residency

Two estuarine zones were delineated within iFB: BR (6.6 km^2) and SG (1.5 km^2). *BR* included all inter/sub-tidal receivers within the AR outflow to the low tide mark and included receivers 1 km alongshore from the tidal channel mouth. *SG* included two receivers 3.5 km from the innermost cove at the base of SG Falls. All other receivers in iFB were considered 'extra-estuarine' (Fig. 2.1a & b). During the 2009 marine migration, the total number of individuals detected in both *BR* and *SG* estuaries were displayed as percentages of all tracked individuals and of those tracked individuals that survived the marine phase (i.e. re-entered fresh water).

Estuarine residence for individual *S. alpinus* was determined by calculating the total and consecutive (continuous presence) amount of time present at *BR* or *SG* estuarine zones. Any estuarine continuous presence < two minutes (two detections) was omitted (Collins *et al*., 2007). The ratio between an individual's total time present at either estuarine zone to total time monitored was calculated to provide a residency index. Residency values range from 0 to 1, with values close to 0 indicating low residence and values close to 1 indicating high residence (Knip *et al*. 2012). Absence from either estuarine zone was considered any period ≥ 24.8 h (ie. one lunar day). The number of times an individual char returned to *BR* or *SG* after an absence was tallied (Knip *et al*., 2012) and standardized to number of returns per days monitored.

Estuarine continuous presence, residency, number of returns and return rates were calculated for each individual during fifteen-day intervals using freshwater entry as the endpoint to determine if *S. alpinus* were present in either estuarine zone for different lengths of continuous presence periods, residency and returned more often during a specific interval. If an individual did not survive the marine migration or no freshwater entry date was determined, the mean freshwater entry date of 20 August was used. The final date of an individual's marine migration included time until 11:59:59 pm. Presence indices during migration intervals were tested for normality using Shapiro-Wilks tests. Normal and non-normal distributed data sets were compared using ANOVA or Kruskal-Wallis ANOVA, respectively (Baran & Warry, 2003).

2.3.4 MOVEMENT PATTERNS

2.3.4.1 Tidally influenced

Detection distribution data was mapped relative to tide phase: high, ebb, low and flood (Curry *et al*., 2006). High and low tides were defined as predicted tide time ± 1 h. Ebb was falling water levels between high and low tides, whereas flood was rising water levels between low and high tides (Materna *et al*., 2000). The dependent variable of individual straight-line distance (SLD) from the AR or SGR mouth and independent variable of tide phase were examined with descriptive statistics, tested for normality using a Shapiro-Wilks test, and compared using ANOVA or Kruskal-Wallis ANOVA depending on normal or non-normal data distribution, respectively (Baran & Warry, 2003).

2.3.4.2 Travel rates

Travel rate, expressed as kilometers traveled per hour ($km.h^{-1}$) and per day ($km.d^{-1}$), were estimated by dividing the distance between two receivers (expressed in kilometres and excluding 2x the receiver detection range for transmitters used) by the time (hours) it took for that fish to swim between the two receivers. Body lengths per second ($bl \cdot s^{-1}$) was calculated by dividing the distance traveled between receivers (m) by individual L_F (m) and the time (seconds) it took for that fish to swim between the receivers (Hubley *et al.*, 2008). Receiver detection range for the four transmitters used was assumed to be 100 (V6), 200 (V7), 350 (V9TP) and 500 m (V13TP; Lacroix & Voegeli, 2000; Hubley *et al.*, 2008; Vemco, 2009; pers. comm. Webber D, 2010). Movements between receivers spaced < four times the assumed detection range (0.4 km to 2.0 km) were excluded to avoid potential detection-range overlap between successive receivers and to address potential issues that could arise due to variable receiver spacing (Halfyard *et al.*, 2012). Tide phase was assigned based on the mean time between the two detections used in travel rates calculations. Travel rate estimates with travel times greater than two hours were excluded as they may have spanned more than one tidal phase.

2.4 RESULTS

2.4.1 RANGE TESTING

In 2008, the V13TP transmitter located 47 m from a continuously submerged receiver yielded a detection efficiency of 79% from 13-29 August (16 days) when tagged *S. alpinus* were present. Extending this range testing period to 29 September 2008 (47 days), detection efficiency remained relatively unchanged (83%). Median detection efficiencies during low (96%) and flood tides (92%) were significantly higher than those during high (33%) and ebb (85%) tides (Kruskal-Wallis, $H = 23.64$, $df = 3$, $P < 0.04$; Table 2.2). Range testing of a V7 transmitter and intertidal receiver yielded detections from 200 to 600 m away. Only one detection occurred at 600 m, with all other detections (98%) occurring at 200 m. Considering the receiver was exposed at low tide, range testing detection periods were limited to high water and ranged from 2h 22m to 7h 35m. Detection efficiencies at the 200 m distance ranged from 38% to 63%. Simultaneous detection by adjacent receivers of *S. alpinus* tagged with a V13TP revealed a detection range > 937 m may have been possible for this transmitter type within the study area.

2.4.2 TAGGING

Of the 61 individuals implanted with acoustic tags, 43 (mean ± S.D. $L_F = 523 \pm 97$ mm; minimum-maximum $L_F = 306\text{-}714$ mm; Table 2.1) were detected within two periods: 3 to 29 August 2008 and 1 July to 4 September 2009. Mean ± S.D. tag/body weight ratio was 0.4 ± 0.2%, ranging from 0.1-0.6%.

2.4.3 MARK/RECAPTURES

Of the eighty marine migrating individuals marked (acoustic and/or ID tags) in 2008-09, 28.8% ($n = 23$) were recaptured from August 2008 to July 2012. During this recapture period, seventeen were caught within BR or SG estuaries from 22 July to 26 August, accounting for 73.9% of all recaptures and 21.3% of all marked fish. The remaining six recaptures, 26.1% of all recaptures and 7.5% of all marked fish, occurred in the Armshow River (AR) from 6 October to 14 June. Estuarine recaptures were split 52.9% and 47.1% between BR and SG estuaries, respectively (Table 2.3).

2.4.4 MARINE MIGRATION

2.4.4.1 Duration

River ice break-up in the SGR occurred 18 June 2009 and *S. alpinus* were confirmed to be in the estuary 27 June. Some stomachs sampled were full of marine prey which suggested these fish had been in salt water for some time. A recapture (T19) on 14 June 2009, through lake ice in the northwest branch of the AR (Table 2.3) suggested seaward movement had not yet started. The first 2009 receiver was deployed within the SGR < 600 m upstream of the falls on 24 June and no tagged individuals were detected until 20 Aug when individuals were returning from the sea. Individuals tagged in 2008 (n = 15) and 2009 (n = 18) were detected in salt water from 1 July to 4 September 2009. Of the three individuals detected during early migration, all were tagged in 2008 at BR and first detected 1 to 3 July 2009 in the SG estuary. The first detection occurred within a day of the first 2009 marine receiver being deployed. Final marine detections of eleven individuals occurred 10 to 29 August 2008 in the cove connecting both AR branches. These individuals were not detected on the monitored SW AR branch, thus were assumed to head up the NW AR branch considering it was not monitored by a receiver. Three others were detected migrating up the SW AR branch: two large individuals (L_F = 576 & 596 mm) on 9 and 11 Aug 2008, and one smaller (L_F = 312 mm) on 27 August 2008. Analysis of L_F

relative to all freshwater re-entry detections revealed only a slight trend of decreasing individual L_F with later freshwater re-entries (L_F = -2.8484t + 119779, r^2 = 0.05). All detected individuals re-entered fresh water 9 to 29 August 2008, and 3 August to 4 September 2009. Mean freshwater re-entry dates were 16 August 2008 ± 7 days (*n* = 14), 22 August 2009 ± 6 days (*n* = 26), and 20 August2008/09 ± 7 days (Table 2.1). Assuming the same saltwater entry date (18 June) in both years, marine migration duration was 46 to 78 days for all tracked individuals which survived 2009. Mean ± S.D. durations were 59 ± 6 in 2008, 65 ± 7 in 2009 and 63 ± 7 days for 2008/09.

2.4.4.2 Estuarine residency

Monitoring over two marine migration seasons recorded 38,982 detections, with the majority (87%) within 6.3 km SLD of the AR or SGR mouths. From 3 to 29 August, 2008, and 1 July to 4 September, 2009, mean ± S.D. tracking periods of tagged *S. alpinus* were 9.0 ± 7.0 and 33.9 ± 9.3 days, respectively. Mean ± S.D. total time present at either estuarine zone for all individuals detected in 2008 and 2009 was 4.2 ± 3.9 and 11.8 ± 7.1 days, respectively. Median continuous estuarine presences were compared for all monitored *S. alpinus* in 2008 and 2009 considering both data sets failed normality tests (Shapiro-Wilk, $P < 0.05$). No significant difference was detected (Mann-Whitney U, T = 3510, $P = 0.79$), thus both years' data were pooled, resulting in a mean ± S.D. continuous estuarine presence of 2.3 ± 3.7 days (1.1, 2.4; median, interquartile range) with a minimum continuous presence of 3.5 minutes. A maximum continuous estuarine presence of 33.9 days was recorded for an individual (T47) that never left BR (Table 2.4, Fig. 2.2).

Mean ± S.D. residency to BR and/or SG estuaries during 2008 (0.51 ± 0.29) was higher than 2009 (0.37 ± 0.23) for tracked individuals (t-Test, -1.72, df = 24, P = 0.05), with 2009 residencies ranging from 0.10 to 0.99 (Table 2.4). In 2008 and 2009, 43.7% and 21.2%, respectively, of individuals spent more than half their time tracked within either estuarine zone. For all *S. alpinus* tracked, the number of returns to either estuarine zone were significantly lower in 2008 compared to 2009 (Table 2.4; t-Test, t = -4.10, df = 44, P = 0.001). There was no significant difference in return rates between 2008 and 2009 *S. alpinus* tracks (t-Test, t = -0.65, df = 47, P = 0.26), thus mean ± S.D. return rates for individuals returning to either estuarine zone during both seasons was 0.11 ± 0.09 (*n* =49), approximately one individual returning every 9.1 days.

2.4.4.3 Transition phase – early migration

Of the three individuals detected early in the marine migration, T7 remained near the SG estuary for the entire 22 days tracked (residency index = 0.60). Another (T6) demonstrated some degree of estuarine fidelity (residency index = 0.33), returning 4 times over the twelve days it was tracked (Table 2.4). The individual (T25) detected 1 July remained near the same SG receiver for three days, until departing and returning daily until 9 July, demonstrating a residency index of 0.44 over the first 7.6 days tracked.

2.4.4.4 Mid to late migration

All fifteen-day interval data sets failed Shapiro-Wilk normality tests ($P < 0.05$), thus statistical comparisons were performed using Kruskal-Wallis ANOVA post-hoc Dunn's Method and described using median, interquartile range [minimum, maximum] values (Baran & Warry, 2008). The median number of days individuals were tracked within BR and/or SG estuaries were significantly higher (Kruskal-Wallis, H = 23.76, df = 3, P < 0.001) during the last two (medians 15.0; mean dates: 22 Jul to 5 Aug & 6 to 20 Aug) migration intervals (Dunn's, P < 0.05) compared to the first two (medians 3.7 & 8.8; mean dates: 1 to 6 July & 7 to 21 July). Individuals spent significantly more time (Kruskal-Wallis, H = 17.578, df = 3, P < 0.001) in the estuarine zone during the final 15 days of their marine migrations (median 5.0) compared to the first two intervals (medians 0.9 & 2.4; Dunn's, P < 0.05; Table 2.5; Fig. 2.2). Median continuous presence periods within the migration intervals revealed the final interval having a significantly higher median value compared to the first two intervals (Kruskal-Wallis, H = 14.76, df = 3, P = 0.002; Dunn's, P < 0.05; Table 2.5). Considering the number of days tracked capped continuous presence periods, each continuous presence period was de-trended by dividing it by the total number of days that individual was tracked within each interval. Median continuous presence residual comparisons between migration intervals revealed no significant differences (Kruskal-Wallis ANOVA, H = 5.839, df = 3, P = 0.12). The final fifteen-day migration interval's residency (median 0.41) was only significantly higher than the previous fifteen-day interval (median 0.18; Kruskal-Wallis ANOVA post-hoc Dunn's Method, H = 10.45. df = 3, P = 0.02; Table 2.5). Interval comparisons for number of returns and return rates revealed no significant differences (Kruskal-Wallis ANOVA: H = 7.459, df = 3, P = 0.06 and H = 2.953, df = 3, P = 0.40, respectively; Table 2.5) with multiple returns occurring for the majority of individuals throughout their monitored migration (Fig. 2.2).

2.4.5 MOVEMENT PATTERNS

2.4.5.1 Tidally influenced

Detected *S. alpinus* moved in and out of the intertidal zone with the tide (Fig. 2.3 & 2.4), often using deeper channels as staging areas to access flooding shallows (A.D. Spares pers. obs.), demonstrated by T18 detected by VR2W-180 KHz receivers limited to a 100 m listening range (Fig. 2.3a). Illustrated percent detections during ebb/low tides revealed individuals retreated from intertidal to sub-tidal zones (Fig 2.4b, d), with some individuals subsequently detected along coasts further away from river mouths (Fig. 2.3b, d & 2.4). A higher % of detections occurred nearer river mouths within the intertidal zone during flood tides (Fig. 2.4c). Mean ± S.D. SLD of *S. alpinus* from either AR or SGR mouths during high and low tidal phases were 2.6 ± 2.8 km (n = 7849) and 5.4 ± 4.8 km (n = 5515), respectively (Fig. 2.4). Significant differences (Kruskal-Wallis, H = 3881, df = 3, $P < 0.001$) in SLD from either river mouth occurred during all tidal phases (Dunn's, $P < 0.05$). Percentage of detections revealed 72% occurred < 2 km SLD away during high tide. The highest percentage of detections during ebb, low and flood tides occurred < 2 km, 4 to 6 km and 2 to 4 km SLD, respectively, from river mouths (Fig. 2.4). Travel rates ($km.h^{-1}$, $bl.s^{-1}$) during high and ebb tide phases were significantly higher than during flood (Kruskal-Wallis, H = 23.84, df = 3, $P < 0.001$, post-hoc Dunn's Method, $P < 0.05$; Table 2.6). Tidally influenced movement pattern was recorded throughout the marine migration period, but occurred more frequently during estuarine residency periods (i.e. late migration; Fig. 2.2, 2.5 & 2.6).

2.4.5.2 Inter-estuarine

Evidence of inter-estuarine movements was provided by three individuals tagged at BR in 2008 and recaptured by SG fishers that same season (Table 2.3). Another three 2008 BR tagged individuals were detected only in the SG early the following 2009 season (Table 2.1). Based on these recaptures and detections, six (15%) of the 41 BR tagged individuals made the journey to SG. Of the 33 individuals tracked in 2009, 15% visited both estuaries. Of those surviving the 2009 migration (*n* = 26; Table 2.1), 19% were detected in both estuaries (Table 2.4). Four survivors tagged at BR made the trip to the SG (17%) and 3 returned (Fig. 2.3c). One of two survivors tagged at the SG in 2009 traveled to BR (Fig. 2.3b). Of all *S. alpinus* marked with acoustic or ID tags in 2008-09 (*n* = 80), 11 (14%) were either detected or recaptured in the opposite estuary between July 2008 and August 2011 (Table 2.3 & 2.4).

2.4.5.3 Extra-estuarine

Movement beyond monitored estuaries occurred mid-migration (mid-late July to mid-August; Fig. 2.3b-d; Fig. 2.5; Fig. 2.6), although many individuals still returned to either estuary throughout this period (Fig. 2.3d). One individual (T51) demonstrated estuarine fidelity during its initial and final 2 monitored migration days and extra-estuarine movements 29 July to 16 August (Fig. 2.5). Individuals spent more overall time and longer periods outside either BR and/or SG estuaries during 2009 compared to 2008 (Table 2.7).

Total time in the extra-estuarine zone was significantly higher in the second last fifteen-day migration interval compared to both adjacent intervals (Wallis-Kruskal post-hoc Dunn's, H = 10.7, df = 2, P = 0.005). There was no significant differences in the duration of extra-estuarine excursions during all three intervals (H = 5.81, df = 2, P = 0.06; Table 2.5). Extra-estuarine residency during the final fifteen-day migration interval revealed similar values in 2008 and 2009 (0.52 & 0.60, respectively; Mann-Whitney U, T = 319.5, P = 0.45), thus both years were pooled for residency interval comparisons. A significantly higher median extra-estuarine residency (Kruskal-Wallis, H = 12.01, df = 3, P = 0.007) occurred during the second last migration interval compared to the final fifteen days of the migration (Dunn's, $P < 0.05$; Table 2.5).

Of the 33 *S. alpinus* tracked in 2009, 14 (42%) ventured over 11 km SLD away from either estuary. Assuming the same migration endpoint of 20 August, individuals ventured over 10 km SLD from either the AR and/or SGR mouths 7 July to 16 August, and reached 27 km SLD away 19 July to 13 August. During the final four migration days, all detected individuals were within 10 km SLD of either river mouth (Fig. 2.6). Original tracking timestamps revealed four individuals (L_F = 521-540 mm) were 27 km SLD away from the AR mouth from 21 July to 13 August, 2009. These individuals remained at or near this receiver for periods of three hours up to 22 days before returning to BR (Fig. 2.3d). A receiver placed ~13 km further along the same coastline recorded no detections (Fig. 2.1b).

2.4.5.4 Travel rates

Mean ± S.D. and median, interquartile travel rates for all tracked individual's consecutive marine detections 2008/09 ($n = 994$), excluding calculations with inter-receiver distance < 4 times the respective detection range ($n = 326$), were $0.9\ \mathrm{km.h^{-1}} \pm 1.0$ ($22.7 \pm 24.1\ \mathrm{km.d^{-1}}$) and 0.6, $1.1\ \mathrm{km.h^{-1}}$ (14.6, $26.9\ \mathrm{km.d^{-1}}$), respectively; with a maximum rate of $9.5\ \mathrm{km.h^{-1}}$ ($227\ \mathrm{km.d^{-1}}$). Travel rates expressed as body lengths.$\mathrm{s^{-1}}$ ($\mathrm{bl.s^{-1}}$) were 0.50 ± 0.52 and 0.33, 0.60; with a maximum of 4.27 (Table 2.8). Median travel rates differed significantly (Kruskal-Wallis, $H = 16.92$, $df = 2$, $P < 0.001$) with the second-last 15-day interval being significantly lower than the intervals before and after it (Fig. 2.7). First interval travel rates were excluded from statistical analysis due to a low sample size ($n = 5$).

2.4.6 FRESHWATER RE-ENTRY

Of forty-one migrations monitored until freshwater re-entry, 39 (95.1%) ended with individuals choosing the river closest to their tagging site, while two individuals used the opposite estuary's river. Of two individuals tagged at SG, one each entered the SGR and AR. Six individuals were detected using the AR in both 2008 and 2009 (Table 2.1). One individual (T60) traveled from its tagging site at BR to the SG and returned to enter the southwest branch of the AR within the final 6 days of its marine migration (Fig. 2.3c). Surprisingly, after 5 days in the southwest AR, T60 briefly returned to the cove connecting the two river branches on 7 September to enter the northwest AR, where it overwintered, further confirmed by its recapture under lake ice by gill net on 6 December (Table 2.3).

2.5 DISCUSSION

2.5.1 RANGE TESTING

Detection range varied considerably considering use of four different transmitters, and highly variable environmental factors such as study site bathymetry; water column stratification, density, current velocity, levels and temperature; and wind speed and direction. Range tests conducted were limited due to inaccessibility of open water or inadequate equipment. Poor detection efficiency during high tide may have resulted in underestimates of estuarine residencies for tracked *S. alpinus*, however considering multiple receivers were deployed within the estuarine zones, individual presence was most likely detected during ebb & flood tides, even during periods of poor detection efficiency. One possible reason for lower detection efficiencies during high and ebb tide may be due to the receiver's location in a tidal channel which was protected from winds until water level rose well above the surrounding intertidal flats. Another possibility may have been the dramatic change in water density and temperature as colder marine water surrounded the test site during high and ebb tides (Chapter 3). On the Ocean Tracking Network's New Minas Passage listening line within the Bay of Fundy (13 m tidal range), Nova Scotia, poor detection efficiency occurred when current velocities were >2 $m.s^{-1}$ due to excessive noise interference (Reddin *et al*., 2014). Current velocities were not concurrently recorded at range test sites within this study, yet the macrotidal nature of iFB (11 m tidal range; Chapter 3) suggests similar interference occurred. According to criteria used for a standardized assessment of how well detection range was accounted for, this study scored 25/45, which may be described as 'passable' compared to a maximum score of 39 from 378 passive acoustic telemetry studies scored (Kessel *et al*., 2014).

2.5.2 MARINE MIGRATION

The migration of anadromous *S. alpinus* has been proposed to have three phases: (1) freshwater overwintering site to the sea; (2) estuarine transition residency; and (3) marine migration and feeding (Bégout Anras *et al*., 1999). Marine migration aspects were examined in this study (see Chapter 3 for marine diving behaviour, feeding and temperature preference), as receiver deployment and fish tracking were difficult during estuarine transition due to sea-ice break-up and high potential for recaptures in the SG fishery. Although few individuals were tracked during the first two weeks at sea, of those detected, all remained within five km of the Sylvia Grinnell River (SGR) mouth, suggesting estuarine transition occurred.

2.5.2.1 Duration

The marine migrations of iFB *S. alpinus* lasted 46 to 78 days; however, if an estuarine transition phase of approximately 10 days is recognized (Bégout Anras *et al*., 1999), the actual marine migration phase may be as short as 36 days. Migration duration varies depending on seasonal ice break-up and latitude, with iFB (63^{o}N) falling between the recorded minimum of 28 days in the central Arctic (68^{o}N; Johnson, 1989) and maximum of 109 days in northern Labrador (58^{o}N; Dempson & Kristofferson, 1987).

2.5.2.2 Estuarine residency

Estuarine residency of anadromous salmonids reduces osmoregulation stresses associated with movement between fresh and salt water, and provides a rich foraging environment resulting in faster growth and often higher marine survival (Miller & Sadro, 2003). Juvenile salmonids, coho *Oncorhynchus kisutch* (Walbaum 1792) and chinook *Oncorhynchus tshawytscha* (Walbaum 1792), spend days to months in the estuarine zone before entering and remaining in the open sea until migration end (Miller & Sadro, 2003; Bottom *et al*., 2005). As first-time individuals, small *S. alpinus* (mean L_F <150 mm) resided in estuaries due to poor osmoregulation while larger individuals successfully entered full strength salt water (Gulseth *et al*., 2000). Anadromous iFB *S. alpinus* were large enough to endure cold marine waters beyond intertidal zones and surface waters (Chapter 3), thus estuarine fidelity should not be taken as evidence of poor osmoregulation (Gulseth *et al*., 2000). Other *S. alpinus* populations have been documented migrating year-round in salinities ≥ 32 and temperatures ranging from -1.5^{o}C to 1.0^{o}C **(**Bystriansky *et al*., 2007; Jensen & Rikardsen, 2008; 2012)**.**

Estuarine use by *S. alpinus* does occur year-round, as demonstrated by a Norwegian fjord population remaining within the estuarine zone during winter (Jensen, 2013). Within iFB, *S.*

alpinus spent on average 37% of their total time tracked during summer 2009 in the estuaries. Estuarine residency was significantly higher in 2008, yet this was believed to be due to tracking covering the final 3 to 4 weeks of the marine migration when individuals were returning to fresh water. Individual estuarine residence indices in 2009 ranged from 0.10 to 0.99, suggesting some individuals roamed while others stayed home (Knip *et al*., 2012). In one case, high estuarine fidelity was demonstrated by an individual that remained within BR virtually the entire time monitored (34 days continuous presence), suggesting a low degree of anadromy (Dempson & Kristofferson, 1987). Yet the majority of individuals (78.8%) spent more than 50% of their time tracked beyond either estuary monitored, suggesting alternative warm water refuges and/or feeding grounds were used (Chapter 3). Interestingly, most individuals (81.8%) returned to either estuary multiple times throughout their migration, averaging once every 9 days. Similar behaviours of continuous (approximately 2 months) and intermittent (cumulative 1 month) presence were recorded for anadromous bull trout *Salvelinus confluentus* Suckley 1859, with estuarine returns averaging once per week (Goetz *et al*., 2004). Estuaries with large intertidal zones may serve as rich foraging grounds and aid in osmoregulation, and may also act as heat recovery arenas, encouraging estuarine residency of individuals which forage in significantly colder extra-estuarine waters. The optimum temperature for efficient digestion in *S. alpinus* occurred within iFB's intertidal/estuarine zones, further reinforcing estuarine residency as a behavioural thermoregulation adaptation (Chapter 3).

2.5.3 MOVEMENT PATTERNS

2.5.3.1 Tidally influenced

Tidally influenced movement has been documented for *S. confluentus* which moved between shoreline and estuarine zones with changing tides, particularly during flooding tide. Individuals were hypothesized to exploit the intertidal zone at high tide and return to permanently submerged tidal channels during ebb/low tide, remaining until flooding resumes (Goetz *et al*., 2004). Lower travel rates during flood tides suggested iFB *S. alpinus* waited for the intertidal zone to flood, with significantly higher travel rates occurring during high and ebb tides possibly indicating active hunting and/or rapid exits, respectively. Individuals' use of tidal channels, confirmed by tracking/personal observations, and increased catchability during flooding tides further supported these results. A previous study revealed these inter/sub-tidal movement patterns were possibly motivated by increased prey availability and behavioural thermoregulation (Chapter 3). Studies of other anadromous salmonid populations (cutthroat trout *Oncorhynchus clarki* (Richardson 1836), *O. kisutch*, *S. alpinus, Salvelinus fontinalis* (Mitchill 1814) have shown the same link to tidal periodicity (Moore, 1975; McCart, 1980; Power, 1980; Castonguay *et al*., 1982; Trotter, 1989; Montgomery *et al*., 1990; Miller & Sadro, 2003) with individuals remaining near shore during low tide to exploit the littoral zones during high tide (Curry *et al*., 2006).

2.5.3.2 Inter-estuarine

Past tagging has revealed summer coastal movements are geographically localized (Dempson, 1995), with the majority of *S. alpinus* recaptures in northern Labrador occurring within 70 km of tagging sites (Dempson & Kristofferson, 1987). Individuals may use different rivers from year to year, with dispersal of migrating individuals ranging from 0 to 66% and absences from original tagging river lasting 1 to 2 years (Dempson & Kristofferson, 1987;

Gyselman, 1994; Moore *et al*., 2013). Distinct populations exist on a microgeographic scale (less than 10 km) considering sufficient genetic divergence occurs. This implies most straying involves non-spawning individuals overwintering (Bernatchez *et al*., 1998; Moore *et al*., 2013).

Moore *et al*. (2013) found dispersal of anadromous *S. alpinus* varied from 15.8% to 25.5% among rivers within Cumberland Sound, Nunavut, which agrees with this study's results (14% to 19%). In a 2009-2011 study, VanGerwen-Toyne *et al*. (2013) marked *S. alpinus* at the SG with all recaptures occurring within SG or just east or west of the estuary, and no individuals recaptured at BR. Of 72 individuals marked at BR, only two (3%) were recaptured at the SG or Iqaluit (VanGerwen-Toyne *et al*., 2013), which is considerably lower compared to this study (15% to 17%). This study revealed individuals tagged in either BR or SG moved between both estuaries, with one of two SG tagged individuals detected within BR. Perhaps lower recapture returns by fishers versus acoustic tracking detection rates accounted for the inter-estuarine dispersal difference estimated in these two studies.

One individual completed a 40 km SLD return trip between the estuaries within its final week of migration, suggesting site fidelity to BR (i.e. Armshow River [AR]). It was possible this individual was seeking its natal river, and its subsequent river branch switch soon after entering an overwintering site (A.D. Spares pers. obs.) may have been due to homing to a specific spawning site (Sprules, 1952; Johnson, 1980) and/or relative density of individuals present within the first site triggering a migratory response (Tsukamoto *et al*., 2009). Genetic analyses revealed BR and SG stocks to be genetically distinct, but with some mixing (VanGerwen-Toyne *et al*., 2013), which may lend support to this individual homing to a specific spawning site.

2.5.3.3 Extra-estuarine

Large *S. alpinus* (L_F >300 mm) have averaged travel rates of 0.6 km.h^{-1} (maximum 4.3 km.h^{-1}) during their first 2 weeks at sea in the Canadian Arctic (Bégout Anras *et al*., 1999). Travel rates for iFB *S. alpinus* during the second-last 15-day interval were significantly lower than the intervals before and after. An explanation for this apparent behavioural difference may be longer periods between detections as many individuals were within the extra-estuarine zone where receiver coverage was lower. Other studies have estimated mean marine migration travel rates of 1.1 km.h^{-1} (maximum 5.3 km.h^{-1}) and 1.6 km.h^{-1} (maximum 3.6 km.h^{-1}) for dolly varden *Salvelinus malma* (Walbaum 1792) and *S. alpinus*, respectively (Armstrong & Morrow, 1980; Jensen, 2013). Inner Frobisher Bay *S. alpinus* travel rates were similar, averaging 0.9 km.h^{-1} (maximum 9.5 km.h^{-1}). Considering sustained swimming speeds for salmonids average 2-3 bl.s^{-1} with burst speeds up to 10 bl.s^{-1} (Brett, 1965), this study's estimated rates (mean ± S.D. = 0.5 ± 0.5; maximum 4.3 bl.s^{-1}) were well within the capability of *S. alpinus* and mirror marine migrating Atlantic salmon *Salmo salar* L. 1758 (0.6 bl.s^{-1}; Jákupsstovu, 1988).

Maximum distances traveled by *S. alpinus* during one marine migration season varies considerably (Klemetsen *et al*., 2003), with iFB *S. alpinus* matching the lower end of recorded maximums (< 30 km). Many studies have shown *S. alpinus* follow coastlines evidenced by recaptures and/or detections occurring near river mouths and/or along shorelines, even at distances up to 30 km SLD from origin river mouths (Bégout Anras *et al*., 1999; Jensen *et al*., 2014). Marine distribution of *S. confluentus* was similar, with captures occurring in river delta and/or near shore marine habitats and acoustic tracking revealing paths following shorelines and/or island coasts (Goetz *et al*., 2004). Tracking of iFB *S. alpinus* revealed an estuarine and near shore (< 3 km) distribution during the final two to three weeks of the marine migration (Chapter 3). Maximum distance detections from the two monitored rivers still occurred < one km from shore, suggesting a preference for near shore/littoral zones. Tracking of *S. confluentus* revealed individuals remained in deeper water just off shore during the day to move into the shallows near shore at night (Goetz *et al*., 2004). Although iFB *S. alpinus* used the littoral zone, this was synchronized by tidal rather than diel cycles as migration occurred during the annual period of perpetual daylight. It was still possible individuals ventured into pelagic zones of iFB, as *S. alpinus* has been caught up to five km off shore in other regions (Dempson & Kristofferson, 1987; Rikardsen & Amundsen, 2005), however, no long-term pelagic monitoring was conducted to verify this.

2.5.4 FRESHWATER RE-ENTRY

It has been suggested *S. alpinus* undergo physiological modifications (*i.e.* reverse smoltification) before freshwater re-entry, often moving in and out of estuaries while slowly accumulating salts to be diluted once in fresh water (Bystriansky *et al*., 2007). Chum salmon *Oncorhynchus keta* demonstrate this process where osmoregulatory processes are shut down and vertical ‘parr’ marks develop prior to freshwater entry (Uchida *et al*., 1997). Stomach content examination of *S. alpinus* re-entering fresh water revealed minimal occurrence of estuarine prey and undigested marine prey, suggesting little to no estuarine feeding and rapid transit from the marine environment (Bégout Anras *et al*., 1999). Rapid freshwater re-entry was demonstrated by T60 traveling from the SG to the southwest AR during its final 2 marine migration days, yet this individual may have undergone reverse smoltification during its final 6 days within both estuaries. The majority of individuals demonstrated a significantly higher estuarine residency during their final fifteen-day migration interval, with extra-estuarine movements restricted to within ten km of the river mouth (Chapter 3).

Individuals tagged at BR demonstrated preference (97%) for overwintering in the AR, with six individuals detected re-entering the AR in consecutive years, suggesting high site fidelity. Although *S. alpinus* have been documenting overwintering in the nearest freshwater system towards the end of their marine migration (Dempson & Kristofferson, 1987), there appeared to be specific homing in the case of some monitored individuals. Considering tagging of individuals occurred within the estuaries 2 to 4 weeks following saltwater entry, natal and/or previous overwintering river origin could not be verified, except for the six individual consecutive re-entries. Detections in 2008 of two large *S. alpinus* re-entering fresh water earlier than a smaller individual suggested larger individuals returned first, agreeing with Moore (1975), yet overall analysis revealed only a slight trend which may have been due to size selective tagging ($L_F > 300$ mm).

2.5.5 CONCLUSIONS

Detected *S. alpinus* spent on average approximately ⅓ of their time tracked within either monitored estuaries, with individuals displaying continuous or intermittent presence. Inner Frobisher Bay's macrotides directed *S. alpinus* intertidal/estuarine movements, with the lowest mean travel rates during flood tides suggesting staging of individuals before movement into intertidal zones. Although the estuaries were approximately 22 km apart, a portion of tagged individuals used both (19%). Individuals remained relatively close to freshwater overwintering systems, although late-migration inter-estuarine movements may have indicated natal homing. Approximately half of individuals exhibited extra-estuarine travel, mostly during mid-migration, but remained within three km of shore ranging < 30 km SLD of either estuary. Tracking evidence suggested an estuarine transition phase may also occur towards the end of marine migration prior to freshwater re-entry, similar to saltwater entry at the migration's beginning (Bégout Anras *et al*., 1999). It was concluded iFB *S. alpinus* (1) spent a significant portion of their migration within or adjacent to the estuaries, and (2) had a restricted marine distribution within 30 km SLD of the river mouths. An effective *S. alpinus* marine management plan should address anthropogenic pressures on adjacent as well as the focal estuary due to inter-estuarine mixing of different populations (Moore *et al*., 2013; VanGerwen-Toyne *et al*., 2013).

Table 2.1 - Summary of *S. alpinus* tagged at *Bay of Two Rivers* estuary and detected (*n* = 43) from July to September 2008/09 within inner Frobisher Bay, Nunavut, Canada.

ID #	**L_F (cm)**	***M* (Kg)**	**Tag Type**	**Tag/*M* Ratio (%)**	**Tagging Date (dd-mmm-yy)**	**Estuary detected in**	**FW entry '08/'09**
T2*	57.6	2.5	V9TP	0.25	22-Jul-08	BR	10-Aug/
T4	54.0	2.1	V13TP	0.57	22-Jul-08	BR	/30-Aug
T5	52.1	1.9	V9TP	0.34	22-Jul-08	BR	29/23-Aug
T6^{t}	61.2	3.0	V13TP	0.4	22-Jul-08	SG	-
T7^{t}	64.0	3.4	V13TP	0.35	22-Jul-08	SG	-
T11	59.6	2.8	V13TP	0.43	23-Jul-08	-	09-Aug/
T12*	54.0	2.1	V13TP	0.57	23-Jul-08	BR	/24-Aug
T13	58.6	2.7	V13TP	0.45	23-Jul-08	BR	/04-Sep
T14*	56.1	2.3	V9TP	0.27	23-Jul-08	BR	16-Aug/2-Sep
T18	51.9	1.9	V6	0.06	24-Jul-08	BR	-
T20	58.5	2.6	V6	0.05	24-Jul-08	BR	-
T25^{t}*	56.6	2.4	V13TP	0.5	25-Jul-08	SG	-
T27*	54.6	2.2	V13TP	0.55	25-Jul-08	BR	/23-Aug
T28	48.6	1.5	V9TP	0.41	09-Aug-08	BR	21/29-Aug
T29	45.0	1.2	V9TP	0.52	09-Aug-08	BR	14/28-Aug
T30	36.2	0.7	V6	0.18	09-Aug-08	BR	-
T31	53.0	2.0	V13TP	0.6	09-Aug-08	BR	10/18-Aug
T32	56.6	2.4	V13TP	0.5	10-Aug-08	BR	19-Aug/
T33	52.8	2.0	V13TP	0.61	10-Aug-08	BR	12-Aug/
T34	32.8	0.5	V6	0.24	10-Aug-08	BR	16-Aug/
T35	30.6	0.4	V6	0.3	10-Aug-08	BR	12-Aug/
T37	31.2	0.4	V6	0.28	10-Aug-08	BR	27-Aug/
T39	61.6	3.1	V13TP	0.39	11-Aug-08	BR	20-Aug/

T40	53.8	2.1	V13TP	0.58	11-Aug-08	BR	22/23-Aug
T41*	54.4	2.1	V9TP	0.3	11-Aug-08	BR	12/8-Aug
T44[sg]	49.2	1.0	V9TP	0.64	08-Jul-09	SG	/20-Aug
T45[s]	32.9	0.3	V7	0.58	09-Jul-09	BR, SG	/28-Aug
T46	71.4	3.8	V9TP	0.17	17-Jul-09	BR	/03-Aug
T47*	60.0	2.2	V9TP	0.29	17-Jul-09	BR	/20-Aug
T48	56.7	1.8	V9TP	0.35	17-Jul-09	BR	/14-Aug
T49*	61.9	2.4	V9TP	0.26	17-Jul-09	BR, SG	-
T50*	53.4	1.5	V9TP	0.42	17-Jul-09	BR	/24-Aug
T51	61.6	2.4	V9TP	0.27	17-Jul-09	BR	/18-Aug
T52	61.8	2.4	V9TP	0.26	17-Jul-09	BR, SG	-
T53	56.6	1.8	V9TP	0.35	17-Jul-09	BR	-
T54[g]	50.7	1.3	V7	0.14	18-Jul-09	BR, SG	/21-Aug
T55*	57.9	2.0	V7	0.09	18-Jul-09	BR	/22-Aug
T56	52.5	1.4	V7	0.12	20-Jul-09	BR	/16-Aug
T57	32.0	0.3	V7	0.6	20-Jul-09	BR	/25-Aug
T58	50.9	1.3	V7	0.14	21-Jul-09	BR	/20-Aug
T59	37.0	0.5	V7	0.38	21-Jul-09	BR	/25-Aug
T60*	54.5	1.6	V7	0.11	21-Jul-09	BR, SG	/02-Sep
T61*	53.3	1.3	V7	0.14	14-Aug-09	BR	/20-Aug
mean	**52.3**	**1.9**		**0.35**			
± SD	**± 9.7**	**± 0.9**		**± 0.17**			
min	**30.6**	**0.3**		**0.05**			
max	**71.4**	**3.8**		**0.64**			

* fish recaptured; AR Armshow River; BR Bay of Two Rivers estuary; FB inner Frobisher Bay; FW fresh water; [g] fish entered Sylvia Grinnell River at end of marine migration, all others entered the Armshow River; MR## ID tagged fish only; SG Sylvia Grinnell River/estuary; T## acoustically & ID tagged fish; TP Temperature/Pressure (depth) sensor tag; [s] fish tagged at SG (*n* =2); [t] fish tagged at BR ‘08, but only detected at SG ‘09.

Table 2.2 - Mean ± S.D., median, interquartile range (IQ), minimum, maximum and number (*n*) of detection efficiencies (%) calculated during high, ebb, low and flood tide phases for a V13TP acoustic transmitter 47 m away from a continuously submerged VR2W receiver located in an intertidal zone tidal channel at *Bay of Two Rivers*, inner Frobisher Bay, Nunavut, Canada from 13 to 29 August, 2008.

tide phase	**mean ± S.D.**	**median, IQ**	**min**	**max**	***n***
high	47 ± 42	33, 86	0	100	32
ebb	80 ± 17	85, 27	46	100	31
low	93 ± 10	96, 9	53	100	32
flood	92 ± 5	92, 9	76	99	32

Table 2.3 - Recaptures of *S. alpinus,* (*n* = 23) tagged at *Bay of Two Rivers* estuary, inner Frobisher Bay, Nunavut, Canada, from July to August 2008/09.

ID	**Tagging date**	**Recapture date**	**Recapture location**
T1	21-Jul-08	Late Aug-09	BR
T2	22-Jul-08	26-Aug-09	BR
T8	22-Jul-08	11-Aug-08	SG
T12	23-Jul-08	4-Aug-10	BR
T14	23-Jul-08	20-Apr-10	AR
T15	24-Jul-08	14-Aug-08	SG
T19	24-Jul-08	14-Jun-09	AR
T21	25-Jul-08	11-Aug-08	SG
T25	25-Jul-08	23-Jul-09	SG
T27	25-Jul-08	25-Aug-09	BR
T41	11-Aug-08	4-Aug-10	BR
T47	17-Jul-09	22-Jul-12	BR
T49	17-Jul-09	14-Aug-09	SG
T50	17-Jul-09	16-Aug-11	BR
T54	18-Jul-09	12-Jul-12	SG
T55	18-Jul-09	10-Oct-10	AR
T60	21-Jul-09	6-Dec-09	AR
T61	14-Aug-09	16-Aug-10	SG
MR10	31-Jul-09	6-Oct-09	AR
MR13	31-Jul-09	25-Jun-10	SG
MR14	31-Jul-09	11-Oct-09	AR
MR16	31-Jul-09	23-Aug-10	BR
MR--	31-Jul-09	25-Aug-09	BR

AR Armshow River; BR Bay of Two Rivers estuary; MR## Floy ID tagged fish only; SG Sylvia Grinnell estuary; T## acoustically & ID tagged fish.

Table 2.4 - Tracking summary of individual *S. alpinus* from 3 to 29 August, 2008 (*n* = 16), and 1 July to 4 September, 2009 (*n* = 33), showing total number of days tracked and total and continuous presence [days; mean ± S.D., (minimum, maximum)], residency, number of returns and return rates (# returns.day^{-1}) within Bay of Two Rivers and/or Sylvia Grinnell estuarine zones. Residency index values range from 0 to 1 (low to high residency), calculated as the ratio of an individual's total time present at either estuarine zone to total time monitored (Knip *et al.* 2012).

ID	# Days	Total Presence	Continuous Presence	Residency	# Returns	Return Rate
2008						
T2	7	0.004	0.004	0.001	0	0.00
T5	26	12.48	2.08 ± 2.40 (0.004, 6.56)	0.48	5	0.19
T14	11	9.88	4.94 ± 1.24 (4.06, 5.81)	0.90	1	0.09
T18	18	5.48	1.10 ± 0.94 (0.002, 2.44)	0.31	5	0.28
T28	12	9.96	3.32 ± 0.99 (2.52, 4.43)	0.85	2	0.17
T29	5	3.88	3.88	0.80	0	0.00
T30	7	3.56	1.78 ± 1.19 (0.94, 2.62)	0.54	1	0.15
T31	1	0.72	0.72	0.89	0	0.00
T32	9	3.12	1.55 ± 2.01 (0.14, 2.98)	0.34	1	0.11
T33	2	1.80	1.80	0.91	0	0.00
T34	6	2.48	1.24 ± 1.33 (0.30, 2.18)	0.42	1	0.17
T35	2	0.71	0.71	0.37	0	0.00
T37	17	1.45	1.45	0.09	1	0.06
T39	9	3.13	1.04 ± 0.71 (0.35, 1.76)	0.35	2	0.22
T40	11	7.50	2.50 ± 2.92 (0.009, 5.71)	0.69	2	0.18
T41	1	0.25	0.25	0.30	0	0.00
mean	9	4.2	1.90	0.51	1.3	0.10
SD	7	3.9	1.77	0.29	1.7	0.10
min	1	0.004	0.002	0.0006	0	0
max	26	12.5	6.56	0.91	5	0.28
2009						
T2	42	4.24	0.85 ± 0.35 (0.36, 1.18)	0.11	4	0.10
T4	46	16.03	2.29 ± 4.94 (0.006, 13.46)	0.35	6	0.13
T5	39	6.26	1.04 ± 0.69 (0.15, 2.10)	0.16	5	0.13
T6	12	3.89	0.78 ± 0.46 (0.01, 1.17)	0.33	4	0.33
T7	22	13.28	2.21 ± 1.76 (0.53, 5.09)	0.60	5	0.23
T12	39	12.63	1.15 ± 0.99 (0.003, 2.81)	0.32	10	0.26
T13	50	20.03	4.01 ± 5.30 (0.07, 11.30)	0.40	4	0.08
T14	40	14.72	2.94 ± 2.84 (0.11, 6.82)	0.37	4	0.10
T25	22	5.59	0.70 ± 0.99 (0.03, 2.81)	0.26	7	0.32
T27	38	3.80	0.63 ± 1.25 (0.03, 3.17)	0.10	5	0.13
T28	44	19.94	1.81 ± 1.79 (0.03, 6.08)	0.46	10	0.23
T29	45	8.19	2.05 ± 3.50 (0.07, 7.29)	0.19	3	0.07
T31	33	3.53	1.18 ± 1.38 (0.005, 2.70)	0.11	2	0.06

T40	39	10.58	1.06 ± 1.59 (0.04, 4.95)	0.27	9	0.23
T41	23	19.53	2.05 ± 6.51 (0.03, 19.28)	0.86	2	0.09
T44	42	6.02	3.01 ± 2.56 (1.19, 4.83)	0.14	1	0.02
T45	48	11.98	2.30 ± 4.01 (0.20, 8.82)	0.25	3	0.06
T46	18	11.64	5.82 ± 3.78 (3.14, 8.50)	0.67	1	0.06
T47	35	33.88	33.88	0.99	0	0.00
T48	28	12.20	6.10 ± 4.01 (3.26, 8.94)	0.43	1	0.04
T49	27	5.14	1.71 ± 1.89 (0.02, 3.75)	0.19	2	0.06
T50	39	13.00	4.33 ± 5.10 (1.04, 10.21)	0.34	2	0.05
T51	32	6.48	1.30 ± 1.09 (0.007, 2.65)	0.20	4	0.12
T52	21	9.50	3.17 ± 3.14 (0.99, 6.77)	0.45	2	0.10
T53	36	7.34	1.83 ± 0.95 (0.61, 2.92)	0.21	3	0.09
T54	34	8.55	2.85 ± 2.22 (0.50, 4.90)	0.25	3	0.09
T55	35	12.85	1.84 ± 1.98 (0.36, 5.93)	0.37	6	0.17
T56	27	24.30	12.15 ± 5.32 (8.39, 15.91)	0.92	1	0.04
T57	36	25.16	3.59 ± 3.60 (0.03, 8.69)	0.71	6	0.17
T58	30	6.00	3.00 ± 2.25 (1.41, 4.59)	0.21	1	0.03
T59	34	17.56	1.95 ± 1.92 (0.30, 6.61)	0.51	8	0.23
T60	43	10.19	3.40 ± 3.73 (0.80, 7.67)	0.24	2	0.05
T61	21	5.76	1.92 ± 2.00 (0.008, 4.00)	0.27	2	0.09
mean	34	11.8	2.44	0.37	3.9	0.12
S.D.	9	7.1	3.98	0.23	2.7	0.09
min	12	3.5	0.003	0.10	0	0
max	50	33.9	33.88	0.99	10	0.33

Table 2.5 - Median, interquartile range (minimum, maximum) for number of days tracked, estuarine and extra-estuarine total/continuous presence (days), continuous presence residuals, residency, number of returns, return rates (returns.day^{-1}) and travel rates (km.h^{-1}, body lengths.s^{-1}) for *S. alpinus*, tracked within inner Frobisher Bay, Nunavut, Canada, during fifteen-day intervals based on the mean migration endpoint of 20 August. Residency index values range from 0 to 1 (low to high residency), calculated as the ratio of an individual's total time present at either estuarine or extra-estuarine zone to total time monitored (Knip *et al*. 2012).

Mean Interval Dates	**1 – 6 July**	***n***	**7 – 21 July**	***n***	**22 July – 5 August**	***n***	**6 – 20 August**	***n***
# days tracked	3.7, 2.0 (0.5, 5.4)	6	8.8, 8.8 (2.3, 15.0)	27	15.0, 2.8 (1.5, 15.0)	35	15.0, 6.0 (0.8, 15.0)	46
Estuarine zones								
total presence (days)	0.9, 1.5 (0.01, 2.8)	6	2.4, 2.5 (0.08, 7.8)	27	3.5, 6.0 (0.02, 15.0)	25	5.0, 6.9 (0.004, 14.5)	45
continuous presence (days)	0.47, 0.88 (0.006, 2.8)	10	0.97, 1.3 (0.005, 7.7)	53	0.67, 2.6 (0.001, 15.0)	51	1.8, 3.0 (0.002, 14.5)	97
continuous presence residuals	0.13, 0.22 (0, 0.58)	10	0.09, 0.19 (0, 1.0)	53	0.06, 0.25 (0, 1.0)	51	0.14, 0.28 (0, 0.97)	97
Residency	0.26, 0.43 (0, 0.58)	6	0.30, 0.40 (0, 1.0)	27	0.18, 0.45 (0, 1.0)	35	0.41, 0.48 (0, 0.97)	46
# returns	0.5, 1 (0, 2)	6	1, 2 (0, 4)	27	1, 1 (0, 5)	35	1, 1 (0, 5)	46
return rate (returns.day^{-1})	0.09, 0.21 (0, 0.41)	6	0.12, 0.26 (0, 0.36)	27	0.07, 0.13 (0, 1.4)	35	0.13, 0.11 (0, 0.56)	46
Extra-estuarine zone								
total presence (days)	2.6, 1.5 (0, 4.3)	5	4.7, 7.5 (0, 14.8)	24	10.1, 10.2 (0, 15.0)	33	5.7, 6.9 (0, 15.0)	46
continuous presence (days)	1.5, 1.0 (0, 3.1)	8	2.0, 2.9 (0, 12.7)	46	2.6, 6.7 (0, 15.0)	60	2.0, 2.2 (0, 15.0)	86
Residency	0.63, 0.49 (0, 0.90)	5	0.66, 0.34 (0, 0.99)	24	0.81, 0.47 (0, 1.0)	33	0.54, 0.49 (0, 1.0)	46
Migration travel rates								
km.h^{-1}	0.3, 0.3 (0.1, 0.5)	5	0.7, 1.2 (0.02, 6.3)	205	0.5, 0.9 (0.007, 9.5)	442	0.7, 1.4 (0.02, 4.9)	461
body lengths.s^{-1}	0.2, 0.1 (0.05, 0.2)	5	0.4, 0.6 (0.01, 3.3)	205	0.3, 0.5 (0.004, 4.3)	442	0.4, 0.7 (0.01, 2.5)	461

Table 2.6 - Median, interquartile range, minimum and maximum travel rates ($km.h^{-1}$, body length.s^{-1}) of *S. alpinus*, relative to tide phases (high, ebb, low and flood) within inner Frobisher Bay, Nunavut, Canada, from 1 July to 4 September, 2008-09.

Tide phase	**km.h^{-1}**	**min**	**max**	**bl.s^{-1}**	**min**	**max**	***n***
High	1.8, 0.9	0.5	6.3	0.93, 0.48	0.28	3.26	69
Ebb	2.0, 1.3	0.2	4.6	0.99, 0.65	0.11	2.45	109
Low	1.4, 1.6	0.4	8.5	0.76, 0.82	0.22	3.81	36
Flood	1.2, 0.9	0.3	9.5	0.60, 0.49	0.17	4.27	143

Table 2.7 - Mean ± S.D. and median, interquartile range (IQ) of extra-estuarine total and continuous presence (days) and residency indices for *S. alpinus*, tracked from 3 to 29 August, 2008, and 1 July to 4 September, 2009, in inner Frobisher Bay, Nunavut, Canada. Residency index values range from 0 to 1 (low to high residency), calculated as the ratio of an individual's total time present in the extra-estuarine zone to total time monitored (Knip *et al*. 2012).

Extra-estuarine	**mean ± S.D.**	**median, IQ**	**min**	**max**	***n***
2008					
Total presence	6.1 ± 4.5	5.2, 4.8	1.1	15.3	11
Continuous presence	2.9 ± 3.0	1.7, 2.1	1.0	14.2	23
Residency	0.39 ± 0.33	0.48, 0.57	0	1.0	16
2009					
Total presence	22.5 ± 10.2	25.0, 14.2	2.0	35.9	32
Continuous presence	5.1 ± 6.8	2.1, 3.1	1.0	35.0	140
Residency	0.62 ± 0.23	0.67, 0.26	0	0.92	33

Table 2.8 - Calculated travel rates ($km.h^{-1}$, $km.d^{-1}$, body length.s^{-1}) of *S. alpinus*, tracked within inner Frobisher Bay, Nunavut, Canada, from 1 July to 4 September, 2008-09. S.D. standard deviation IQ interquartile range

Travel rate	**mean ± S.D.**	**median, IQ**	**min**	**max**	***n***
km.h^{-1}	0.9 ± 1.0	0.6, 1.1	0.007	9.5	994
km.d^{-1}	22.7 ± 24.1	14.6, 26.9	0.17	227.5	994
body lengths.s^{-1}	0.50 ± 0.52	0.33, 0.60	0.004	4.27	994

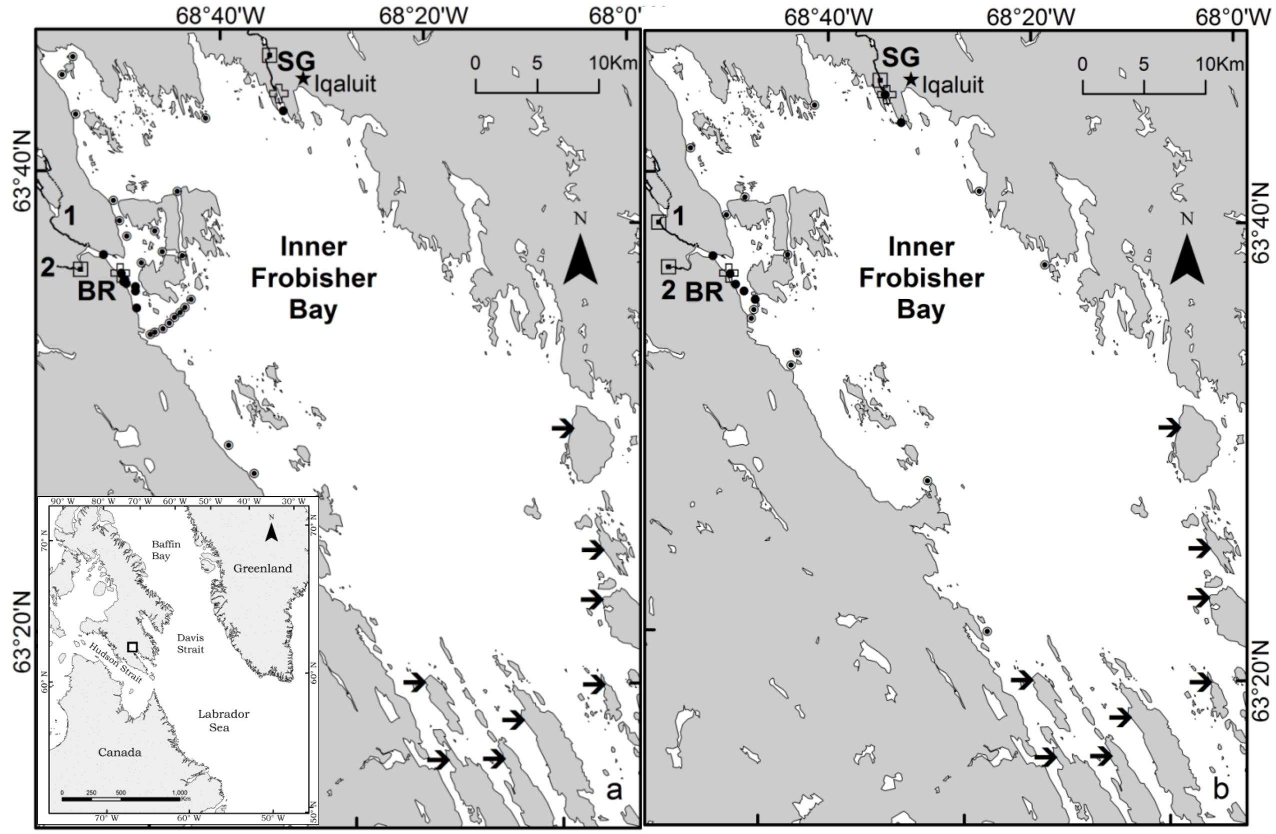


Figure 2.1 - Location of inner Frobisher Bay, Nunavut, Canada, showing the tag sites (✚) at Bay of Two Rivers (BR) and Sylvia Grinnell (SG) estuaries, northwest (1) and southwest (2) branches of the Armshow River, city of Iqaluit (★), and Channel Islands (➔). Estuarine (●), extra-estuarine (◉) and fresh water (▣) zone acoustic receivers (VR2/VR2W) are shown for 2008 (a) and 2009 (b).

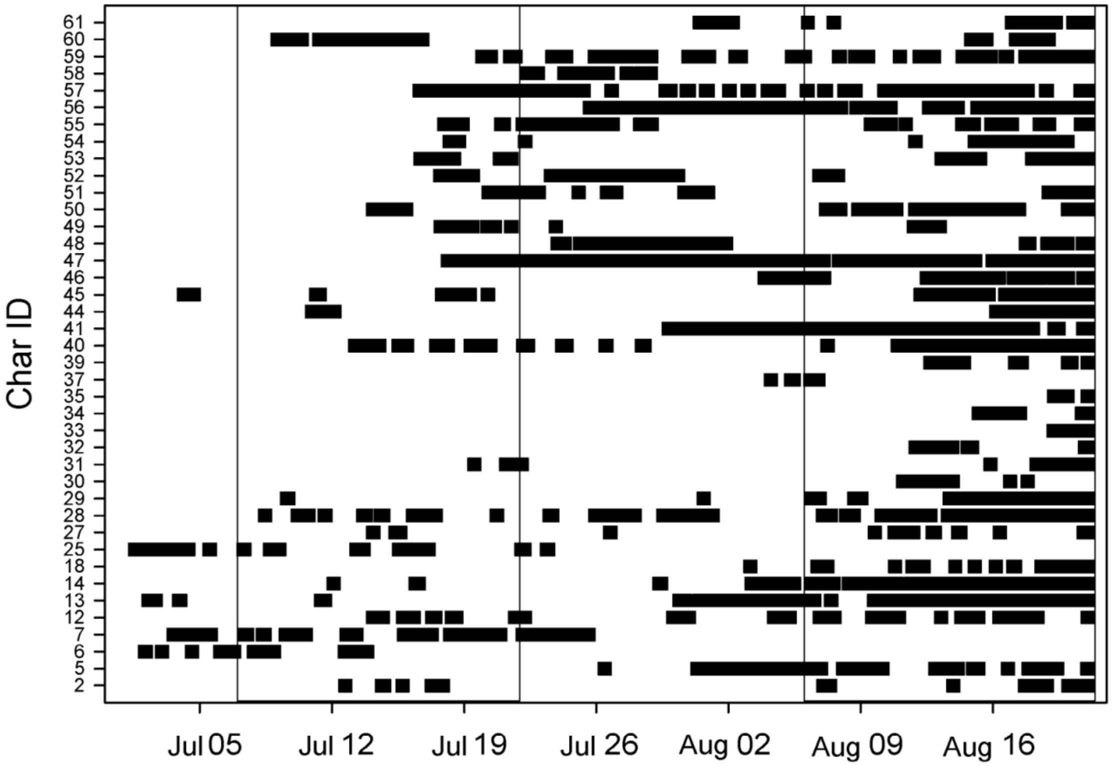
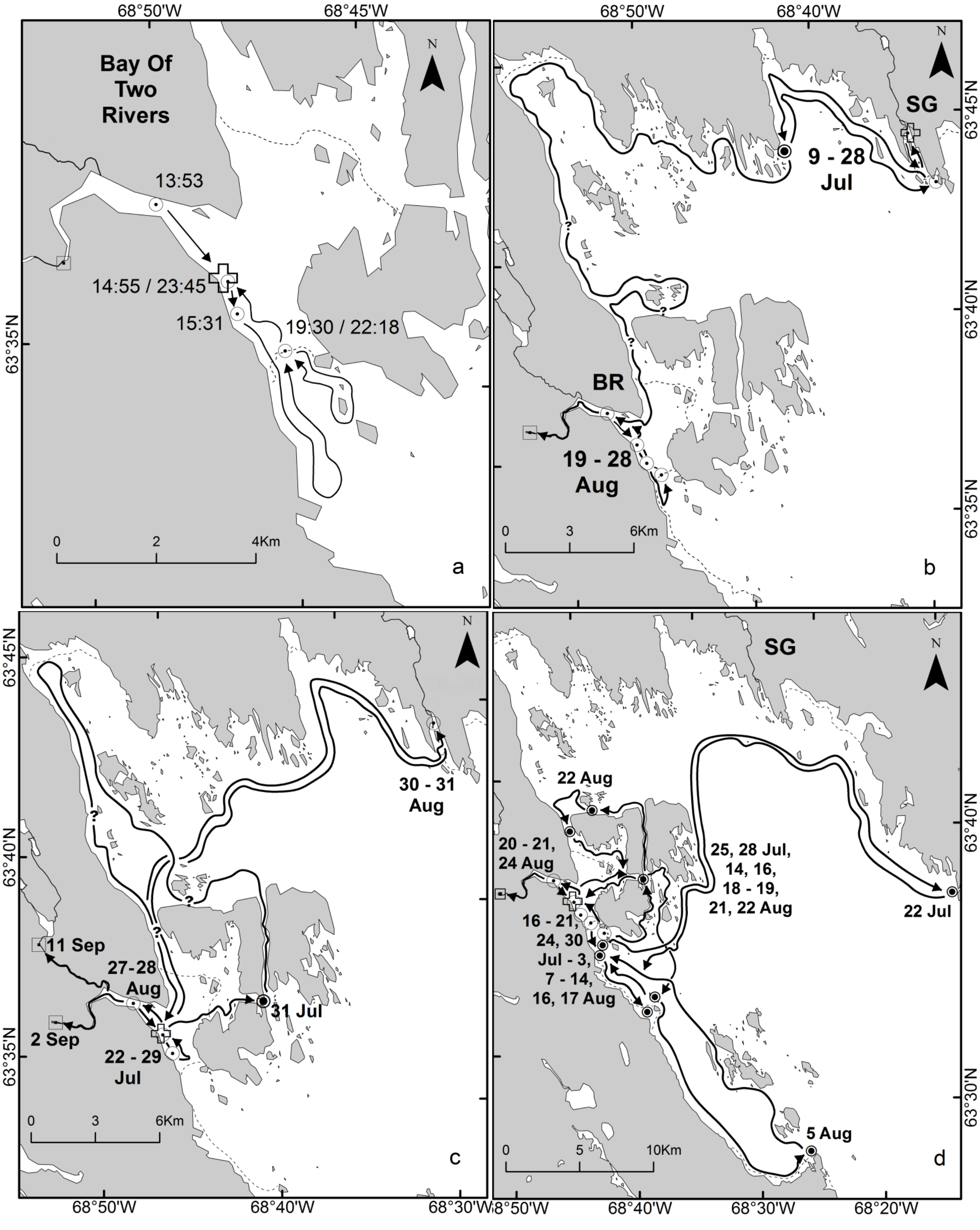


Figure 2.2 - Presence of individual S. alpinus, at either Bay of Two Rivers and/or Sylvia Grinnell estuarine zones within inner Frobisher Bay, Nunavut, Canada, 2008/09. For all individuals who completed their marine migration and/or survived beyond a mean endpoint of 20 August, timestamp data were adjusted accordingly. Any individual removed from the migration before 20 August retained original timestamps. Vertical lines represent start and end dates of fifteen-day intervals used for residency analyses.



68°50'W
68°45'W
Bay Of Two Rivers
N
13:53
14:55 / 23:45
15:31
19:30 / 22:18
63°35'N
0
2
4Km
a
68°50'W
68°40'W
63°45'N
SG
9 - 28 Jul
?
63°40'N
BR
19 - 28 Aug
63°35'N
0
3
6Km
b
63°45'N
N
30 - 31 Aug
63°40'N
?
11 Sep
27-28 Aug
31 Jul
2 Sep
22 - 29 Jul
63°35'N
0
3
6Km
c
68°50'W
68°40'W
68°30'W
SG
N
22 Aug
63°40'N
20 - 21, 24 Aug
25, 28 Jul, 14, 16, 18 - 19, 21, 22 Aug
22 Jul
16 - 21, 24, 30 Jul - 3, 7 - 14, 16, 17 Aug
63°30'N
5 Aug
0
5
10Km
d
8°50'W
68°40'W
68°30'W
68°20'W

Figure 2.3 - Tidally influenced, inter-estuarine, possible homing and maximum range migration movements of *S. alpinus* tracked in inner Frobisher Bay, Nunavut, Canada, 2008/09. Detection times (UTC) and locations (⊙estuarine, ◉extra-estuarine) of individual T18 relative to high (14:25 UTC) and low (20:42 UTC) tides at Bay Of Two Rivers on 21 August 2008 (a), T45 showing movement between Sylvia Grinnell and Bay Of Two Rivers estuaries (b), T60 showing a return trip between Bay of Two Rivers and Sylvia Grinnell (c) and T12 showing maximum straight line distance traveled away from either estuary (d). Arrows show known direction of travel with hypothetical tracks between receivers. Dashed lines represent approximate position of the low tide mark. Question marks represent VR2 receivers which were unable to detect the V7 transmitter carried by T45 & T60. Open cross represent tagging site for each tracked individual.

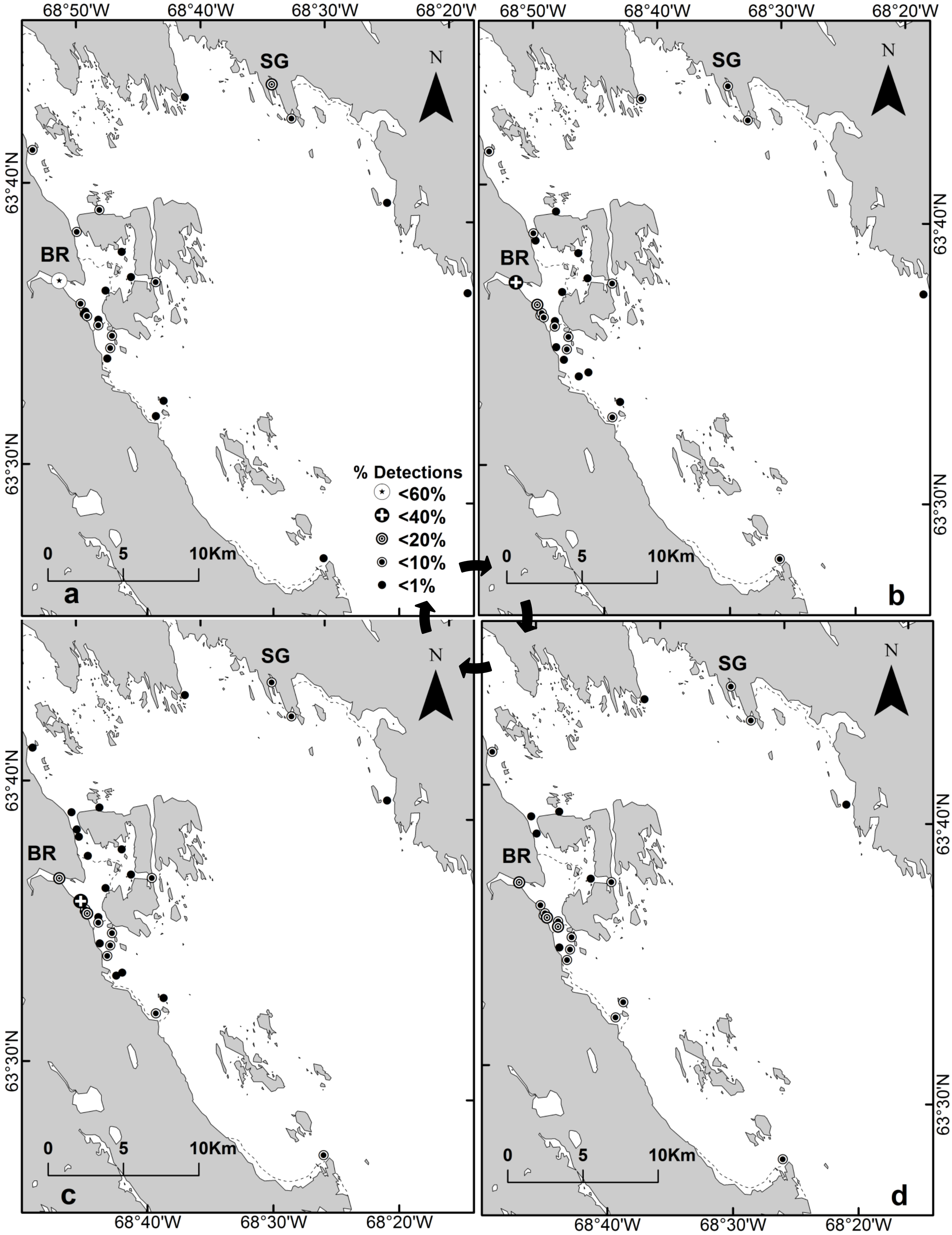

68°50'W
68°40'W
68°30'W
68°20'W
63°40'N
63°30'N
SG
BR
N
% Detections
<60%
<40%
<20%
<10%
<1%
0
5
10Km
a
b
c
d

Figure 2.4 - Percentage of detections recorded at each receiver relative to total number of detections recorded for tracked anadromous S. alpinus during high (a), ebb (b), flood (c) and low (d) tide phases in inner Frobisher Bay, Nunavut, Canada, from July to September, 2008/09.

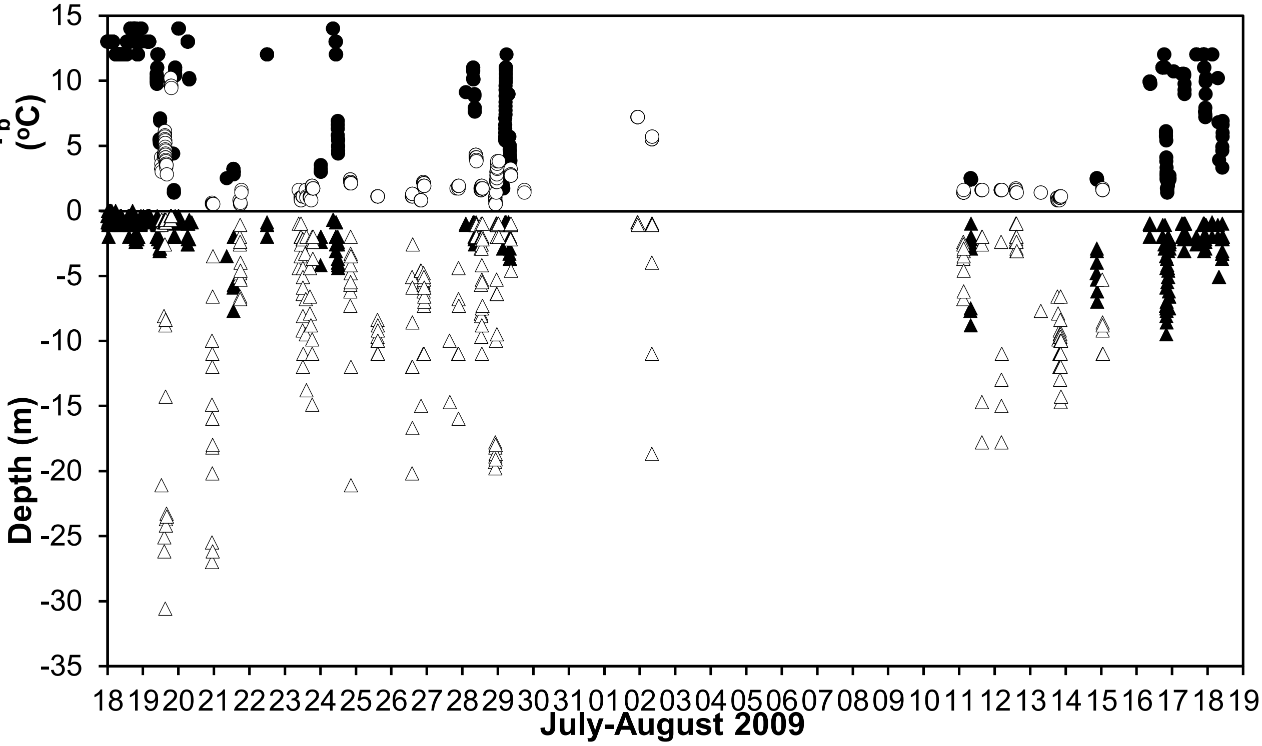


Figure 2.5 - Depth (m; triangle) and body temperature (°C; circle) of S. alpinus T51 relative to intertidal (solid symbols) and sub-tidal (open symbols) zones during marine migration in inner Frobisher Bay, Nunavut, Canada, from 18 July to 18 August, 2009.

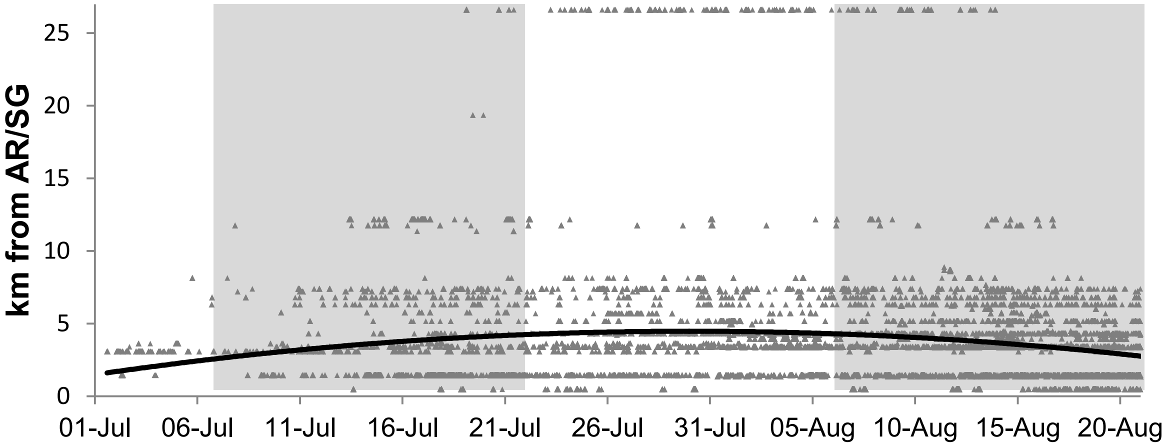


Figure 2.6 - Distance from Armshow and/or Sylvia Grinnell river mouths (km) relative to dates adjusted to mean freshwater entry of 20 August.

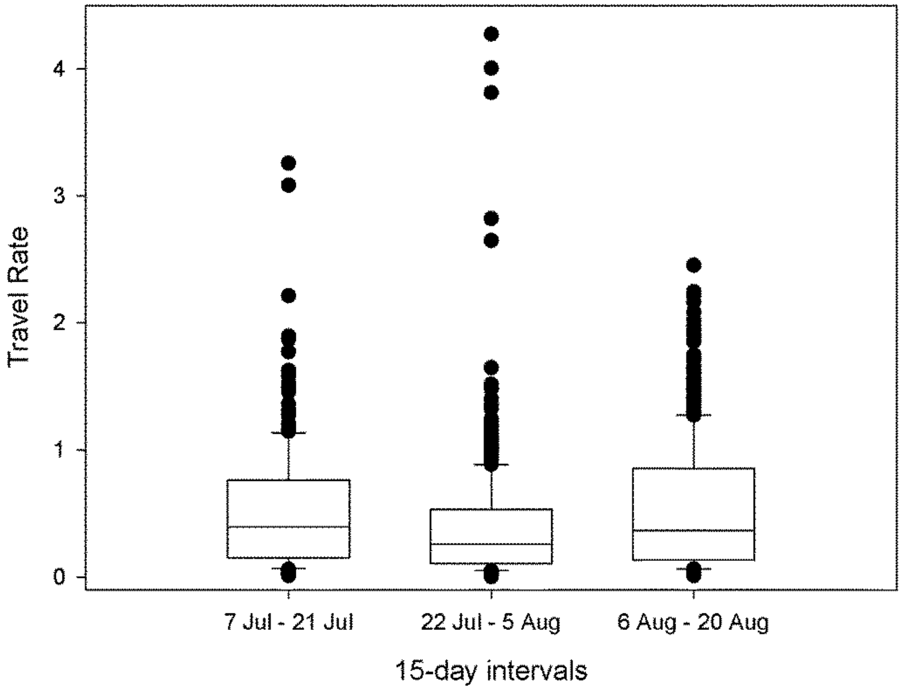


Figure 2.7 - Box-and-whisker plot showing median travel rate (body length.second-1) during fifteen-day intervals with freshwater entry as marine migration endpoint for S. alpinus tracked within inner Frobisher Bay, Nunavut, Canada. Box ends and whiskers represent interquartile range and minimum/maximum values, respectively. Outliers shown by solid circles. Interval dates labeled using mean freshwater entry of 20 August.

CHAPTER 3

TEMPERATURE, SALINITY AND PREY AVAILABILITY SHAPE THE MARINE MIGRATION OF ARCTIC CHAR, *Salvelinus alpinus*, IN A MACROTIDAL ESTUARY.

3.1 ABSTRACT

The influence of salinity, temperature and prey availability on the marine migration of anadromous fishes was determined by describing the movements, habitat use and feeding behaviours of Arctic char (*Salvelinus alpinus*). The objectives were to determine if char are restricted to the upper water column of the inter/subtidal zones due to higher temperatures. Twenty-seven char were tracked with acoustic temperature/pressure (depth) transmitters from June to September, 2008/09, in inner Frobisher Bay, Canada. The majority of detections were in surface waters (0 to 3 m). Inter/sub-tidal movements and consecutive repetitive dives (maximum 52.8 m) resulted in extreme body temperature shifts (-0.2 to18.1°C). Approximately half of intertidal and subtidal detections were between 9 to13°C, and 1 to 3°C, respectively. Stomach contents and deep diving suggested feeding in both inter/sub-tidal zones. We suggest that char tolerate cold water at depth to capture prey in the subtidal zone, then seek warmer water to enhance feeding/digestion physiology.

3.2 INTRODUCTION

Abiotic (ie. depth, salinity, temperature) and biotic (ie. prey availability) factors can influence marine migration patterns. A basic migration model for salmonid fishes shows movement, stock mixing and duration influenced by environmental conditions (depth, light, salinity, temperature); prey availability; and fish size, sex and state of maturation (Dempson & Kristofferson, 1987; Dadswell *et al*., 2010). To gain an understanding of how depth, salinity, temperature and prey availability influence marine migration patterns of anadromous fishes; the movements, habitat use and feeding behaviours of the Arctic char (*Salvelinus alpinus*), were examined using acoustic tracking, stomach content analysis and environmental monitoring from late June to early September in inner Frobisher Bay (63°N 68°W), Canada.

Anadromous Arctic char emigrate to sea as soon as rivers are ice-free (Moore, 1975). The majority of marine migrating char travel along shorelines (Moore, 1975), although some have been caught up to five km offshore (Dempson & Kristofferson, 1987; Rikardsen & Amundsen, 2005). Migrants have been recaptured up to 940 km away from natal rivers within one season (Klemetsen *et al*., 2003), however the majority average 30 km from natal river mouths (Moore, 1975; Bégout Anras *et al*., 1999). Inner Frobisher Bay migrants have been observed moving into the intertidal zone and up to river mouths with flooding tides (pers. obs.).

Anadromous Arctic char require a transition phase both to and from the ocean to adjust to changing salinity. Salinity tolerance increases with fish size (Bystriansky *et al*., 2007). Small char (fork-length <12 cm) can tolerate salinities of 20 or less, for periods up to four days in temperatures ranging from -1.1 to 12.0°C, whereas in salinities greater than 30 and temperatures below 0°C, survival depends on access to fresh or brackish water (Dempson, 1993). A recent study reported adult char (fork-length 38 to 50 cm) from a Norwegian riverine population overwintering in an estuary with salinities up to 24 and tidal exposure to salinity of 33 at temperatures down to 0°C (Jensen & Rikardsen, 2008). Large Arctic char (mean 3.8 ± 0.56 kg) returning to Somerset Island, Nunavut, Canada in August travelled through open ocean in a salinity of 32 with SST at 0°C, and yielded in an estuary with salinities of 25 to 32 and SSTs of -

1.5 to 1°C (Bystriansky *et al*., 2007). The majority of char overwinter in fresh water (Moore, 1975) leaving saltwater before temperatures drop to 0°C (Dempson & Kristofferson, 1987).

Ectotherm physiology is largely controlled by ambient temperatures, thus animals may move to alter physiological processes such as digestion (ie. behavioural thermoregulation; Bégout Anras *et al*., 1999). In fresh water, Arctic char can remain active at 0°C (Klemetsen *et al*., 2003), with growth occurring from -1.7 to 23.2°C (Larsson *et al*., 2005). Anadromous char from Nauyuk Lake, Arctic Canada entered saltwater with sea ice still present and water temperatures below -1°C (Klemetsen *et al.,* 2003). Saltwater tracking during summer revealed adult char (fork-length 37 to 51 cm) from Norway experienced water temperatures of 6.3 to 13.6°C (Rikardsen *et al*., 2007). In Cambridge Bay, Nunavut, Canada, acoustic tracking of char (fork-length 40 to 65 cm) during their first 10 days at sea revealed fish in water temperatures ranging from 5.8 to 11.4°C (Bégout Anras *et al*., 1999). Freshwater tracking of southeast Baffin Island landlocked adult char (fork-length 53 to 63 cm) revealed a temperature preference of 5.1 to 7.5°C during July and August (Dick *et al*., 2009). Landlocked Arctic char from New Brunswick, Canada demonstrated a preferred temperature of 9.2°C (Peterson *et al*., 1979), while laboratory studies showed juvenile freshwater char from Scandinavia selected a preferred temperature of 10.9°C from spring to autumn which was suggested to optimize food conversion efficiency (Larsson, 2005; Mortensen *et al*., 2007).

Marine feeding by Arctic char is intense, with migrants consuming up to 7.5% of their body mass per day (Klemetsen *et al*., 2003) and some individuals doubling their mass in just over a month (Dempson *et al*., 2002). Stomach contents have included fishes, including smaller char (Rikardsen & Amundsen, 2005), crustaceans, polychaete worms, insects, isopods, bivalve clams (Moore, 1975; Hunter, 1976; Grønvik & Klemetsen, 1987; Isinguzo *et al*., 2002;

Klemetsen *et al*., 2003) and zooplankton (Klemetsen *et al*., 2003). Depending on location, char feed primarily on invertebrates, predominantly amphipods; or fish, with *Ammodytes* spp. (sandlance), *Mallotus villosus* (capelin), *Gadus* spp. (cod), *Triglops* spp. and *Myoxocephalus* spp. (sculpins), as the most common prey (Dempson *et al*., 2002).

Due to regional variation in anadromous salmonid life histories (Brenkman *et al*., 2007), marine movement and habitat use should be correlated to ambient abiotic/biotic factors to enhance future fisheries management and conservation efforts, especially for populations potentially isolated from outside recruitment (ie. straying, immigration) and/or subjected to increasing human demands. Thus, we chose to study the increasingly exploited population of Arctic char from inner Frobisher Bay, Canada (Gallagher & Dick, 2010). Intertidal foraging in macrotidal estuaries has been documented in other anadromous fishes, such as Atlantic sturgeon (*Acipenser oxyrhynchus*) in the Bay of Fundy (Dadswell, 2006), thus we predicted Arctic char movements into the intertidal zone of inner Frobisher Bay would be influenced by prey availability. Based on depth preferences of char in past studies, we expected migrants to be restricted to intertidal/upper water column habitats due to higher temperatures.

3.3 MATERIAL AND METHODS

3.3.1 STUDY AREA

Located in southeast Baffin Island, Nunavut, Canada, Frobisher Bay is a semi-enclosed, macrotidal estuary divided by islands into a larger outer and a smaller inner bay. Inner Frobisher Bay (63^oN 68^oW) is approximately 25 by 70 km and less than 250 m deep (DFO 2008; Fig. 3.1). A maximum tidal amplitude of 11 m moves approximately 17 km^3 of water at a mean velocity of 1 m s^{-1} (3.6 km h^{-1}) in and out of the bay during a single, large tidal cycle (Grainger, 1975). Sea-ice cover occurs from November to June, with break-up beginning around mid-June, leaving waters relatively ice free July to October (pers comm Thomas 2008). Sea surface temperature rarely exceeds 4^{o}C (Moore, 1975).

Two major river systems within inner Frobisher Bay, the Sylvia Grinnell (Iqaluit; 63^{o}44'N 68^{o}34'W) and Armshow (63^{o}36'N 68^{o}50'W), are located about 20 km apart at the upper end (Fig. 3.1). The mouth of the Sylvia Grinnell River consists of a set of three waterfalls depending on tide and season. Two of the plunge pools form the innermost extent of the inlet. High tide rises to the base of all falls, and can reduce flow to a set of rapids during spring tides. During low tide, approximately two km of the inner inlet is exposed, yet shallow runoff continues to the low tide mark. The Armshow River consists of two main branches, the Northwest and Southwest. Both empty into the same cove approximately 450 m apart at the head of Bay of Two Rivers estuary. At high tide, the cove floods, and retains this water, along with freshwater inputs, at low tide. Overflow continuously empties into the estuary over a large tidal flat at low tide, yet run-off is too shallow for passage of large char. Approximately two km from the cove, run-off funnels into a major tidal channel (maximum depth 2 m) beginning at Bay of Two Rivers tag site and running approximately two km, tide dependent, to the low tide mark. Approximately 12 km^{2} of the benthic zone is exposed at low tide (pers obs). Both the Sylvia Grinnell and Armshow rivers contain overwintering populations of anadromous Arctic char (pers comm Amarok HTA 2008).

3.3.2 ACOUSTIC TRACKING

Acoustic transmitters with temperature/pressure (depth, TP) sensors were surgically implanted into marine migrating anadromous Arctic char to determine their horizontal and vertical movements and habitat use (inter/subtidal, temperature/depth preferences) relative to ambient environmental conditions. Char were captured in late and early Jul, 2008 and 2009, respectively, in the intertidal zone at Bay of Two Rivers with a 4.5" gill net, and by spin casting at Bay of Two Rivers and the Sylvia Grinnell River. Fish were triaged and candidates sedated (Aquacalm, 40 mg L^{-1}) before anaesthetizing (MS-222, 30-50 mg L^{-1}). Procedures, including fork-length measurement, external Floy ID tag insertion, and surgical implantation of a transmitter into the abdominal cavity, lasted less than four min per fish. One of two temperature/pressure (TP) coded sensor acoustic transmitters (V9TP, V13TP [69 kHz]; Vemco 2009) was selected so that tag mass was less than 2% of the fish's estimated body mass (Jepsen *et al*., 2002). Recovering fish were monitored one to four hours in a well-aerated cooler and/or tide pool before release.

Tagged char were tracked with passive acoustic receivers (Amirix/Vemco Ltd., Nova Scotia, Canada) 2 August to 30 September, 2008, and 24 June to 26 September, 2009. In 2008, thirty VR2W receivers were deployed 2 to 8 August (Fig. 3.2a). Receivers monitored Bay of Two Rivers estuary, its adjacent coastlines extending approximately 15 km northwest and southeast, and one km upstream the Southwest Armshow River. Three receivers were relocated to the Sylvia Grinnell River estuary 21 to 22 August. Receivers were recovered September 20-30. In 2009, twenty-eight VR2/VR2W receivers were deployed 24 June to 23 July and recovered 9 to 26 September. The array monitored Bay of Two Rivers and Sylvia Grinnell River estuaries, their respective rivers, the coastline between them, and inner Frobisher Bay's coastline extending towards the Channel Islands, approximately 40 km southeast of Armshow River and 20 km southeast of the Sylvia Grinnell River (Fig. 3.2b). Five receivers were lost, likely due to ice movements, sunken floats (pers obs) and/or human interference (pers comm. hunters 2009).

The intertidal was considered to be the zone between high tide and low tide, including tidal channels, which flowed continuously during ebb and low tide until flood tide. The subtidal zone was below mean low tide, including benthos exposed during spring tides. Freshwater was any waterway above high tide. Receiver locations were categorized as intertidal, subtidal or fresh water and coordinates were marked with a global positioning system. Receivers were tied directly to anchors and safety lines, or secured to a vertical line floated with a trawl float approximately three m above a rock anchor. A swivelled riser extended to the surface with one or two floats. Receiver placement was based on a minimum detection radius of 300-400 m (Vemco, 2009). However, detection range varies from 45-620 m (Heupel *et al*., 2006), thus a limited range test of an intertidal receiver and V7 acoustic transmitter was conducted testing ranges of 200-800 m.

3.3.3 STOMACH CONTENT ANALYSIS

Feeding behaviour was inferred from stomach content analysis of marine migrating char obtained opportunistically from fishers and by gill net. Fork-length to the nearest 0.1 cm and mass to the nearest 0.1 kg were recorded. Excised stomachs were individually wrapped, labelled and stored on ice until freezing at -20°C. In the laboratory, stomachs were thawed, contents removed, separated and identified to the lowest taxon possible. Due to advanced digestion, some contents were numerically estimated from identifiable body parts (Power *et al*., 2002). Excess moisture was blotted dry prior to counting and weighing (nearest 0.001g). Percentage of empty stomachs estimated feeding activity. Indices of occurrence (*%O*), number (*%N)*, and weight (%*W*) were used to determine frequency of each prey type consumed and relative importance of each (Hyslop, 1980).

3.3.4 DEPTH PROFILES

To determine the influence of ambient salinity and temperature on migrant movements, depth profiles of water temperature (^{o}C), salinity, pH and dissolved oxygen (mg L^{-1}), were taken from the surface every one m to a maximum depth of 20 m using a calibrated HYDROLAB Surveyor/DS5 or YSI85 sonde. Additional intertidal water temperature data were obtained with a temperature/pressure acoustic transmitter moored next to a receiver in a tide channel near BR tag site 13 August to 29 September, 2008 (Fig. 3.1). In 2008, a Slocum submersible glider fitted with a conductivity-temperature-depth sensor array profiled inner Frobisher Bay subtidal sites. All sites and dates were chosen based on watercraft and water monitoring equipment available for use, and ice/tide/wind conditions. Freshwater input temperature data was obtained from char returning to monitored pools in the Armshow and Sylvia Grinnell Rivers.

3.3.5 DATA ANALYSES

Undetected and stationary transmitters, possibly due to fish death, tag expulsion (Jepsen *et al.*, 2002) or malfunction, were removed from analyses. Sensor detections recorded beyond transmitter's calibrated range and/or temperatures recorded below salt water freezing point (-1.9^{o}C; DeVries & Cheng, 2005) were omitted. Distribution data were displayed relative to receiver location using ArcGIS software. Migrant mean body temperature and median swimming depth relative to intertidal and subtidal zones, were compared using a T and Mann-U Whitney test, respectively (Systat, 2009).

3.4 RESULTS

3.4.1 TRACKING

Range testing of a V7 transmitter and intertidal receiver yielded detections from 200 to 600 m away, however almost all (98%) occurred at 200 m. These detection periods were limited to high water, ranging from 2h22m to 7h35m, and resulted in detection efficiencies of 38 to 63%. Simultaneous detection by adjacent receivers of char tagged with a V13TP revealed a detection range greater than 972 m may have been possible within the study area. Tag/body mass ratio was 0.4 ± 0.1%, ranging from 0.2-0.6% (N = 27). Of the 36 char tagged with TP tags, 75% (mean ± SD = 56.6 ± 5.4 cm; min-max = 45-71.4 cm FL, N = 27) were detected 26,499 times 3 to 27 August, 2008 and 1 July to 4 September, 2009. The majority of detections (65%) were within 4 km straight line distance of the Armshow River or Sylvia Grinnell River mouths (Fig. 3.2c & d). From 21 July to 13 August, 2009, four char (fork-length 52.1 to 54 cm) ventured 26.6 km straight line distance from the Armshow River mouth. Individuals were in this area for 3 hours up to 22 days before returning to Bay of Two Rivers. No char were detected ~13 km further along the same coast (Fig. 3.2d). Intertidal detections occurred from 3 to 27 August, 2008 and 1 July to 4 September, 2009, and subtidal from 10 to 16 August, 2008, and 1 July to 30 August, 2009.

3.4.2 DEPTH PREFERENCE

In the intertidal and subtidal zone, 10,434 and 2,850 pressure detections were recorded from 13 July to 30 August, 2008-09, with median (interquartile range) depths of 0.7 (1.0) m and 3.0 (7.0) m, and maximum depths of 10 m and 52.8 m, respectively (Table 3.1). The majority of detections were within the top 3 m of the water column (86.6%; median depth = 0.9 (1.6) m, N = 11,504) with over half within the top metre (52.7%). When subdivided into intertidal and subtidal, however, 95.1% and 55.6% occurred within the top 3 m, and 57.2% versus 36.3% were in the top metre, respectively (Fig. 3.3a & b). The majority of tagged char (67%) descended to or below 10 m, accounting for 17.9% of subtidal detections (Fig. 3.3b). A significant difference in depth preference between inter/sub-tidal zones was determined (Mann U Whitney test, $t_{0.05,\,1}$ = 786, P <0.00). During subtidal excursions from mid-July to mid-August (Fig. 3.4), specific diving behaviour was recorded for multiple individuals as periodic series of consecutive, repetitive dives. Many dives were deeper than 30 m and short in duration, less than 7 minutes. Each series was followed by a period near the surface (Fig. 3.5).

3.4.3 BODY TEMPERATURE

From 13 July to 30 August, 2008-09, body temperature (T_b) detections in the intertidal (10,368) and subtidal (2,847) zones showed migrants experienced extreme body temperature shifts (-0.2 to 18.1°C). Mean intertidal body temperature was 9.4 ± 3.4°C (range -0.2 to 18.1°C, N = 10,368) compared to subtidal at 3.7 ± 3.1°C (-0.1 to 14°C, N = 2,847; Table 3.1). Approximately half (48.5%) of intertidal detections were between 9 to 13°C (Fig. 3.3a), whereas subtidal (55.5%) ranged from 1 to 3°C (Fig. 3.3b). Only 0.09% of inter/sub-tidal detections were at or less than 0°C. A significant difference in body temperature between intertidal and subtidal zones was determined (T test, $t_{0.05,\,1} = 3.21$, P = 0.04). Combined 2008-09 detections demonstrated mean migrant body temperature decreased linearly over the marine detection period (1 July to 4 September; Fig. 3.6; $F_{df=1} = 2746$, $R^2 = 0.2095$, intertidal; $F_{df=1} = 1232$, $R^2 = 0.3022$, subtidal; $p<0.05$).

3.4.4 STOMACH CONTENTS

Char were collected opportunistically from fishers at the Sylvia Grinnell River 27 to 29 June (N = 12) and 4 July (N = 13), 2009, and by intertidal gill netting at Bay of Two Rivers basecamp 11 to 12 July (N = 20), 2008, and 13 August (N = 13), 2009. Sizes ranged from 33.8 to 74.5 cm FL (mean 54.7 ± 8.3 cm, N = 58) and 0.5 to 4.1 kg (1.8 ± 0.7 kg, N = 58). Fifty-six stomachs contained prey (3.4% empty stomachs) from four major taxa: fish, crustaceans (mysids, amphipods, decapods), polychaetes and insects (Table 3.2). Crustaceans dominated, occurring in 87.5% of the stomachs, as 99.7% by number of items, and 94.8% wet weight of contents. Amphipods were consumed the most, constituting 95.2*%N* and 72.2*%W*, of which *Themisto libellula* (hyperiid amphipod; 14.9*%N*, 29.3*%W*) and *Onesimus littoralis* (gammarid amphipod; 70.8*%N*, 26.2*%W*) the dominant species. Mysids (*Mysis mixta*) also constituted a significant proportion (4.5*%N*; 22.6*%W*). Fish constituted the remainder, occurring in 26.8% of the stomachs as 5.0*%W*. Spiny lumpsuckers (*Eumicrotremus spinosus)* and pricklebacks (Stichaeidae) occurred most frequently (8.9%O) and were associated with *Mysis mixta* 11 to 12 July, and *Themisto libellula* 13 to 14 August, respectively. Insects were noted in 21.4% of all stomachs sampled, but only in samples collected 27 to 29 June (N = 9), 4 (N = 2) and 11 July (N = 1).

3.4.5 DEPTH PROFILES

Depth profiles (0-20 m) were taken in the intertidal zone on 2 August, temperature only from 13 August to 29 September, 2008; and 10 July, 1, 7 August, 2009. Subtidal profiles were taken on 2 August, 14 September, 2008; and 11, 31 July, 27 September, 2009. Glider depth profiles (0-30 m) occurred at subtidal sites 6-9 km from the Armshow River mouth on 25 and 26 July, and 8-10 km from the Sylvia Grinnell River mouth on 26 and 27 July, and 19 and 20

August, 2008. A cyclical pattern of warm and cold water dominated the intertidal zone, corresponding to tide ebb and flood. A cumulative intertidal profile revealed a warm (mean 6.4 ± 2.4°C, N = 2,042), brackish (mean 15.5 ± 11.6 , N = 16) layer in the top 3 m of the water column. Below 3 m, cold (mean 1.6 ± 0.6°C, N = 1,087), marine (mean 31.9 ± 0.2 , N = 6) water occurred to the bottom. Depending on stratification, subtidal salinity ranged from 2.1 to 33.0 in the top 3 m, but compared to intertidal waters remained relatively cool (mean 2.6 ± 1.4°C, N = 271) and saline (mean 30.1 ± 3.5, N = 271). Below 3 m to 30 m, water temperature fell below 3.0°C to -0.9°C (Table 3.3). Profiles on 10 July revealed a warm (0.9 to 12.1°C), brackish (0.1 to 29.4) 3 m top layer of melt water extending over 4 km from the Sylvia Grinnell River mouth. Below this, a well-mixed, cold (<0°C), marine (>30) water mass extended to the bottom. The upper subtidal layer became increasingly saline and colder following the melt and as summer progressed. From 6 August to 4 September, 2008/09, freshwater input temperatures ranged from 6.6 to 15.9°C (mean 10.6 ± 1.4 °C, N = 26,697).

3.5 DISCUSSION

Marine movement and habitat use studies are important for predicting species-specific responses to climate change (Rikardsen *et al.*, 2007). Unfortunately the ocean migration of many diadromous fishes remains one of the most poorly known portions of their life cycles. Advances in acoustic tracking technology have enabled such studies (Dadswell, 2009). However field tracking still faces financial, logistical and time limitations, which in the case of this study did not permit extensive sampling and resulted in more qualitative rather than quantitative comparisons.

3.5.1 DEPTH PREFERENCE

Our results showed Arctic char occupied the top 3 m of the water column most of the time. It was unclear, however, whether this was influenced by selection of an optimum temperature (ie. behavioural thermoregulation) to aid physiological processes, a feeding response to available prey, or a combination of both (Bégout Anras *et al.*, 1999; Rikardsen *et al.*, 2007). Our tracking revealed a preference for the warm upper layer from late June to early July during an apparent 'transition phase' to saltwater (Bégout Anras *et al.*, 1999). Stomach contents revealed two intertidal amphipod prey species, *Onesimus littoralis* (26.2%*W*) and *Gammarus duebeni* (15.4%*W*), which are near bottom and surface foragers (Sars, 1890). Availability of these prey could have influenced shallow depth preference, however, access would have been tide dependent. Benthic, shallow water, piscivorous prey, such as sculpins, could also have supported prey selection as a potential influence to dive to depth. Rikardsen *et al*. (2007) mentioned prey selection and preferred temperature as influences, with near surface feeding on vertically migrating planktonic crustaceans, and piscivory at greater depths (max. 16 m); or selection of slightly cooler water during the warmest period of the day, respectively, as evidence for both. Other marine migrating salmonids, such as Atlantic salmon (*S. salar*) predominantly used the top 40 m (prey selection) combined with extended periods in the upper 10 m (temperature preference; Jákupsstovu, 1988). Large landlocked Arctic char on southeast Baffin Island have shown a depth preference in the mid-water column of a small lake during summer with vertical movements both above and below this preferred zone, which suggested preferred temperature and prey selection as factors (Dick *et al*., 2009). Based on these examples and our findings, we suggest a combination of preferred temperature and prey selection controlled depth preference, as migrants utilized deeper subtidal water for prey selection, yet still returned to relatively warmer waters of the subtidal surface layer and intertidal brackish run-off layer (temperature preference).

3.5.2 INTERTIDAL/SUBTIDAL MOVEMENTS

The bimodal distribution of char body temperature reflected the two dominant thermal niches of warm intertidal estuarine and cold subtidal marine waters. Both zones experienced each niche due to substantial flushing (Grainger, 1975), yet access to both niches existed at all tide phases (high, ebb, low, flood) due to brackish/riverine run-off in intertidal channels/creeks, and a pool at the Armshow and Sylvia Grinnell river mouths (pers obs). Thus, migrants were not restricted to a thermal niche at any time. Thermoclines existed both horizontally between the intertidal and subtidal zones, and vertically in the upper water column (2 to 4 m) in each zone, through which migrants could have selected a preferred temperature. These natural gradients were used to estimate temperature preference for inner Frobisher Bay char.

The high frequency of intertidal detections throughout marine residency may have indicated a preference for significantly warmer water. Compared to smaller freshwater char with preferred temperatures ranging from 9.2 to 11.8^{o}C, larger fish have a lower temperature preference (Peterson *et al*., 1979; Reddin & Shearer, 1987; Jákupsstovu, 1988; Holm *et al*., 2003; Larsson, 2005; Mortensen *et al*., 2007). Mean intertidal body temperature of 9.4^{o}C in our study agreed with similar sized char tracked in 8.6^{o}C after salt water entry and remaining in relatively warm water, 6.8 and 7.5^{o}C, as they moved away from the river mouth (Bégout Anras *et al*., 1999). These data suggested 9.4^{o}C was an accurate estimate of temperature preference in the wild. Whether intertidal occupancy was motivated by prey availability and/or preferred temperature remains unclear.

Only one study to our knowledge estimated subtidal temperature preference, however its location (Alta Fjord, Norway) was substantially warmer (min 4.8°C at 24 m, max 14.7°C at 0 m; Rikardsen *et al*., 2007) compared to inner Frobisher Bay (min -0.9°C at 16 m, max 10.9°C at 0 m). Any extended period in the subtidal zone of inner Frobisher Bay lowered body temperature below 4°C, a mean body temperature decrease of 5.7°C compared to intertidal body temperature. Larger char (mean 3.8 ± 0.56 kg) migrated through even colder water (SST -1.5 to 1°C) off Somerset Island, NU (Bystriansky *et al*., 2007), which suggested thermal tolerance rather than selection of a preferred temperature. Interestingly, of all body temperature detections, hardly any (0.1%) were at or below 0°C, which agreed with other studies (Dempson & Kristofferson, 1987, Dempson, 1993, Jensen & Rikardsen, 2008), and suggested this may be a thermal limitation in full saltwater. Char captured in the intertidal zone had extremely full stomachs. Many contained subtidal prey only (pers obs), which suggested feeding before flood tide. Intertidal feeding alone would have significantly reduced potential energy gain during the short migration period, thus we believe subtidal feeding was essential, and appeared to be a plausible behavioural influence.

Rikardsen *et al*. (2007) noted Arctic char experienced a decreasing water temperature during their first 10 days at sea, and suggested prey preference, habitat selection and ⁄or their optimal temperatures for growth as reasons. However, we noted decreasing body temperature throughout the tracking period in both tidal zones. Most likely this reflected the ‘summer-fall recession’ of freshwater input, with the highest body temperatures correlating to the spring freshet. A brackish water layer on top of a saltwater layer often results in a warming greenhouse effect which increases the temperature of the upper thermocline between the layers (Spares & Dadswell, 2001). Thus decreasing solar radiation (ie. shorter days) and decreasing volume of the upper brackish layer combined with heat loss to the lower marine layer, may explain overall decreasing char body temperatures during the marine migration period.

3.5.3 SALINITY

It was uncertain how long char can tolerate full strength salt water at temperatures close to zero without compromising physiology. Char overwintered in a Norwegian estuary for a period of months in temperatures near 0°C (Jensen & Rikardsen, 2008). Our tracking revealed a decreasing frequency of return trips to the intertidal zone over the migration period, and migrants remaining within 30 km of the nearest major river mouth, thus it appeared large char were capable of tolerating extended periods of time in cold, marine waters (hours to days), yet were still invariably linked to warmer, brackish water associated with freshwater inputs as are juveniles (Dempson, 1993). Decreased salinity and increased temperature in the intertidal zone may have aided osmoregulation. Extended intertidal occupancy towards the end of the marine migration may have been an important behavioural adaptation which allowed migrants to shut down active Na^+ ion excretion pathways before re-entering fresh water (Bystriansky *et al.*, 2007). We acknowledged monitoring voids as a source of error for determining the frequency of visits to warmer water and/or the intertidal zone. Our summer distribution pattern agreed with a study in the Alta Fjord, Norway, which placed recaptured fish within 30 km of the river mouth (Rikardsen *et al.*, 2007). Other studies found this distance increased up to 80 km (Moore, 1975; Dempson & Kristofferson, 1987) with a maximum of 940 km for one char (Klemetsen *et al.*, 2003). These varying distances could have related to regional marine climate and availability of freshwater inputs.

3.5.4 DEEP DIVING

Feeding, more efficient digestion at lower temperatures, predator avoidance or olfactory orientation while homing, have all been suggested as reasons for diving behaviour. Homing orientation was suggested for char diving 16 m to get underneath the thermocline while returning to natal rivers in stratified estuary (Rikardsen *et al*., 2007). The same was suggested for salmonids diving before entering fresh water (Westerberg, 1982; Døving *et al*., 1985; Sturlaugsson & Thorisson, 1997). However, char in our study dived frequently to 10 m or deeper (18% subtidal detections), considerably lower than the thermocline at 2 to 4 m, thus an alternative to homing was more likely.

We dismissed predator avoidance, as char in this study were too large for capture by loons (*Gavia spp;* pers obs), and although mammals (seals, *Phoca* spp.; belugas (*Delphinapterus leucas*), killer whales (*Orcinus orca*; Richard, 2001); Polar bears (*Ursus maritimus*; Dyck & Romberg, 2007) are capable hunters, it was doubtful diving behaviour would have evolved as an effective defence strategy. Aiding efficient digestion was rejected considering an isothermal column of cold water (-1 to 1°C) was accessible 2 to 4 m from the surface. In addition, the energetic cost of diving may have countered energy saved by more efficient digestion.

Migrant stomach contents revealed young and adult *T. libellula* pelagic amphipods as staple prey items (29.3*%W*). Juvenile *T. libellula* have been shown to occupy surface waters, with adults inhabiting deeper water (Sars, 1890), which suggested char were feeding throughout the subtidal water column. Nectobenthic pelagic mysids, *Mysis mixta*, have been shown to undergo diel vertical migrations, remaining near the bottom in cold, relatively darker waters (~ 50m) to avoid predation, but rising towards the surface during lower light intensity periods to forage (Viherluoto, 2001). Considering 24 hrs of light occurred most of the study period, with low light intensity lasting approximately 4 hrs (0300 to 0700 h UTC, pers obs), it's very likely char had to dive deep in order to hunt mysids.

Pelagic fishes, Arctic cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) supported feeding throughout the water column, as both have been shown to inhabit surface waters down to depths below those of inner Frobisher Bay (Scott & Scott, 1988). Predation of Arctic cod may have occurred near drifting sea ice as both cod and char have been shown to associate with these habitats (Scott & Scott, 1988; Bégout Anras *et al*., 1999). As an interesting zoogeographical note, our study may have documented the first account of capelin as char prey in the fjords of southeastern Baffin Island (63°N; Grainger, 1953, FB; Moore & Moore, 1974, Cumberland Sound; Isinguzo *et al*., 2002, inner Frobisher Bay). To our knowledge, capelin have not been found in char stomachs sampled further north than northern Labrador (59°N; Dempson *et al*., 2002). Atlantic Spiny lumpsuckers and pricklebacks offered benthic feeding evidence. Both have been shown to inhabit high salinity (>30), cold (0°C) water, at depths of 5 to 200 m. Lumpsuckers are poor swimmers and often stick to substrates with pelvic fins modified into a suction disc (Scott & Scott, 1988). The co-occurrence of lumpsuckers and pricklebacks with mysids and adult hyperiid amphipods, respectively, in individual stomachs, further supported deep water feeding (Sars, 1890; Scott & Scott, 1988; Viherluoto, 2001). Arctic Staghorn sculpin have been shown to occupy depths below 1.8 m, but are most abundant below 18 m (Scott & Scott, 1988). Although fish comprised only 5*%W*, they have been shown to be a high energy food (total nutrients per gram and increased digestibility) and may have required less energy for capture as larger prey means fewer items need to be consumed (Isinguzo *et al*., 2002; Morinville & Rasmussen, 2006). Considering increased digestibility of fishes relative to crustaceans (Isinguzo *et al*., 2002) and the fact fish prey were often in a greater state of digestion compared to crustaceans (pers. obs.), there was a possibility of underestimating the actual *%N* and *%W* of fishes consumed. Sedentary, benthic species, such as sculpins, may have also been easier targets. Considering all these points, benthic piscivory likely acted as a natural selection pressure to dive deeper. We suggested feeding on relatively larger pelagic crustaceans and slow-moving benthic fishes was the main influence of deep diving.

The reasons for repetitive, rapid dives of char between surface waters and maximum dive depth were unclear. Energetically, we assumed a fish remaining at depth to feed until full would increase energy gain. Dive repetition may have been explained as a trade-off between energy demand to remain at depth and prey encounter rate (Rikardsen *et al*., 2007). Studies have shown some fish species must actively swim against their swim bladder's positive buoyancy at depths greater than their neutral buoyancy (Harden Jones & Scholes, 1985). Based on our results, this was 2 m for Arctic char. However, increasing pressure with depth would have decreased swim bladder volume (Horne *et al.,* 2009), thus positive buoyancy effects may have been minimized.

Rikardsen *et al*. (2007) noted deep dives were frequently followed by a marked drop in Arctic char body temperature. This was also noted in our study as char encountered sub-zero temperatures (mean -0.1 ± 0.6 ^{o}C) from 10 to 30 m, yet avoided decreasing their body temperature to or below 0^{o}C (0.1% of all detections). The narrow subtidal surface zone of relatively warmer water (mean 2.6 ± 1.4 ^{o}C) from 0 to 3 m may have explained dive repetition, as an ectothermic fish would have warmed, enhancing muscle activity, and subsequently, conferring an advantage in swimming performance which would allow greater hunting success in cold water (Moyle & Cech, 1996). This advantage has been readily demonstrated by endothermic predatory pelagics such as tuna (*Thunnus* spp.) and great white sharks (*Carcharodon carcharias*; Scott & Scott, 1988; Holland *et al*., 1992; Teo *et al*., 2007). Char returning to warmer surface waters may have delayed the overall decrease in body temperature by slight warm-ups between dives and dive series. This behavioural thermoregulation (Holland *et al*., 1992) may have also explained migrants' affinity for significantly warmer intertidal waters before and after subtidal hunting trips. We suggested near surface time between dives may have been a rest/heat recovery phase at neutral buoyancy, whereas higher temperatures enhanced overall physiological function, aiding systems critical for marine feeding, such as digestion, locomotion, osmoregulation and respiration.

3.5.5 CONCLUSIONS

Overall migrant movements were influenced by inner Frobisher Bay's macrotides, but behaviour suggested prey availability was the main influence for intertidal/subtidal movements, with temperature-based physiology shaping their repetitive nature. Estuaries with large intertidal zones may serve as rich foraging grounds and heat recovery arenas. With warming of the Arctic, intertidal zones near the optimum temperature for efficient digestion in char (9.4^{o}C) may be a limiting factor for growth. Warmer water may enhance foraging ability, but essentially decrease efficient food conversion (Larsson & Berglund, 2005). This may have a delayed effect of these anadromous char having comparatively lower energy reserves while overwintering in fresh water, ultimately decreasing fitness and overall survival. This study demonstrated Arctic char's tolerance of low temperatures while foraging at depth. It also showed char are linked to comparatively warmer near surface waters, in both intertidal and subtidal zones. We suggested this behavioural thermoregulation aided physiology associated with foraging. Based on our study and others (Dempson & Kristofferson, 1987, Dempson, 1993, Bystriansky *et al*., 2007, Jensen & Rikardsen, 2008), it appeared that char, once acclimatized to salt water, were more than capable of surviving high salinities in low temperatures for extended periods of time (hours to days), yet avoided decreasing their body temperature to or below 0^{o}C. Marine migrating char were not restricted to intertidal or upper water column habitats due to warmer water. We suggest they tolerate cold water due to prey availability, yet seek warmer water to enhance feeding/digestion physiology. The plasticity of anadromous Arctic fishes marine migration strategies may have allowed these fishes to exploit extreme environments. Wider habitat and thermal tolerances may offer a crucial survival advantage to Arctic animals faced with rapid climate change.

Table 3.1 - Mean ± SD (min, max) and number of detections (N) for body temperature (°C), and median, interquartile range (min,max) and number of detections (N) for swimming depth (m) of individual Arctic char, *Salvelinus alpinus* (N = 27), tracked in the intertidal (IT) and subtidal (ST) zones of inner Frobisher Bay, Nunavut, Canada, 1 July to 4 September, 2008/09

ID	**IT Body Temperature**	**N**	**ST Body Temperature**	**N**	**IT Swimming Depth**	**N**	**ST Swimming Depth**	**N**
T2	7.1 ± 4.7 (0.9, 12.9)	37	2.2 ± 1.2 (0.5, 8)	159	1.5, 2.6 (0, 6.2)	36	4.4, 7.6 (0, 52.8)	145
T4	6.4 ± 3.9 (0.6, 12.8)	101	2.0 ± 1.0 (0.7, 5.2)	123	0.9, 1.0 (0, 6.6)	98	8.4, 16.6 (0, 35.6)	115
T5	7.8 ± 3.0 (1.4, 13.8)	572	2.7 ± 1.2 (0.8, 6.6)	133	0.4, 1.3 (0, 7.0)	576	3.0, 6.6 (0, 42.2)	138
T6	11.6 ± 0.1 (11.5, 11.6)	2	9.4 ± 2.6 (4.8, 12.7)	40	1.0, 0.1 (0.9, 1.0)	4	0.9, 2.0 (0, 3.0)	44
T7	10.5 ± 1.1 (7.5, 12.0)	18	9.0 ± 1.8 (4.0, 12.3)	76	1.0, 0.4 (0.9, 2.2)	21	0, 0.9 (0, 9.7)	73
T12	8.5 ± 4.4 (-0.2, 13.7)	67	2.2 ± 1.2 (0.3, 7.9)	140	0, 0.9 (0, 9.2)	79	3.0, 9.2 (0, 37.4)	134
T13	5.1 ± 2.8 (1.0, 11.2)	363	1.6 ± 1.4 (-0.1, 8.0)	107	0.9, 1.0 (0, 8.8)	370	4.8, 16.1 (0, 36.9)	113
T14	7.8 ± 3.1 (2.1, 13.7)	407	1.8	1	0.4, 0.9 (0, 4.0)	404	0.9	1
T25	-	0	6.9 ± 1.9 (3.1, 12.3)	109	-	0	0.5, 2.2 (0, 12.0)	114
T27	6.2 ± 3.2 (1.7, 12.8)	57	2.0 ± 1.0 (1.4, 6.4)	22	1.0, 2.2 (0, 6.6)	47	2.0, 6.1 (0, 11.0)	21
T28	8.0 ± 3.2 (1.0, 12.0)	208	2.3 ± 1.3 (0.9, 7.6)	107	0, 0.9 (0, 6.2)	191	4.0, 7.4 (0, 19.0)	100
T29	6.9 ± 3.4 (1.1, 14.1)	218	1.8 ± 0.7 (1.0, 3.8)	31	0.9, 1.8 (0, 7.9)	219	9.7, 16.3 (0, 26.0)	31
T31	8.7 ± 3.1 (1.6, 11.9)	70	3.4 ± 1.1 (1.4, 6.1)	55	0.4, 0.9 (0, 2.2)	73	1.0, 3.8 (0, 18.0)	55
T32	11.0 ± 1.5 (6.6, 14.9)	75	2.3	1	0.4, 0.5 (0, 1.8)	72	-	0
T33	11.2 ± 2.2 (6.8, 16.3)	27	-	0	0, 0 (0, 0.4)	27	-	0
T39	10.9 ± 2.4 (3.2, 16.2)	69	-	0	0.9, 0.5 (0, 1.8)	64	-	0
T40	8.8 ± 3.7 (0.3, 15.7)	202	2.3 ± 1.3 (0.2, 7.3)	204	0.4, 1.3 (0, 7.5)	208	2.2, 7.5 (0, 29.0)	221
T41	9.5 ± 2.9 (0.9, 16.8)	199	-	0	0.9, 1.5 (0, 6.6)	219	-	0
T44	9.8 ± 3.1 (1.9, 13.0)	604	7.7 ± 3.1 (1.3, 13.0)	237	0.9, 0.7 (0, 8.1)	582	0.9, 0.7 (0, 27.0)	250
T46	10.6 ± 2.3 (3.6, 17.1)	1036	-	0	1.1, 1.3 (0, 4.0)	1026	-	0
T47	9.8 ± 3.1 (0.8, 18.1)	2104	-	0	1.0, 1.3 (0, 5.9)	2131	-	0
T48	9.7 ± 2.9 (1.4, 15.0)	812	1.9 ± 0.6 (1.3, 4.4)	50	1.1, 1.1 (0, 8.1)	883	2.0, 3.5 (0, 13.0)	43
T49	10.3 ± 2.8 (1.3, 13.0)	380	3.4 ± 3.4 (1.1, 13.0)	133	0.9, 0.4 (0, 10.0)	378	3.7, 6.5 (0, 24.6)	142
T50	8.8 ± 3.5 (1.3, 13.0)	819	2.1 ± 1.4 (1.0, 9.1)	331	0.7, 0.7 (0, 5.9)	799	4.0, 9.3 (0, 24.4)	308
T51	10.7 ± 3.7 (1.4, 14.0)	647	2.4 ± 1.9 (0.5, 10.2)	365	1.0, 1.3 (0, 9.5)	678	5.3, 8.3 (0.4, 30.6)	369
T52	11.4 ± 2.0 (4.6, 16.5)	595	8.3 ± 2.9 (2.4, 14.0)	205	0.7, 0.5 (0, 3.5)	594	0.9, 0.7 (0, 14.3)	211
T53	9.2 ± 3.8 (1.4, 14.0)	679	2.3 ± 0.9 (1.3, 4.4)	218	0.7, 0.7 (0, 6.8)	655	2.0, 9.3 (0, 23.7)	222
ALL	**9.4 ± 3.4 (-0.2, 18.1)**	**10368**	**3.7 ± 3.1 (-0.1, 14.0)**	**2847**	**0.9, 0.0 (0, 10.0)**	**10434**	**2.0, 7.0 (0, 52.8)**	**2850**

Table 3.2 - Summary of stomach contents of anadromous Arctic char (N=58) sampled 27 June to 14 August, 2008-09, from inner Frobisher Bay, Nunavut, Canada. Indicies used are frequency of occurrence (*%O*), percent by number (*%N*), and percent by weight (*%W*). Frequency of occurrence is expressed relative to the total number of stomachs containing food (N = 56)

Prey Organism	**Relative importance of prey organisms**		
	%O	***%N***	***%W***
Pisces (Total)	26.79%	0.19%	5.01%
Mallotus villosus (Capelin)	5.36%	0.01%	1.35%
Cottidae (sculpins)	5.36%	0.01%	0.87%
Myoxocephalus quadricornis (Fourhorn sculpin)	3.57%	0.01%	0.05%
Gymnocanthus tricuspis (Arctic Staghorn sculpin)	1.79%	0.004%	0.82%
Lumpenus spp. (Stichaeidae - Pricklebacks)	8.93%	0.15%	0.13%
Boreogadus saida (Arctic cod)	1.79%	0.01%	1.83%
Eumicrotremus spinosus (Atlantic Spiny lumpsucker)	8.93%	0.01%	0.07%
Unidentified fish remains	5.36%	0.01%	0.77%
Crustacea	87.50%	99.70%	94.78%
Mysidacea (Mysids; *Mysis mixta*)	46.43%	4.46%	22.55%
Amphipoda (Amphipods)	87.50%	95.24%	72.15%
Hyperiidae (*Themisto libellula*)	50.00%	14.94%	29.26%
Gammaridea (Gammarid amphipods)	73.21%	80.27%	41.64%
Onesimus littoralis	58.93%	70.81%	26.23%
Gammarus duebeni	50.00%	9.41%	15.39%
Gammaracanthus loricatus	8.93%	0.05%	0.02%
Amphithopsis longicaudata	1.79%	0.004%	0.001%
Unidentified amphipod remains	8.93%	0.03%	1.25%
Decapoda	1.79%	0.004%	0.16%
Annelida (Polychaeta)	12.50%	0.03%	0.03%
Insecta (Miscellaneous insects)	21.43%	0.08%	0.12%
Unidentified and miscellaneous debris	16.07%	-	0.06%

Table 3.3 - Mean (± SD), minimum, maximum and number (N) of water temperature (T, °C), salinity, pH, and concentration (mg L^{-1}) and percent saturation (%) of liquid dissolved oxygen (LDO) readings in the intertidal (10 July to 4 September) and subtidal (11 July to 20 August) zones within inner Frobisher Bay, Nunavut, Canada, 2008-09

	Intertidal					**Subtidal**				
Z (m)	**T (°C)**	**Salinity**	**pH**	**LDO (mg L^{-1})**	**LDO (%)**	**T (°C)**	**Salinity**	**pH**	**LDO (mg L^{-1})**	**LDO (%)**
0-1										
Mean ± SD	7.2 ± 1.9	12.1 ± 11.3	8.0 ± 1.1	12.2 ± 1.0	115 ± 1	3.4 ± 1.4	28.7 ± 4.2	8.2 ± 1.4	12.4 ± 0.6	117 ± 1
Min	0.9	0.1	6.9	11.7	114	0.8	2.1	6.5	11.5	117
Max	12.9	31.5	10.4	14.0	116	10.9	32.1	10.4	13.3	118
N	1405	8	8	5	4	109	109	11	7	2
0-3										
Mean ± SD	6.4 ± 2.4	15.5 ± 11.6	8.2 ± 1.1	12.3 ± 0.7	119 ± 8	2.6 ± 1.4	30.1 ± 3.5	8.2 ± 1.1	12.2 ± 0.6	118 ± 1
Min	0.8	0.1	6.9	11.7	114	0.4	2.1	6.5	11.5	116
Max	12.9	31.8	10.4	14.0	137	10.9	33.0	10.4	13.3	120
N	2042	16	16	10	7	271	271	35	22	7
3-10										
Mean ± SD	1.6 ± 0.6	31.9 ± 0.2	9.6 ± 0.2	11.7 ± 0.1	-	1.0 ± 0.8	32.1 ± 0.6	8.2 ± 0.8	12.0 ± 0.4	110 ± 3
Min	0.6	31.6	9.4	11.5	-	-0.6	29.4	7.0	11.7	108
Max	5.0	32.0	9.8	11.9	-	3.0	33.5	9.6	13.1	114
N	1087	6	6	6	-	332	332	62	42	7
10-30										
Mean ± SD	-	-	-	-	-	-0.1 ± 0.6	32.2 ± 0.2	8.5 ± 0.4	11.6 ± 0.2	-
Min	-	-	-	-	-	-0.9	31.4	7.5	11.4	-
Max	-	-	-	-	-	1.1	32.7	9.1	12.1	-
N	-	-	-	-	-	173	173	56	52	-

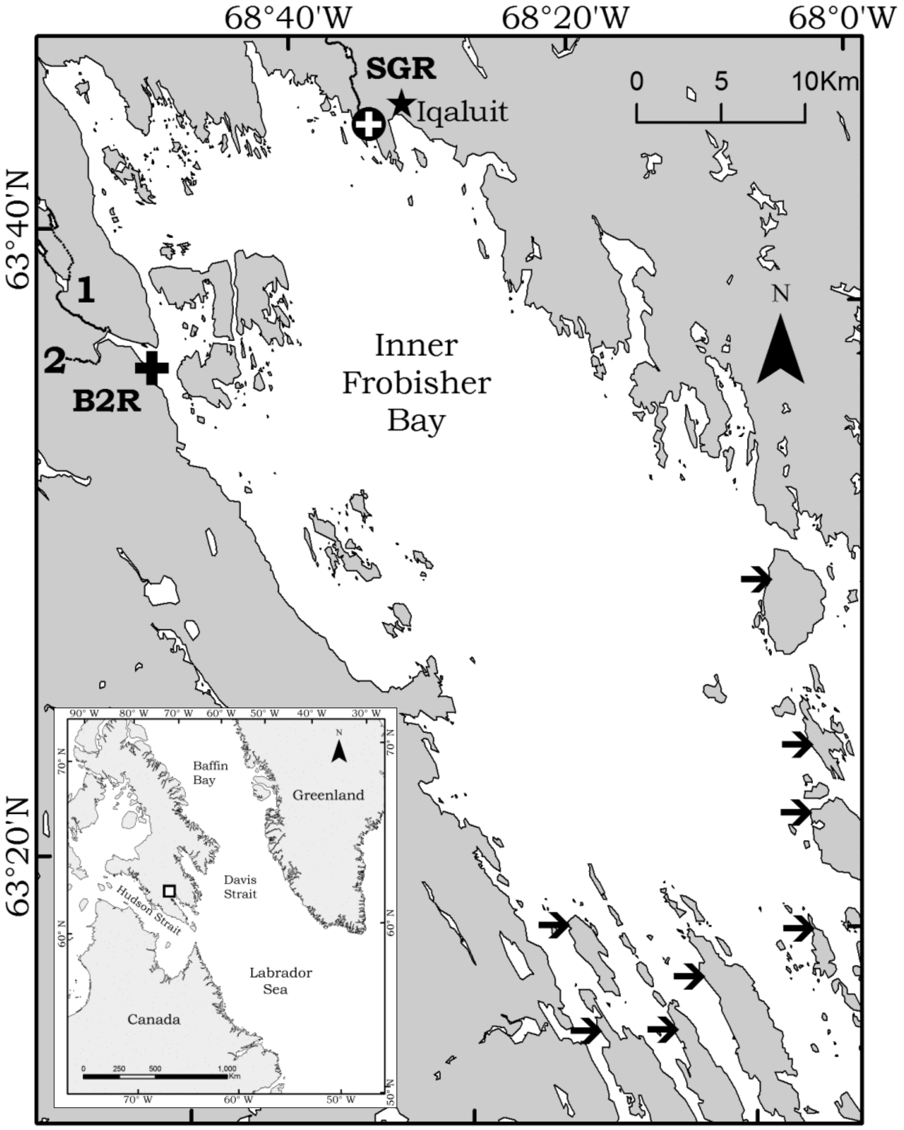
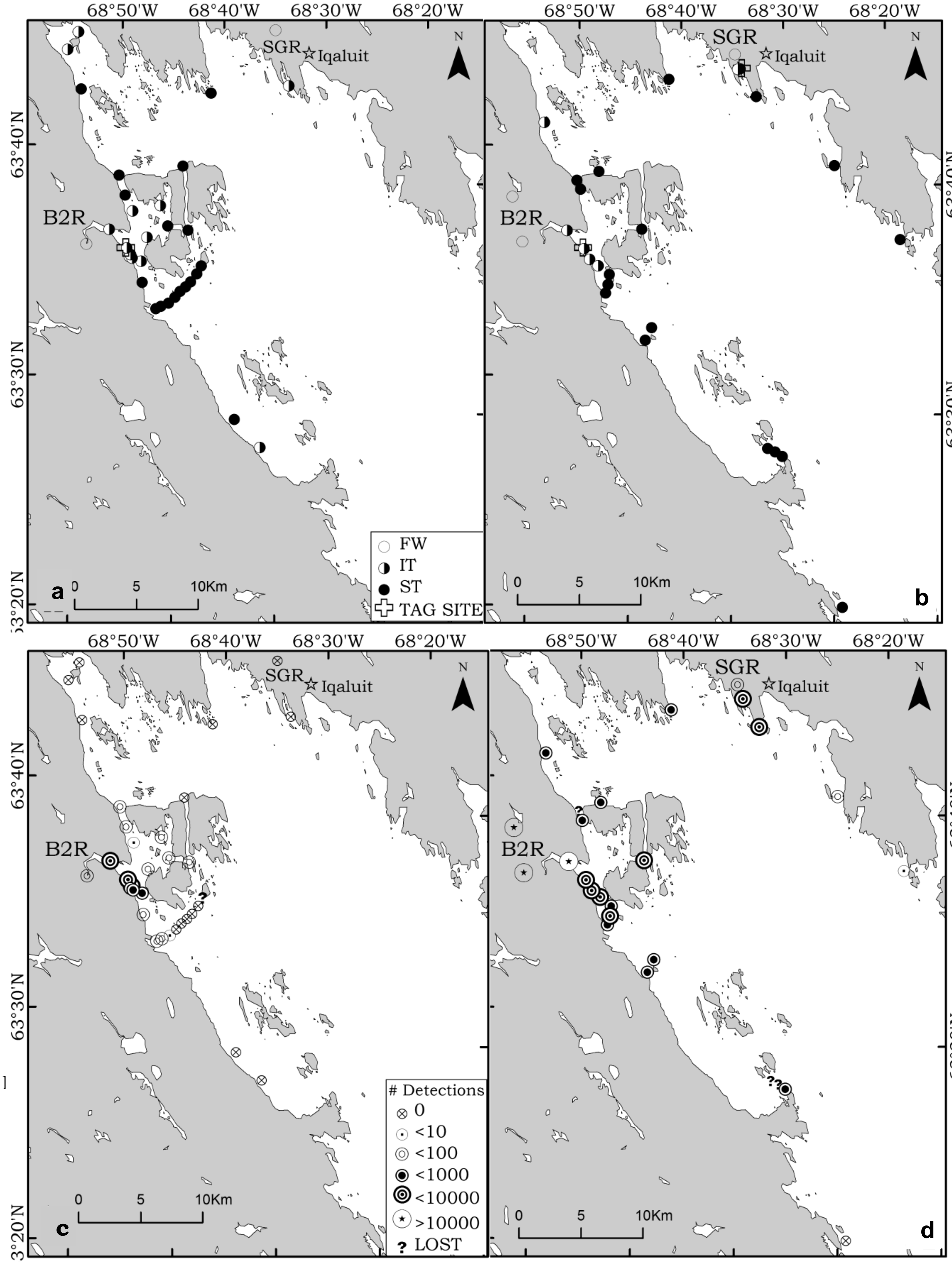
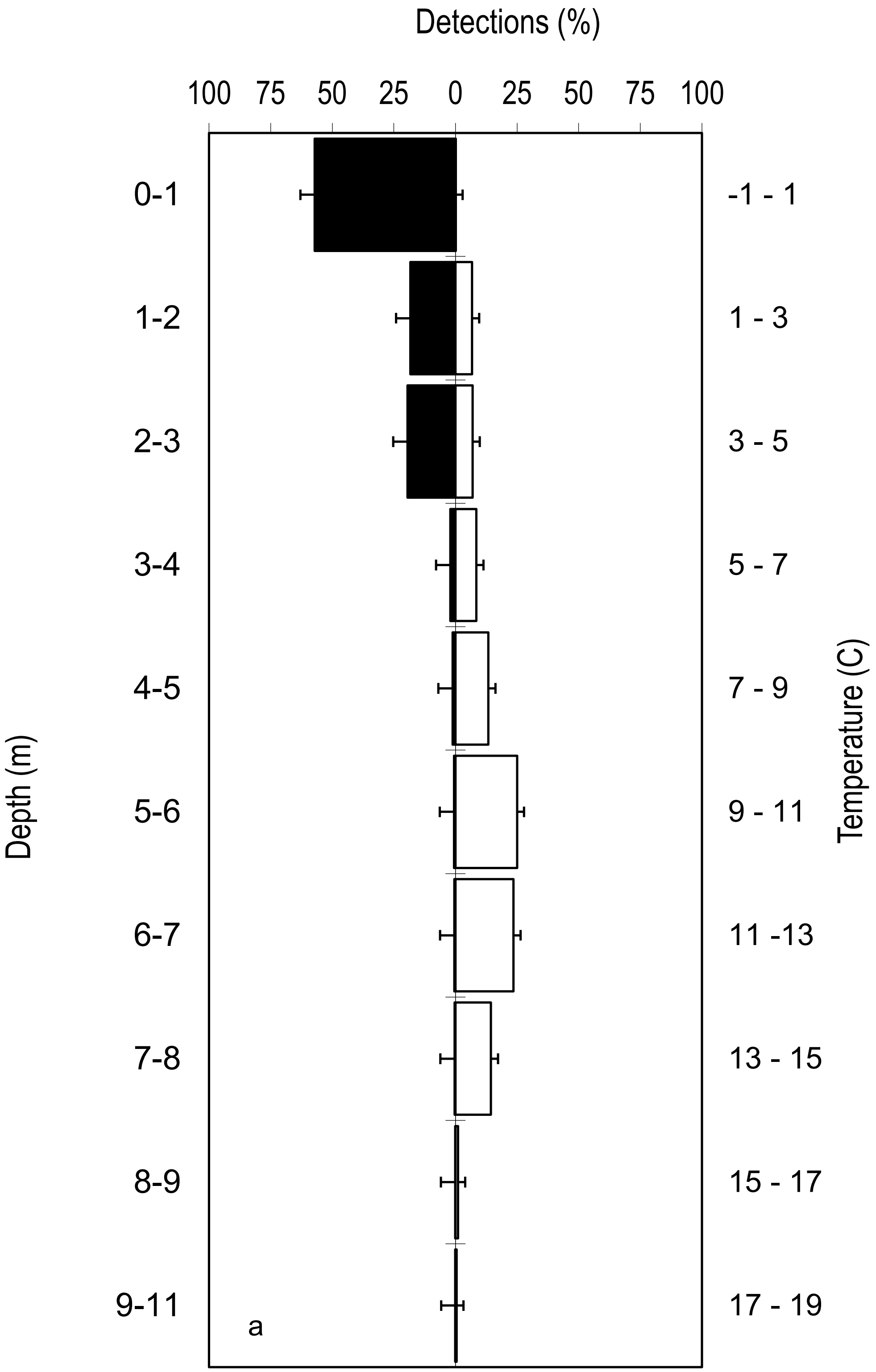


Figure 3.1 - Location of inner Frobisher Bay, Nunavut, Canada, showing tag sites at Bay of Two Rivers (B2R;✚) and the Sylvia Grinnell River (SGR; ⊕), the northwest (1) and southwest (2) branches of the Armshow River, the city of Iqaluit (★), and the Channel Islands (➔)



68°50'W
68°40'W
68°30'W
68°20'W
63°40'N
63°30'N
63°20'N
SGR
Iqaluit
B2R
N
FW
IT
ST
TAG SITE
0
5
10Km
a
b
c
d
Detections
0
<10
<100
<1000
<10000
>10000
? LOST

Figure 3.2 **-** Deployment of acoustic receivers relative to fresh water (○), intertidal (◗), and sub-tidal (●) zones in inner Frobisher Bay, Nunavut, Canada 2008 (a) and 2009 (b) and number of detections recorded for anadromous Arctic char, *Salvelinus alpinus*, tracked from 2-29 Aug, 2008 (c) and 2 Jul-29 Aug, 2009 (d). Lost receivers (?) were not recovered.


Detections (%)
100
75
50
25
0
25
50
75
100
Depth (m)
0-1
1-2
2-3
3-4
4-5
5-6
6-7
7-8
8-9
9-11
Temperature (C)
-1 - 1
1 - 3
3 - 5
5 - 7
7 - 9
9 - 11
11 -13
13 - 15
15 - 17
17 - 19
a

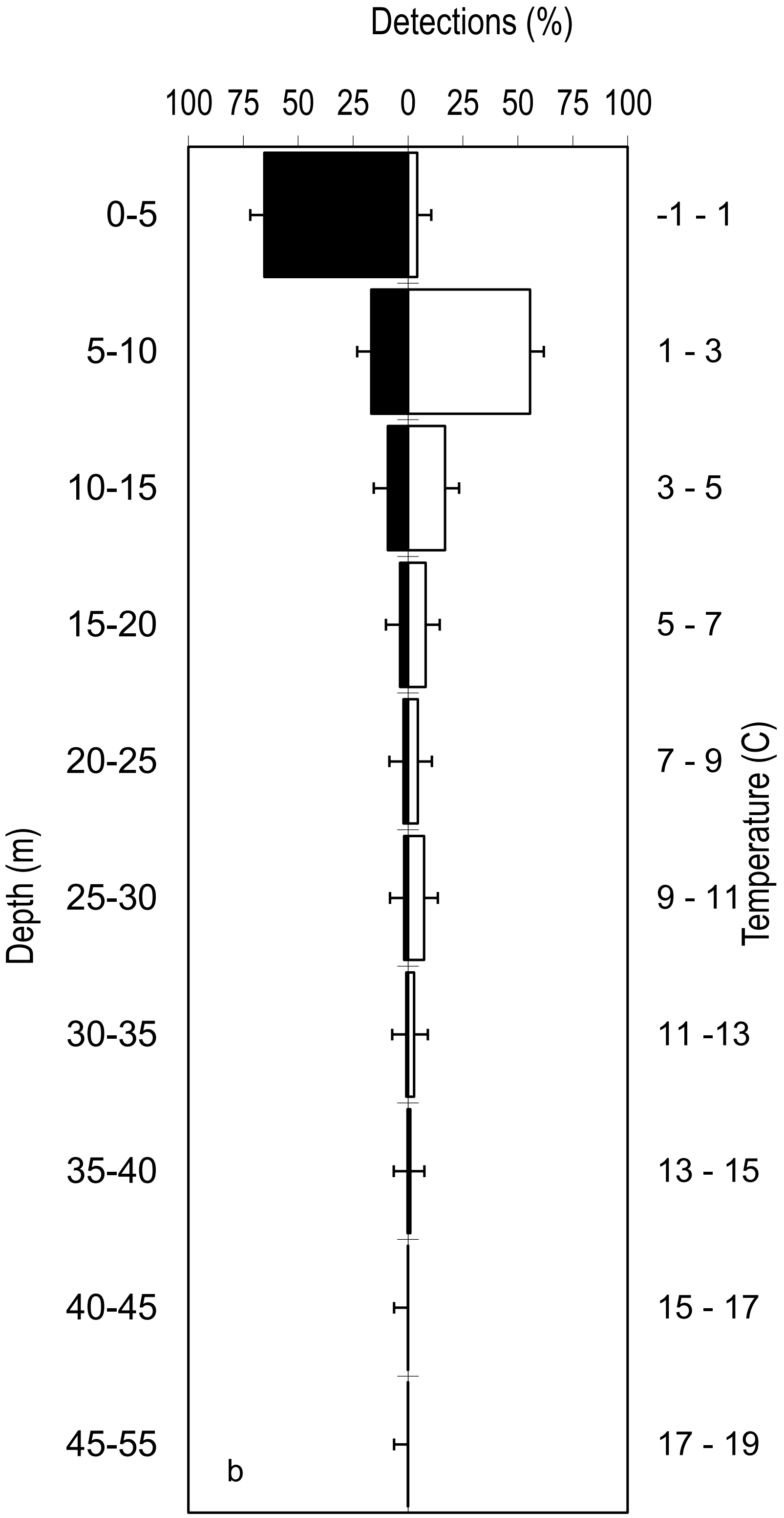

Detections (%)
100 75 50 25 0 25 50 75 100
Depth (m)
0-5
5-10
10-15
15-20
20-25
25-30
30-35
35-40
40-45
45-55
Temperature (C)
-1 - 1
1 - 3
3 - 5
5 - 7
7 - 9
9 - 11
11 -13
13 - 15
15 - 17
17 - 19
b

Figure 3.3 - Frequency histograms of detections for depth (m) and body temperature (^{o}C) of Arctic Char in intertidal (a) and subtidal (b) zone of inner Frobisher Bay, NU, Jul-Aug 2008/09. Histograms are combined for display only. No relationship between adjacent depth and temperature bins is inferred.

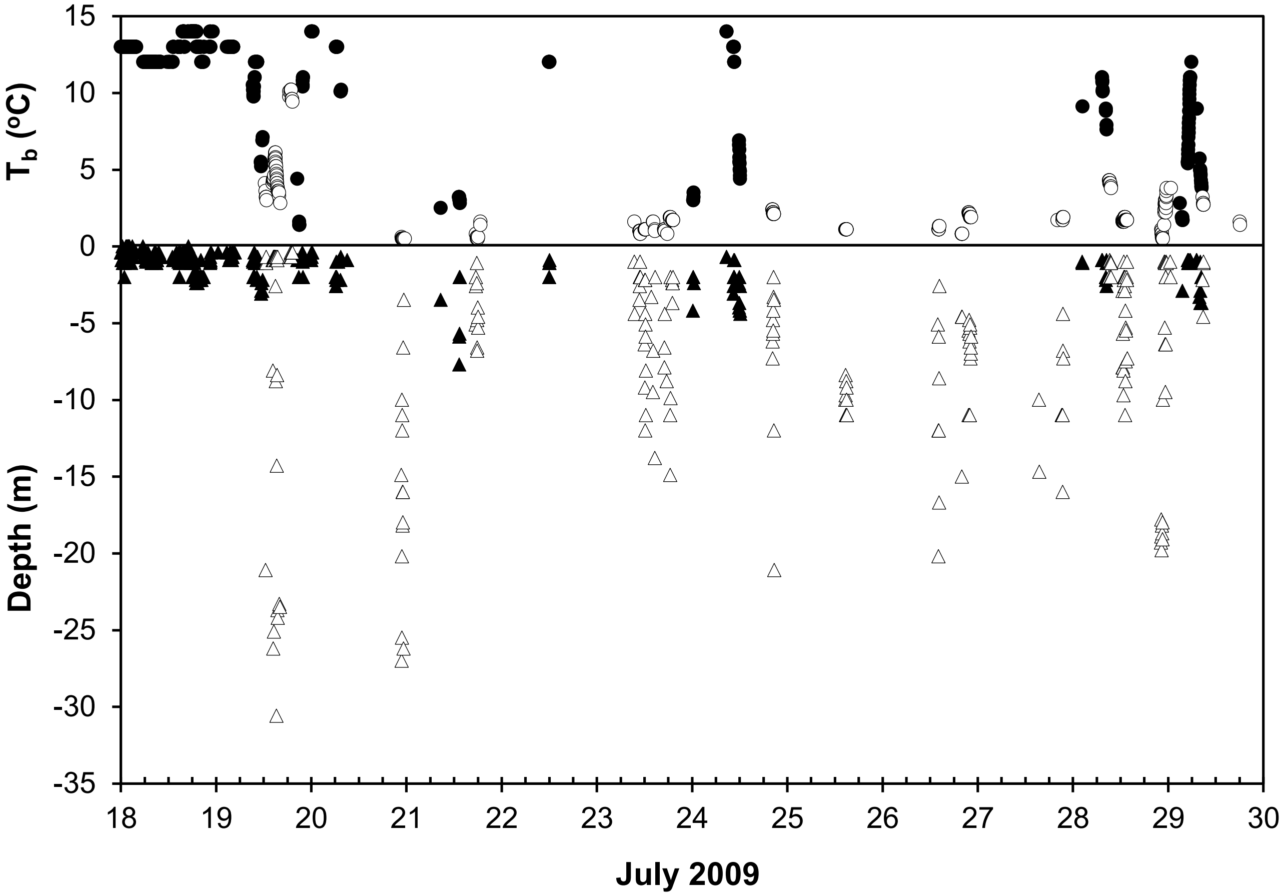


Figure 3.4 - Depth (m; triangle) and body temperature (^{o}C; circle) of Arctic char T51 relative to intertidal (solid symbols) and sub-tidal (open symbols) zones during marine migration in inner Frobisher Bay, NU, from 18-30 Jul, 2009.

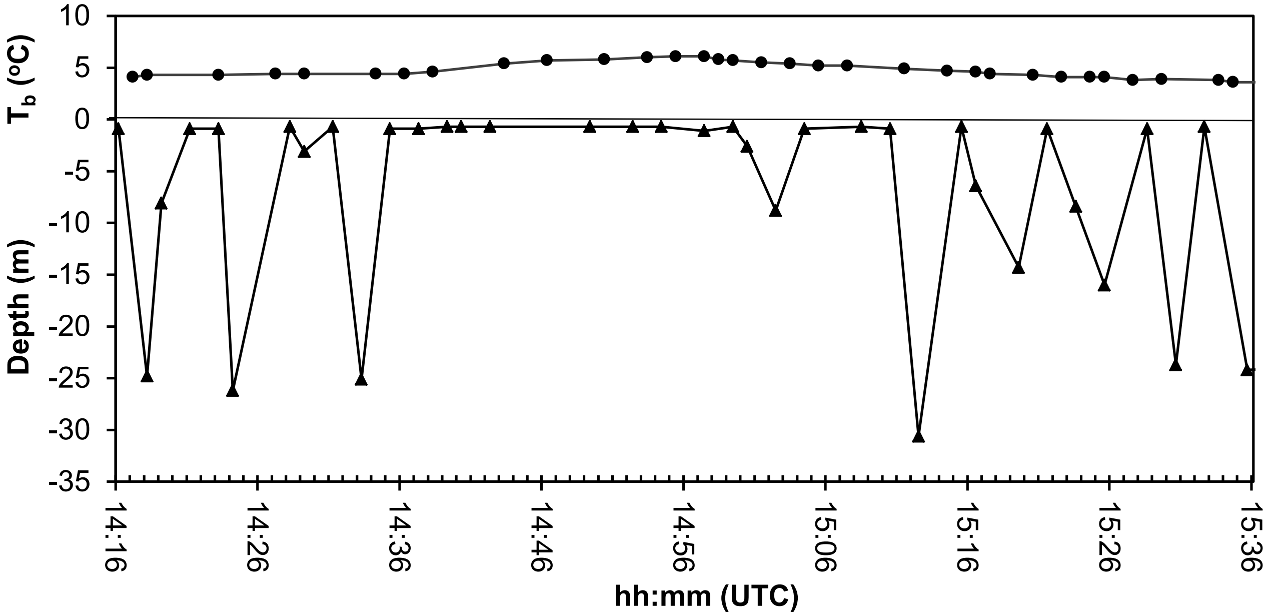


Figure 3.5 - Depth (m; triangle) and body temperature (°C; circle) of Arctic char T51 displaying repetitive diving behaviour in the sub-tidal zone near Bay of Two Rivers, inner Frobisher Bay, NU, on 19 Jul, 2009.

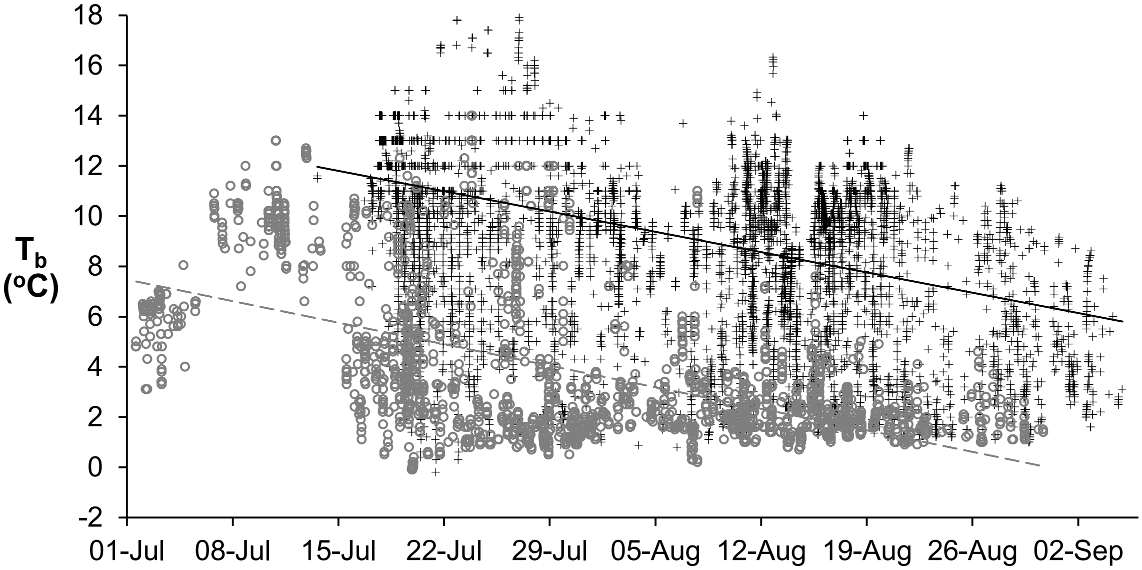


Figure 3.6 - Body temperature (T_b, °C) of Arctic char in the intertidal (+; $R^2 = 0.2095$) and subtidal (○; $R^2 = 0.3022$) zones of inner Frobisher Bay, Nunavut, Canada, from 1 Jul to 4 Sep, 2008-09.

CHAPTER 4

TO FAST OR FEED: AN ALTERNATIVE LIFE HISTORY FOR ANADROMOUS BROOK TROUT *Salvelinus fontinalis* OVERWINTERING WITHIN A HARBOUR.

4.1 ABSTRACT

The seasonal feeding pattern of sea-run brook trout *Salvelinus fontinalis* was studied from November to May during 2010, 2011 and 2012 in Antigonish Harbour, Nova Scotia, Canada (45^o 38N, 61^o 55W). Sixty-three *S. fontinalis* (330 ± 70 mm, 536 ± 351 g, mean ± SD) captured had fed predominantly on fishes (Fundulidae & Gasterosteidae). Percentage of empty stomachs was highest during autumn (18%) and winter (22%) and lowest in spring (7%). Stomach fullness increased from autumn to a maximum during winter, relating to near-zero body temperatures which may have effectively stopped gastric evacuation. Although feeding occurred during winter (December-March), consumption rates were calculated as negative values, and subsequently returned to positive values in spring (April-May). The over-winter life history strategy of this sea-run *S. fontinalis* population appears to be a feeding marine migration in which fish continually increase body condition, representing an alternative to the more common over-wintering strategy of starvation in fresh water until spring.

4.2 INTRODUCTION

The marine migration of salmonids is largely influenced by more favorable feeding conditions leading to rapid growth, enhanced fecundity and increased survival (Nikolsky, 1963;

Harden Jones, 1968; Northcote, 1978; 1984). Most marine migrations commence in spring with a return to fresh water for autumn spawning, and overwintering for iteroparous species, with migrants often decreasing or ceasing feeding activity within fresh water (Klemetsen *et al*., 2003; Quinn, 2005; Thorstad *et al*., 2011). However, there are documented accounts of salmonid populations residing in brackish to full-strength saltwater during winter, including Atlantic salmon *Salmo salar* L. 1758 (Jonsson & Jonsson, 2002; Lacroix, 2013), brown trout *Salmo trutta* L. 1758 and Arctic char *Salvelinus alpinus* (L. 1758) (Rikardsen *et al*., 2006; Jensen & Rikardsen, 2008, 2012). It has also been observed that some anadromous brook trout *Salvelinus fontinalis* (Mitchill 1814) return to estuaries in autumn and remain there over winter (Bigelow & Welsh, 1925; Smith & Saunders, 1958; Gaudreault *et al*., 1982; Curry *et al*., 2002; Morinville & Rasmussen, 2006). This appears to be the case of an anadromous population of *S. fontinalis* overwintering in Antigonish Harbour, Nova Scotia, Canada.

Few studies document the marine diet of anadromous *S. fontinalis*, and most only provide a description of prey items found in stomachs, such as crustaceans (especially *Crangon* sp., *Gammarus* sp. and *Mysis* sp.), insects, mammals (deer mouse *Peromyscus* sp.) and polychaetes *Nereis* sp.. Fishes consumed included capelin *Mallotus villosus*, hake *Urophycis* sp., killifishes (*Fundulus* sp.), *S. fontinalis,* sand lance *Ammodytes* sp., sculpins (Cottidae), smelt *Osmerus mordax*, sticklebacks (Gasterosteidae), rock gunnel *Pholis gunnellus*, and whitefishes *Coregonus* spp. (White, 1940; 1942; Dutil & Power, 1980; O'Connell, 1982; Gaudreault *et al*., 1982; Morinville & Rasmussen, 2006). Morinville and Rasmussen (2006) found crustaceans and fishes to be the dominant prey items for first and second year migrants, respectively, with *S. fontinalis* >250 mm L_F employing piscivory.

Only two studies in the northwest Gulf of St. Lawrence (48^{o}N) documented estuarine winter feeding (Gaudreault *et al*., 1982; Morinville & Rasmussen, 2006). To our knowledge, there are no diet studies of *S. fontinalis* populations overwintering in estuaries of the southern Gulf (45^{o}N). To address the lack of detailed knowledge on marine migration and life history strategies of northern anadromous salmonids, including information during winter (Huusko *et al*., 2007), we aimed to 1) describe the diet of *S. fontinalis* from autumn to spring, and 2) determine if *S. fontinalis* are feeding under sea ice during winter. To do this, we examined seasonal changes in diet and feeding intensity (% empty stomachs, stomach fullness, consumption rates & body condition) of *S. fontinalis* captured within Antigonish Harbour from November to May. We hypothesized that *S. fontinalis* diet would vary with the seasons, with piscivory occurring in migrants >250 mm L_F, with winter feeding focused on *Osmerus sp*. which are abundant from December to January. Feeding intensity during winter was expected to decrease with colder water, with percentage of empty stomachs being the highest, and stomach fullness and consumption rates being the lowest. Body condition was expected to be lowest in autumn due to post-spawning and increasing until the end of the migration in late spring.

4.3 MATERIALS AND METHODS

4.3.1 STUDY SITE

Antigonish Harbour, Nova Scotia, Canada (45^{o} 38N 61^{o} 55W), is a semi-enclosed, Y-shaped, estuarine system with three rivers draining into the inner harbour, the South River in its southern end and the West and Wrights in its western extent (Fig. 4.1). The inner harbour is characterized by shallow (water depth $Z < 2$ m), silted, cordgrass *Spartina* sp saltmarsh delta containing numerous inlets, coves and tidally influenced ponds. The mid-harbour has shallow inlets and multiple islands with a deep basin (Z_{max} = 11 m) and channels ($Z < 3$ m) fringed with blue mussels *Mytilus* sp and American oysters *Crassostrea virginica.* The outer harbour is dominated by a barrier beach with two channels ($Z < 5$ m) connecting to St. George Bay, Gulf of St. Lawrence. The outer harbour contains multiple islands, shallow shoals blanketed by eel grass *Zostera* sp (Thériault *et al*., 2006) and a large salt marsh pond. The harbour is known to contain a population of sea-run *S. fontinalis* which support a popular recreational spring fishery (MacMillan & Madden, 2007).

4.3.2 FISH SAMPLING

Sixty-three *S. fontinalis* were captured during day and night with a 5.1 cm mesh size gill net, live-trap fyke net, rod and/or obtained opportunistically from fishers, from 19 November to 5 May, 2010-12. Although fishing occurred, there were no captures in February. Autumn samples were captured near the head of the tide in the South and West rivers using fyke and gill nets (n = 11). Winter samples were captured by ice rod at the east harbour in January (n=6) and by gill net near the head of the tide in the West River in March (n = 3). Spring samples were caught throughout the inner harbour (n = 43), with the majority captured in West and South river estuaries (Fig. 4.1).

Fork-length (L_F) to the nearest mm and mass, including stomach contents, to the nearest 10 g (M) were recorded. Excised stomachs were individually wrapped, labelled and stored on ice until freezing at -20 °C. In the laboratory, stomachs were thawed, contents removed, separated and identified to family (Carlander, 1950; Borror & Delong, 1954; Needham & Needham, 1962; Bromley & Bleakney, 1984; Marshall, 2006) or alternative grouping (*i.e.* fish remains). Due to advanced digestion, some contents were numerically estimated from identifiable body parts (Power *et al*., 2002). Excess moisture was blotted dry prior to counting and weighing (nearest 0.001 g).

4.3.3 STOMACH CONTENT ANALYSIS

Samples were pooled according to season: autumn (22 September - 20 December), winter (21 December - 19 March) and spring (20 March – 20 June), combining all collection years due to low samples sizes (Morinville & Rasmussen, 2006). For all samples and seasonal categories, indices of occurrence (*% O*), number (*% N*) and mass (*% M*) were used to determine frequency of each prey type consumed and relative importance of each (Hyslop, 1980). The diet of an individual was quantified using the index of relative importance (*IRI*) calculated for each taxon, excluding vegetal matter. The *IRI* is defined as: *IRI* = (*% N* + *% M*) * *% O*; where *% N* is the percent number of certain prey item, *% M* is the percent weight and *% O* is the frequency of occurrence (Pinkas *et al*., 1971). The diets of *S. fontinalis* >250 mm L_F were examined for piscivory. Further seasonal diet differences were compared using total number of taxa, mean number of taxa, and the Shannon-Weiner and Schoener's overlap indices. The Shannon-Weiner diversity index

$$(H') = -\sum_i^n p_i ln p_i$$

, where p_i is the mean *% M* x 0.01 of taxon i. Diet overlap between seasons was compared with Schoener's overlap index (*SI*), so that

$$SI = 1 - 0.5\left(\sum_{i=1}^{n} \left|p_{xi} - p_{yi}\right|\right)$$

, where p_{xi} is the mean *% M* of prey taxon i for season x, and p_{yi} is the mean *% M* of prey taxon i for season y. The index varies from 0 (no overlap) to 1 (complete overlap; Guilbard *et al.*, 2007). Any fish with an empty stomach was excluded from stomach content analyses.

4.3.4 BODY TEMPERATURE (T_B)

Mean seasonal and interval (19 November – 13 December, 13 December – 7 January, 7 January to 29 January, 29 January – 4 March, 4 March – 8 April and 8 April – 5 May) body temperatures of *S. fontinalis* were obtained from a concurrent tracking study using temperature-pressure sensor acoustic transmitters (V9TP & V13TP, Vemco/Amirix Ltd., Halifax, Canada) and active (VR100) and passive receivers (VR2W & VR3-UWM), following procedures outlined in Spares *et al*. (2012). Simultaneous detections on multiple receivers, and temperatures recorded beyond the transmitter's calibrated range and/or below salt-water freezing point (-1.9^{o}C; DeVries & Cheng, 2005) were omitted.

4.3.5 SEASONAL FEEDING INTENSITY

To estimate feeding activity between seasons, percentage of empty stomachs (*%ES*) and indices for stomach fullness (I_r) and body condition factor (K) were calculated using all sampled fish (Rikardsen *et al.*, 2006); whereas means for number of prey, mass of prey, mass of vegetal/miscellaneous matter, and consumption rate (C_{24}; Richter *et al.*, 2004), were calculated from fish with prey or vegetal/miscellaneous matter present in their stomachs (Guilbard *et al.*, 2007). The degree of stomach fullness was calculated using Hureau's index (I_r), where I_r = prey mass (g)/body mass (g) x 1000 (mg prey g M^{-1}; Tudela & Palomera, 1995; McLean *et al.*, 2012). Food consumption rate of *S. fontinalis* was estimated as the daily ration (C_{24}; mg prey g M^{-1})

using the Eggers method, so that $C_t = I_r Rt + (I_{rt} - I_{ro})$; where C_t is the consumption over the feeding interval considered, I_r is the mean stomach fullness index for the interval, R is the instantaneous gastric evacuation rate (h^{-1}), t is the interval duration (h), I_{ro} is the mean stomach fullness index at the beginning of the interval and I_{rt} is the mean stomach fullness index at the end of the interval (Tudela & Palomera, 1995; Amundsen & Klemetsen, 1988; Rikardsen *et al*., 2006). Six feeding intervals were considered: 19 November – 13 December, 13 December – 7 January, 7 January to 29 January, 29 January – 4 March, 4 March – 8 April and 8 April – 5 May. Mean I_{ro} and I_{rt} values were calculated from samples captured within 24 hours of the beginning and end dates. The rate of gastric evacuation of *S. fontinalis* and its relation to temperature was estimated by Sweka *et al*. (2004) in laboratory studies using fly and beetle larvae as prey, and these estimates were adopted for this study. Fulton's condition factor (K), was calculated using $K = 10^5 M L_F^{-3}$ (Ricker, 1975). A low K value (0.80) represented a fish in poor condition with a large head and narrow, thin body, whereas a large K value (1.60) indicated a fish in excellent condition with a well-proportioned, thick body, usually trophy class (Barnham & Baxter, 2003).

4.3.6 DATA ANALYSIS

Due to low sample sizes, a cumulative prey taxa abundance curve was generated by randomly ordering stomach samples to estimate the number of samples needed to compare taxa diversity between seasons. For all seasonal comparisons, either a parametric (ANOVA post-hoc Tukey) or non-parametric (Kruskal-Wallis with pairwise comparisons using a Dwass-Steel-Chritchlow-Fligner [D-S-C-F]) test were conducted, with normal and non-normal sample distribution (Shapiro-Wilks test) determining the test, respectively (Baran & Warry, 2008). Outliers were identified using box-and-whisker plots generated by Systat 13 software and removed for hypotheses testing (Systat, 2013). Means for *% O*, *% N* and *% M* were generated. An alpha level of 0.05 was used for all tests.

4.4 RESULTS

4.4.1 FISH SAMPLING

Mean fork-length for all *S. fontinalis* sampled was 330 ±70 mm ($n = 63$; Fig. 4.2). Mean mass was 462 ± 282 g ($n = 56$), with fish masses unmeasured in the field removed from any statistical analysis involving body mass. Minimum and maximum L_F and M were 179 mm and 450 mm, and 42 g and 1235 g, of *S. fontinalis* captured in autumn and spring, respectively (Table 4.1). There was a significant increase in mean L_F and M from autumn to spring (L_F, ANOVA post-hoc Tukey, $F = 4.927$, d.f. = 2, $P = 0.009$, $n = 63$; $\sqrt{M}$, $F = 7.545$, d.f. = 2, $P = 0.001$, $n = 56$; Fig. 4.3).

4.4.2 STOMACH CONTENT ANALYSIS

Stomach content diversity expressed as total *n* of taxa present was highest in spring ($n = 32$) with the median number of taxa highest in autumn (2 [3.3]) and lowest in winter (1 [0.8]; Table 4.1; Kruskal-Wallis post-hoc D-S-C-F: t = 6.763, d.f. = 2, $P \leq 0.046$, 5 outliers removed). The cumulative prey taxa abundance curve revealed the maximum number of taxa to be 34 for the entire sampling period, and minimum of 5 taxa during winter, reaching these sample size asymptotes within 52 and 3 stomachs, respectively (Fig. 4.4). Stomach content indices revealed fish as the dominant component, occurring in 90.6% of all stomachs containing prey, as 58.7% by number of items, 93.1% wet mass of contents, and greater than 85 *% O* and 75 *% M* throughout all seasons, with the highest *% N* (76.1%) occurring in spring. Fundulidae [mummichog *Fundulus heteroclitus* (L. 1766)], Atherinopsidae [Atlantic silverside *Menidia menidia* (L. 1766)] and Gasterosteidae [*Apeltes quadracus* (Mitchill 1815), *Gasterosteus aculeatus* L. 1758, *Pungitius pungitius* (L. 1758)] were consumed the most, constituting 14.4, 2.0 and 12.1 *% N*, and 69.3, 11.2 and 6.2 *% M*, respectively. Atherinopsidae only occurred in stomachs during winter and spring, constituting 10.0 *% N* and 22.9 *% M* of the winter diet (Table 4.2; Fig. 4.5). Surprisingly, the largest prey item was an American eel *Anguilla rostrata* (Lesueur 1817) (220 mm L_F , 22.8 g) coiled inside the stomach of a 448 mm L_F , 1235 g *S. fontinalis*. Seasonal specialties were Gammaridae in autumn (71.4 *% O*, 84.5 *% N* and 20.0 *% M*), Nereidae during winter (14.3 *% O*, 45.0 *% N* and 11.9 *% M*) and fish eggs in spring (2.6 *% O*, 42.1 *% N* and 0.2 *% M*; Fig. 4.5). Insects occurred during all seasons, and included 20 identified families, with caddis (Limnephilidae) and damsel (Coenagrionidae) flies, and ground (Carabidae) and scarab (Scarabaeidae) beetles consumed the most often (Table 4.2).

For *S. fontinalis* > 250 mm $\mathrm{L_F}$ which contained prey (*n* = 49, 9 % ES), piscivory accounted for 93.9 *% O*, 43.2 *% N*, 94.3 *% M* and 129.1 % IRI. Of the *S. fontinalis* < 250 mm $\mathrm{L_F}$ containing prey (*n* = 7, 22 % ES), only one individual had consumed a Fundulidae (14.3 *% O*, 0.3 *% N*, 18.5 *% M*, 2.7 % IRI; Fig. 4.6). Stomach contents of these smaller *S. fontinalis* included estuarine (Crangonidae, Gammaridae, Nereidae) and aquatic (Carabidae, Corydalidae, Dytiscidae, Limnephilidae, Lumbricidae) prey. One individual (213 mm $\mathrm{L_F}$) had consumed 298 unidentified fish eggs (0.7 g wet mass), but these were not considered as fish for this analysis.

Percentage Index of Relative Importance revealed Fundulidae (45.8%), Gasterosteidae (4.8%), Gammaridae (4.0%) and Atherinopsidae (2.2%) as the most valuable prey items year-round, with Gammaridae most prevalent in autumn (74.6%) and Fundulidae in winter (41.3%) and spring (53.9%; Fig. 4.5). The Shannon-Weiner diversity index was highest in autumn (1.28) and lowest in spring (1.06) with complete overlap (1.00) between seasons indicated by Schoener's overlap index (Table 4.1).

4.4.3 BODY TEMPERATURE (T_B)

There was a significant difference between mean body temperatures of *S. fontinalis* for each season (ANOVA post-hoc Tukey, F = 27445, d.f. = 2, $P < 0.000$), calculated as 8.6 ± 3.6°C ($n = 1,147$) during autumn, 0.7 ± 1.2°C ($n = 9,548$) in winter and 9.0 ± 3.4°C ($n = 45,547$) in spring, with an overall T_b of 7.6 ± 4.4°C (min = -0.5°C, max = 20.1°C, $n = 56,242$; Table 4.1).

4.4.4. FEEDING INTENSITY

Prey occurred in 56 of all *S. fontinalis* stomachs sampled: 9 in autumn, 7 in winter and 40 in spring. Percentage of empty stomachs was high during autumn (18%) and winter (22%) and lowest in the spring (7%). The median number of prey per stomach did not change significantly with the seasons (4 to 5 [4 to 9.8], Kruskal-Wallis test, t = 0.868, d.f. = 2, $P = 0.648$, $n = 50$, 6 outliers removed), whereas median prey mass was significantly higher in winter (14.00 g [9.16], $n = 7$), compared to spring (5.37 [11.77], $n = 40$), and autumn (0.44 [2.49], $n = 8$, 1 outlier removed; Kruskal-Wallis post-hoc D-S-C-F, t = 11.76, d.f. = 2, $P \leq 0.039$). The percentage of stomachs containing vegetal/miscellaneous matter was highest in winter (43%) and lowest in spring (20%) with no significant seasonal difference in median vegetal mass (Kruskal-Wallis test, t = 2.885, d.f. = 2, $P = 0.236$, 2 outliers removed; Table 4.1).

There were significant seasonal differences (Kruskal-Wallis post-hoc D-S-C-F, t = 8.304, d.f. = 2, $P \leq 0.02$) in stomach fullness (I_r) with the lowest median index of 0.6 in autumn ([interquartile range = 3.5], $n = 9$, 2 outliers removed), 12.7 during spring ([16.4], $n = 36$, 1 outlier removed), and highest of 22.2 in winter ([43.0], $n = 8$; Table 4.1). Further divisions into approximately monthly intervals (28 ± 5 days) revealed mean stomach fullness indices following a similar pattern (Fig. 4.7), beginning at 11.6 ± 21.3 from 19 November–13 December, increasing to a maximum of 32.6 ± 24.7 from 29 January-4 March, and decreasing to 11.7 ± 11.5 from 4 March-8 April (Table 4.3). Estimates of consumption rate (C_{24}) revealed a reciprocal relationship (Fig. 4.7) with the highest values of 3.67 mg prey g M^{-1} and 5.93 mg prey g M^{-1} occurring during 19 November-13 December and 8 April-5 May, respectively, and negative consumption values occurring from 7 January to the 4 March (Fig. 4.7). Negative consumption corresponded to recorded body temperatures of -0.5^{o}C to 3.8^{o}C (Table 4.3).

Mean condition factors (K) of *S. fontinalis* significantly increased from 0.90 ± 0.12 in autumn ($n = 11$), to 1.10 ± 0.16 in winter ($n = 8$), and peaked at 1.31 ± 0.15 ($n = 37$) in spring (Table 4.1; Fig. 4.8, $K = 0.0028t - 115.59$, $R^2 = 0.5768$, $n = 56$; ANOVA post-hoc Tukey, $F = 34.633$, d.f. = 2, $P \leq 0.016$). Minimum and maximum K indices of 0.73 and 1.61 occurred during autumn and spring, respectively (Table 4.1).

4.5 DISCUSSION

Salmonid populations feeding in marine environments have allocated different proportions of gained energy to somatic growth, body maintenance, gonad development and/or lipid deposition (Rikardsen, 2004; Olsen *et al*., 2006; Rikardsen *et al*., 2006). Considering members of the genus *Salvelinus* display a high degree of life history variability with anadromous populations exhibiting irregular periods of marine residence (Brenkman *et al*., 2007), it is unclear where *S. fontinalis* channel marine energy gained. *Salvelinus fontinalis* feeding in Antigonish Harbour from autumn to spring appear to channel energy gained into somatic growth. An individual (258 mm L_F) tagged 7 April in Antigonish Harbour was recaptured 14 June in the Wrights River, and revealed a L_F increase of 47 mm in 68 days (Spares *et al*. unpublished data), lending evidence to rapid somatic growth. However, significant increases in body mass and condition from autumn to spring also suggested allocation to lipid deposition. More detailed studies would be needed to determine if energy allocation changes with ontogeny and/or season (Olsen *et al*., 2006).

4.5.1 SEASONAL DIET

Amphipods have been a dominant food item during *Salvelinus* spp. marine migrations (Gaudreault *et al*., 1982; Morinville & Rasmussen, 2006; Chapter 3). Gaudreault *et al*. (1982) found crustaceans to occur in the diet of *S. fontinalis* throughout their entire marine migration in the Rivière St-Jean estuary, Québec, with individuals consuming the most during January-February (75.0 *% O*, 94.7 *% N*) whereas crustaceans consisted of 75% Gammaridae and 25% Mysidacea. In contrast, Antigonish Harbour migrants consumed no Gammaridae during winter, and the most during autumn (71.4 *% O*, 84.5 *% N*, 74.6 *% IRI*). Migrants in the Matamek River estuary, Québec, similarly consumed amphipods the most from late-August to early October (Whoriskey *et al*., 1981). Considering amphipods breed during summer (Ruppert & Barnes, 1994), their increased abundance during late summer/autumn due to recruitment was likely taken advantage of by feeding *S. fontinalis*.

Nereidae were considered a major winter diet component (14.3 *% O*, 45.0 *% N*, 11.9 *% M*) of Antigonish Harbour *S. fontinalis*. However, analyses were based on nine *S. fontinalis*, with one consuming 36 *Nereis* sp and 1 *Fundulus* sp, thus, possibly misrepresented Nereidae's importance. Gaudreault *et al*. (1982) found winter polychaete predation to be considerably lower

(7.1 % *O*, 1.5 % *N*, *n* = 28). Occurrence of Nereidae in our study coincided with the highest percentage of vegetal/miscellaneous matter within stomachs (43%), suggesting *S. fontinalis* were cued to benthic feeding. Cueing on neckto-/benthic prey during winter, mainly crustaceans and polychaetes, has been observed in other *S. fontinalis* (Gaudreault *et al*., 1982) and *S. trutta* (Pemberton, 1976; Rikardsen *et al*., 2006) populations. Morinville and Rasmussen (2006) noted polychaetes as a dominant prey of *S. fontinalis* remaining near freshwater inputs of Ste. Marguerite Bay, and suggested estuarine fidelity minimized osmoregulation costs. This may be the case of Antigonish Harbour *S. fontinalis*, since many were captured during winter in the West River estuary where salinities and water temperatures averaged 4.5 ± 6.9 (min 0.1, max 21.5; *n* = 57) and 1.0 ± 1.4°C (min -0.1°C, max 6.1°C; *n* = 57), respectively (Spares *et al*. unpublished data). Conversations with ice fishers added observations of *S. fontinalis* feeding on polychaetes in shallow water (depth < 1 m) near the main river channel during February and March. This was further supported by sea-run *S. trutta*, caught co-currently with *S. fontinalis*, regurgitating *Nereis* sp. only (A.D. Spares pers. obs.). Whether or not our results accurately estimate the contribution of Nereidae to Antigonish Harbour *S. fontinalis* winter diet, the fact Nereidae do not occur as prey in autumn, and are more important in winter compared to spring suggests a seasonal specialty.

Insects occurred as prey during the entire sampling period and included 20 taxa, however their occurrence was limited to a few stomachs. For example, two *S. fontinalis* captured in spring had consumed 13 and 15 taxa, of which 11 (85%) and 14 (93%), respectively, were insects. Most insect prey during spring were Carabidae and Scarabaeidae beetles, likely taken as surface prey (Rikardsen *et al*., 2006) considering terrestrial ecosystems virtually enclose Antigonish Harbour(Fig. 4.1). Aquatic insect prey occurred in all seasons, which suggested individuals had returned to fresh water briefly, or had re-entered saltwater from an extended freshwater stay. The caddisfly tube found in an individual captured on 5 March may have been undigested and/or unevacuated for weeks considering cold water temperatures and the tube's sand grain composition (A.D. Spares pers. obs.). Gaudreault *et al*. (1982) found Ephemeroptera larvae and Trichopterans in January-February *S. fontinalis* stomachs, which suggested migrants were foraging near freshwater inputs. Aquatic insects occurring in early May samples may have also suggested individuals re-entered fresh water temporarily before their main re-entry during mid-May to mid-June for summer/autumn residency (Spares *et al*. unpublished data). The occurrence of aquatic insects from autumn to spring may suggest site-fidelity to freshwater inputs (Chapter 3).

Prey diversity, indicated by *n* of taxa consumed by migrants, varied considerably between a winter minimum ($n = 5$) and spring maximum ($n = 32$). This relative diet difference likely related to increased terrestrial insect activity in spring, which increased abundance of optimally sized prey items (Morinville & Rasmussen, 2006). The median *n* of taxa consumed per stomach still remained the same throughout all seasons.

In fresh water, salmonids must often attain a size of 150-250 mm to employ piscivory, however this minimum size threshold varies by species. *Salmo trutta*, *S. fontinalis*, bull trout *Salvelinus confluentus* (Suckley 1859), cutthroat trout *Oncorhynchus clarki* (Richardson 1836) and *O. nerka* have been shown to employ piscivory at $L_F > 200$ mm (Ibbotson *et al*., 1996; Moyle, 2002; Nowak *et al*., 2004; Miller *et al*., 2007; Browne & Rasmussen, 2009). However, piscivory has been observed in an individual *S. trutta* as small as L_F 85 mm (Sánchez-Hernández *et al*. 2012). *Salmo salar* smolts at $L_F < 150$ mm have been documented feeding extensively on fish larvae upon sea entry, suggesting prey type and availability influences piscivorous behaviour (Rikardsen & Dempson, 2011).

Our results concur with the general rule that anadromous *S. fontinalis* > 250 mm L_F employ piscivory (Dutil & Power, 1980; Whoriskey *et al*., 1981; Gaudreault *et al*., 1982; O'Connell, 1982; Morinville & Rasmussen, 2006). The few *S. fontinalis* Gaudreault *et al*. (1982) found feeding on fish in the upper Rivière St-Jean estuary during winter had focussed on Gasterosteidae (75% *Pungitius* sp. & 25% *Gasterosteus* sp.), yet more *S. fontinalis* switched to piscivory during spring (May-June), adding *Ammodytes* sp. and *Osmerus* sp., and had fishes dominating diets by summer as migrants moved into the lower estuary (July-August; 45.5 *% O*; 50 *% N*). Ste. Marguerite Bay *S. fontinalis* preyed almost entirely on *Osmerus* sp. in the upper Saguenay River from winter to spring, but diversified to also include Fundulidae, *Ammodytes* sp. and Gasterosteidae in Ste. Marguerite Bay from May to September (Morinville & Rasmussen, 2006). Acoustic tracking and stomach content analysis of *S. fontinalis* in Sheet Harbour, Nova Scotia, revealed migrants remained around shoals to feed on spring-spawned Atlantic herring larvae *Clupea harengus* (L. 1758), respectively (pers. comm. E.A. Halfyard). Antigonish Harbour *S. fontinalis* followed a similar pattern, focusing almost entirely on Fundulidae and Gasterosteidae from autumn to spring in the inner harbour, but demonstrated seasonal diet changes to include Atherinopsidae during winter/spring and Anguillidae during spring. *Menidia menidia* occurred only during winter/spring, agreeing with their overwintering under estuarine sea ice (Needler, 1940) and spawning in spring (Scott & Scott, 1988). Antigonish Harbour *S. fontinalis* appear to use piscivory as their dominant feeding strategy, and like other populations (Dutil & Power, 1980; Whoriskey *et al*., 1981; Gaudreault *et al*., 1982; O'Connell, 1982;

Morinville & Rasmussen, 2006) appear to focus on one or two prey types depending on habitat and/or season.

The Shannon-Weiner diversity index (*H'*) were similar to SCA results, being the highest in autumn (1.28) and lowest in spring (1.06), which suggested fish foraged on multiple taxa, with relative differences possibly relating to *S. fontinalis* feeding on both freshwater and saltwater prey during their return from rivers to the harbour in autumn, and their increasing preference for Fundulidae and Gasterosteidae fishes over the entire estuarine residency relating to the lowest diversity in spring. High preference for a few fishes during the entire migration is further indicated by complete seasonal diet overlap using Schoener's Overlap index. Decreasing *H'* from autumn to spring seemingly contradicts the total number of taxa present within seasonal samples, which showed the lowest diversity of prey during winter and highest in spring, however *H'* is largely calculated using *% M*, which further reinforces the importance of a few taxa in Antigonish Harbour *S. fontinalis* diet.

4.5.2 SEASONAL FEEDING INTENSITY

All season samples of Antigonish Harbour *S. fontinalis* had percentages of empty stomachs (<22% *ES*) similar to actively feeding *S. fontinalis* during winter in the upper Saguenay River, Québec (< 20% *ES*; Morinville & Rasmussen, 2006). Indeed, none of our seasonal or overall *% ES* were even close to *S. fontinalis* which had ceased feeding (>75% *ES*; Morinville & Rasmussen, 2006). However, higher occurrence of empty stomachs in autumn (18%) and winter (22%) compared to spring (7%) suggested fish may have been having difficulty feeding during autumn/winter. It should be noted that low sample sizes for autumn/winter may have misrepresented actual percentages. Our results agreed with sea-run *S. trutta* which showed stomach fullness and feeding rates were lowest in autumn, along with a high percentage of empty stomachs (45-48%; Rikardsen *et al*., 2006).

The lowest median *M* of prey and median stomach fullness index of Antigonish Harbour *S. fontinalis* during autumn suggested a low feeding intensity. Gaudreault *et al*. (1982) suggested the low mean stomach fullness index for *S. fontinalis* captured in fresh water was due to low prey availability. This may suggest some Antigonish Harbour *S. fontinalis* had recently re-entered saltwater from fresh water during autumn and/or were experiencing difficulty obtaining prey. However, mean stomach fullness indices were virtually the same for autumn (11.6 mg prey g M^{-1}) and spring (11.7 mg prey g M^{-1}), suggesting similar feeding intensities. Autumn/spring indices were comparable to indices (16.7-18.1 mg prey g M^{-1}) for *S. fontinalis* feeding in the Rivière St-Jean estuary from winter to summer (Gaudreault *et al*., 1982). The difference between autumn median and mean stomach fullness indices for Antigonish Harbour *S. fontinalis* was associated with a low sample size, yet the spread of data agreed with individuals exhibiting varying degrees of feeding intensity at the beginning of their marine migration.

Our winter results appeared to suggest feeding intensity peaked with the highest median prey *M* and median/mean stomach fullness indices, however, these results were contradicted by the highest *%ES* and negative consumption rates. Other *S. fontinalis* seasonal feeding studies have found higher prey *M* in winter (Elliott & Jenkins, 1972) and similar stomach fullness indices in winter and summer (Gaudreault *et al*., 1982). No mid-winter sampling was conducted by Rikardsen *et al*. (2006), however consumption rates for *S. trutta* were decreasing November to December and increasing from March to April, which suggested a minimum consumption rate during mid-winter (January-February) when temperatures approached $1^{o}C$ (Rikardsen, 2004). This appeared to be the case in our study where negative consumption rates corresponded to the coldest *S. fontinalis* body temperatures, which may have essentially lowered feeding (Power, 1980) and decreased digestion to ineffective rates (Gaudreault *et al*., 1982; Sweka *et al*., 2004).

Gastric evacuation periods of *S. fontinalis* indicate that one week is needed to empty a full stomach at 4°C (Sweka *et al*., 2004). Comparing water at 20°C versus 4 and 3°C for common roach *Rutilus rutilus* (L. 1758) and sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) digestion duration increased three and eight times longer, respectively (Brett & Higgs, 1970; Hofer, 1979). Assuming these rates for *S. fontinalis*, gastric evacuation of a full stomach at 3°C would take 5 weeks. Furthermore, gastric evacuation rate is zero or lower at temperatures ≤ 2.8°C according to the model proposed by Sweka *et al*. (2004). Evidence of little to no digestion was further supported by no significant difference in the median number of prey items consumed per season and no unidentified (*i.e.* partially digested) fish remains in winter samples.

No significant difference in the median number of prey items consumed per season also suggested continued feeding during winter, further supported by migrants actively taking ice fishing bait (A.D. Spares pers. obs.). It appeared low body temperatures were not negatively influencing feeding as much as digestion (Chapter 3). Considering *S. fontinalis* have been shown to have lower gastric evacuation rates compared to other salmonids (Sweka *et al*. 2004), Antigonish Harbour *S. fontinalis* may have filled their stomachs, but not emptied them during winter.

Spring median prey *M* and median/mean stomach fullness indices were between autumn and winter or similar to autumn indices, indicating feeding was the most consistent during this season. Although spring and autumn mean body temperatures were the same (9°C), consumption rates were comparatively higher in spring, suggesting high feeding intensity and prey availability (total *n* prey taxa = 32). The consumption rates of sea-run *S. trutta* were the highest from spring to autumn (Rikardsen *et al*., 2006). Mean stomach fullness was highest for *S. fontinalis* in Rivière St-Jean estuary during spring (Gaudreault *et al*., 1982), further suggesting optimum feeding conditions.

The significant increase in mean L_F, M and condition factor (K) from autumn to spring revealed Antigonish Harbour *S. fontinalis* were increasing and/or maintaining body condition during this period. Mean K values indicated autumn *S. fontinalis* were in very poor condition compared to migrants captured in spring, with 16% of spring specimens considered trophy class (Barnham & Baxter, 2003). Even the maximum autumn K of 1.11 was considered a poor to fair fish (Barnham & Baxter, 2003). Poor autumn *CF*s suggested migrants had recently re-entered saltwater following fasting during summer-autumn and autumn spawning in fresh water (Morinville & Rasmussen, 2006). Only two spring *S. fontinalis* (5.4%) had *CF*s ≤ 1.00 representing poor specimens (Barnham & Baxter, 2003), which may have been individuals recently entering the harbour following overwintering in fresh water (Morinville & Rasmussen, 2006). Most spring specimens (81%) had *CF*s ≥ 1.20, which are considered fair to excellent fish (Barnham & Baxter, 2003). Considering many spring migrants (37%) were caught 5-10 April, at least one more month of feeding was possible, subsequently increasing K even more before migrants began returning to fresh water in early May (Spares *et al*. unpublished data).

4.5.3 Sources Of Error

Antigonish Harbour *S. fontinalis* are part of a special trout management area, and are heavily fished during a limited spring recreational fishery (MacMillan & Madden, 2007). Therefore, sample collection was highest during spring, with autumn and winter sampling restricted to fewer specimens to reduce negative impacts on the population (Anon., 2006). The authors acknowledge that low autumn and winter sample sizes represent a potentially large source of error, especially comparing seasonal feeding intensity indices and diet differences, where one or two stomachs containing high numbers of different prey could affect summary analyses. For this reason, outliers identified by Systat (2013) were removed to allow similar variances to be used for seasonal comparisons of stomach fullness, number of prey consumed and vegetal/miscellaneous mass per stomach. The cumulative taxa abundance curve showed the maximum *n* of taxa consumed during autumn and winter were reached with relatively few stomachs, thus diet diversity comparisons should be unaffected by the low sample sizes.

Although fishing occurred, no samples were obtained during February, which potentially missed mid-winter trends in diet and feeding intensity. However, considering samples were collected in late January and early March, the authors feel migrants behaved similarly during the four week void. Gaudreault *et al*. (1982) sampled *S. fontinalis* during February and found similar feeding patterns as spring, with prey selection focussing more on invertebrates than fishes. Other seasonal studies have had difficulty obtaining mid-winter samples (Rikardsen *et al*., 2006), possibly due to low movement rates of migrants (Spares *et al*. unpublished data).

Use of 5.1 cm mesh size gill nets and hooks baited with live Fundulidae during sampling may account for larger size of *S. fontinalis* captured. Fyke nets were only used at the head of the tide, thus smaller fish caught in these may have been inhabiting the transition zone between fresh and marine waters. The resulting low sample size of smaller *S. fontinalis* (< 250 mm L_F) may underestimate the importance of fish in their diet.

Temperature, type and size of prey, predator size and prior starvation have all been shown to influence gastric evacuation rates in salmonids (Elliott, 1972). Sweka *et al*. (2004) used *S. fontinalis* approximately half the length of individuals in our study, however they suggested predator size would not influence gastric evacuation rates for *S. fontinalis* >152 mm L_T. Elliott (1972) found predator size didn't affect gastric evacuation rates in *S. trutta* ranging from 200-300 mm L_F, thus predator size effect may have been a minimal source of error in our calculations.

Elliott (1991) showed *S. trutta* gastric evacuation rates of Gasterosteidae were lower than amphipods, similar to caddisfly larvae and higher than beetle larvae. Based on these data (Elliott, 1991) and the prey of Antigonish Harbour *S. fontinalis* (which included amphipods, caddisfly larvae and Gasterosteidae), actual evacuation rates may have been higher than our estimates using Sweka *et al.'s* (2004) beetle/fly larvae prey model. To our knowledge, no gastric evacuation model for piscivorous *S. fontinalis* exists, thus Sweka *et al*. (2004) was the most appropriate model for our estimates. Other consumption rate studies for fishes have used the entire digestive tract since intestine evacuation rates are lower (Héroux & Magnan, 1996). Since this study used stomach contents only, estimated consumption rates may be overestimates.

4.5.4 ESTUARINE OVERWINTERING

Although there are benefits for anadromous salmonids overwintering in saltwater, such as increased abundance of prey, stable water levels and less hazardous ice conditions (Rikardsen *et al*., 2006), there are associated costs such as increased osmoregulation stress and possible predation (Jensen & Rikardsen, 2008; 2012). Yet despite sea-run *S. fontinalis* experiencing Antigonish Harbour's winter extremes, such as a minimal body temperatures of -0.5^{o}C and maximum salinity of 22.2 (Spares *et al*. unpublished data), migrants maintained and/or increased body condition from November to May. Other studies have documented *S. fontinalis* overwintering in salinities ranging from 0 to 22 depending on the tide (Castonguay *et al*., 1982;

Gaudreault *et al*., 1982; Morinville & Rasmussen, 2006). Even spring migrants within Laval Bay, Québec, tolerated a minimum temperature of 6^{o}C in salinities reaching 34 (Curry *et al*., 2006). Other studies (Jensen & Rikardsen, 2008; 2012) have shown *Salvelinus* sp. overwintering in full-strength saltwater during winter, contradicting views that the Genus is a poor osmoregulator at low temperatures (Saunders *et al*., 1975; Finstad *et al*., 1989; McCormick, 1994; Pennell & Barton, 1996; Claireaux & Audet, 1999). Based on diet and fishing locations, Antigonish Harbour *S. fontinalis* remained in the estuary all winter, frequently moving with the flooding tide to the head of tide mark (A.D. Spares pers. obs.). This behaviour probably aided osmoregulation at lower temperatures (Morinville & Rasmussen, 2006).

4.5.5 Conclusions

Saltwater feeding from autumn to spring represented a valuable and important source of energy; especially for fish whose condition factor significantly decreased after freshwater fasting and/or spawning (Morinville & Rasmussen, 2006; Rikardsen *et al*., 2006). Although Antigonish Harbour *S. fontinalis* diet varied with the seasons, migrants relied on a staple diet of Fundulidae & Gasterosteidae, with seasonal supplements of Gammaridae & Nereidae. Piscivory occurred in migrants >250 mm L_F, however no predation on *Osmerus sp*. was observed, perhaps due to large prey size (A.D. Spares pers. obs.). Stomach fullness was expected to be the lowest during winter, however the opposite was observed, which suggested migrants continued to feed although digestion virtually ceased. Antigonish Harbour *S. fontinalis* were concluded to undertake an autumn to spring feeding migration, during which migrants continuously maintained and/or increased body condition. Such a life history strategy represents an alternative to the more common strategy of overwintering and fasting in fresh water until spring.

Table 4.1 - Seasonal comparison of fork-length (mm), body mass (g), diet diversity, body temperature (°C), feeding intensity and body condition indices for sea-run *S. fontinalis* captured in Antigonish Harbour, Nova Scotia, Canada, 2010-12. Summary statistics expressed as mean ± SD and median, interquartile range; (min, max). *H*' and *SI* are Shannon-Weiner and Schoener's Overlap indices, respectively. Stomach Fullness (I_r) expressed as mg prey g M^{-1}. Outliers were removed for all calculations.

	Autumn	Winter	Spring	All
Mean Fork-length (L_F)	278 ± 89 (179, 443)	317 ± 48 (256, 410)	346 ± 62 (213, 450)	330 ± 70 (179, 450)
n	11	9	43	63
Mean Body Mass (*M*)	270 ± 303 (42, 965)	363 ± 189 (140, 740)	540 ± 262 (150, 1235)	462 ± 282 (42, 1235)
n	11	8	37	56
Total *n* taxa	13	5	32	34
Median *n* taxa	2, 3.3 (1, 6)	1, 0.8 (1, 3)	1, 1 (1, 15)	1, 1 (1, 15)
n	9	7	40	56
Diversity *H*'	1.28	1.12	1.06	1.17
Overlap *SI*		1.00	1.00	
Mean Body Temperature (T_b)	8.6 ± 3.6 (1.3, 20.1)	0.7 ± 1.2 (-0.4, 4.7)	9.0 ± 3.4 (0.2, 19.3)	7.6 ± 4.4 (-0.5, 20.1)
n	1147	9548	45547	56242
***n* with prey**	9	7	40	56
***n* empty**	2	2	3	7
% Empty	18%	22%	7%	11%
Median *n* prey	4, 4.5 (1, 10)	5, 4 (2, 18)	5, 9.8 (1, 28)	5, 8 (1, 28)
n	7	6	37	50
Median Total prey M (g)	0.44, 2.49 (0.001, 3.935)	14.00, 9.16 (1.25, 17.21)	5.37, 11.77 (0.05, 24.69)	4.78, 12.39 (0.001, 24.69)
n	8	7	40	55

***n* with vegetal /miscellaneous matter**	3	3	8	14
Median M vegetal /miscellaneous matter (g)	0.09, 0.10 (0.05, 0.14)	0.30, 0.30 (0.11, 0.50)	0.09, 0.11 (0.04, 0.38)	0.11, 0.17 (0.04, 0.50)
n	2	3	7	12
Median Stomach Fullness (I_r)*	0.6, 3.5 (0, 17.5)	22.2, 43.0 (0, 60.8)	12.7, 16.4 (0, 43.8)	11.5, 18.6 (0, 68.2)
n	9	8	36	53
Mean Condition Factor (K)	0.90 ± 0.12 (0.73, 1.11)	1.10 ± 0.16 (0.82, 1.25)	1.31 ± 0.15 (0.98, 1.61)	1.20 ± 0.22 (0.73, 1.61)
n	11	8	37	56

*includes empty stomachs

Table 4.2 - Summary of stomach contents of *S. fontinalis* (*n* = 63) captured from November to May, 2010-12, in Antigonish Harbour, Nova Scotia, Canada. Indices used are frequency of occurrence (*% O*), percent by number (*% N*), and percent by mass (*% M*). Frequency of occurrence is expressed relative to the total number of stomachs containing food (*n* = 53).

	% O				***% N***				***% M***			
	All	**Fall**	**Winter**	**Spring**	**All**	**Fall**	**Winter**	**Spring**	**All**	**Fall**	**Winter**	**Spring**
n	53	7	7	39	63	11	9	43	63	11	9	43
Estuarine Prey Items												
C. Actinopterygii	90.6%	85.7%	100.0%	89.7%	58.7%	8.8%	53.8%	76.1%	93.1%	75.3%	86.9%	95.6%
F. Anguillidae	1.9%	0.0%	0.0%	2.6%	0.1%	0.0%	0.0%	0.1%	5.2%	0.0%	0.0%	6.7%
F. Atherinopsidae	17.0%	0.0%	14.3%	20.5%	2.0%	0.0%	10.0%	1.8%	11.2%	0.0%	22.9%	9.3%
F. Fundulidae	54.7%	28.6%	57.1%	59.0%	14.4%	3.4%	16.3%	18.0%	69.3%	51.4%	56.0%	73.4%
F. Gasterosteidae	26.4%	28.6%	42.9%	23.1%	12.1%	3.8%	27.5%	13.2%	6.2%	21.5%	8.0%	4.8%
Unidentified fish eggs	1.9%	0.0%	0.0%	2.6%	29.1%	0.0%	0.0%	42.1%	0.2%	0.0%	0.0%	0.2%
Unidentified fish remains	17.0%	28.6%	0.0%	17.9%	1.3%	1.7%	0.0%	1.3%	1.1%	2.4%	0.0%	1.2%
F. Crangonidae	9.4%	0.0%	0.0%	12.8%	1.0%	0.0%	0.0%	1.4%	1.0%	0.0%	0.0%	1.3%
F. Gammaridae	17.0%	71.4%	0.0%	10.3%	22.7%	84.5%	0.0%	4.5%	1.1%	20.0%	0.0%	0.2%
F. Nereidae	5.7%	0.0%	14.3%	5.1%	4.5%	0.0%	45.0%	1.4%	3.0%	0.0%	11.9%	1.3%
Aquatic Prey Items												
F. Amnicolida	1.9%	14.3%	0.0%	0.0%	0.2%	0.8%	0.0%	0.0%	0.0%	0.1%	0.0%	0.0%
F. Lumbricidae	1.9%	0.0%	0.0%	2.6%	0.2%	0.0%	0.0%	0.3%	0.3%	0.0%	0.0%	0.4%
C. Insecta	18.9%	71.4%	14.3%	10.3%	12.7%	5.9%	1.3%	16.3%	1.0%	3.7%	0.1%	1.0%
F. Coenagrionidae	5.7%	14.3%	0.0%	5.1%	1.9%	0.4%	0.0%	2.5%	0.1%	0.3%	0.0%	0.2%
F.Cicadellidae	3.8%	0.0%	0.0%	5.1%	0.3%	0.0%	0.0%	0.4%	0.0%	0.0%	0.0%	0.0%
F.Formicidae	3.8%	0.0%	0.0%	5.1%	0.3%	0.0%	0.0%	0.4%	0.0%	0.0%	0.0%	0.0%
F. Apidae	3.8%	0.0%	0.0%	5.1%	0.1%	0.0%	0.0%	0.1%	0.0%	0.0%	0.0%	0.0%
O. Coleoptera	9.4%	42.9%	0.0%	5.1%	8.7%	2.5%	0.0%	11.7%	0.6%	1.6%	0.0%	0.7%
F. Carabidae	5.7%	14.3%	0.0%	5.1%	3.1%	0.4%	0.0%	4.4%	0.2%	0.0%	0.0%	0.3%

F. Dytiscidae	1.9%	14.3%	0.0%	0.0%	0.3%	1.3%	0.0%	0.0%	0.1%	1.1%	0.0%	0.0%
F. Staphylinidae	3.8%	0.0%	0.0%	5.1%	3.0%	0.0%	0.0%	4.4%	0.2%	0.0%	0.0%	0.2%
F. Elateridae	3.8%	0.0%	0.0%	5.1%	0.5%	0.0%	0.0%	0.7%	0.1%	0.0%	0.0%	0.1%
F. Scarabaeidae	5.7%	14.3%	0.0%	5.1%	0.6%	0.4%	0.0%	0.7%	0.0%	0.2%	0.0%	0.0%
F. Hydrophilidae	3.8%	14.3%	0.0%	2.6%	0.2%	0.4%	0.0%	0.1%	0.0%	0.3%	0.0%	0.0%
F. Curculionidae	3.8%	0.0%	0.0%	5.1%	0.2%	0.0%	0.0%	0.3%	0.0%	0.0%	0.0%	0.1%
F. Chrysomelidae	1.9%	0.0%	0.0%	2.6%	0.1%	0.0%	0.0%	0.1%	0.0%	0.0%	0.0%	0.0%
F. Coccinellidae	1.9%	0.0%	0.0%	2.6%	0.1%	0.0%	0.0%	0.1%	0.0%	0.0%	0.0%	0.0%
F. Pentatomidae	1.9%	0.0%	0.0%	2.6%	0.1%	0.0%	0.0%	0.1%	0.0%	0.0%	0.0%	0.0%
F. Cydnidae	3.8%	0.0%	0.0%	5.1%	0.6%	0.0%	0.0%	0.8%	0.0%	0.0%	0.0%	0.0%
F. Corydalidae	1.9%	14.3%	0.0%	0.0%	0.2%	0.8%	0.0%	0.0%	0.0%	0.8%	0.0%	0.0%
F.Calliphoridae	1.9%	0.0%	0.0%	2.6%	0.1%	0.0%	0.0%	0.1%	0.0%	0.0%	0.0%	0.0%
F. Limnephilidae	5.7%	28.6%	14.3%	0.0%	0.3%	0.8%	1.3%	0.0%	0.0%	0.6%	0.1%	0.0%
F. Leptophlebiidae	1.9%	0.0%	0.0%	2.6%	0.3%	0.0%	0.0%	0.4%	0.0%	0.0%	0.0%	0.0%
F.Acrididae	1.9%	0.0%	0.0%	2.6%	0.1%	0.0%	0.0%	0.1%	0.0%	0.0%	0.0%	0.0%
Unidentified insects	7.5%	42.9%	0.0%	2.6%	0.4%	1.3%	0.0%	0.1%	0.0%	0.3%	0.0%	0.0%
O. Araneae	1.9%	0.0%	0.0%	2.6%	0.1%	0.0%	0.0%	0.1%	0.0%	0.0%	0.0%	0.0%
Unidentified	26.4%	42.9%	42.9%	20.5%	-	-	-	-	0.9%	7.0%	1.2%	0.5%

Table 4.3 **-** Summary of calculations (mean ± SD, min, max, *n*) used to estimate consumption rates (C_{24}; mg prey g M^{-1}) of sea-run *S. fontinalis* during seasonal intervals from 19 November to 5 May, 2010-12, in Antigonish Harbour, Nova Scotia, Canada. Calculations include mean body temperature (T_b, °C), mean stomach fullness at beginning of interval (I_{ro}), mean stomach fullness at end of interval (I_{rt}), mean stomach fullness over entire interval (I_r), instantaneous gastric evacuation rate (R, estimated from Sweka *et al*. 2004) and interval duration (t, h).

Interval	**19 Nov-13 Dec**	**13 Dec–7 Jan**	**7 Jan-29 Jan**	**29 Jan-4 Mar**	**4 Mar-8 Apr**	**8 Apr-5 May**
T_b	6.3 ± 1.7 (3.0, 9.1)	3.9 ± 1.6 (0.5, 9.4)	1.4 ± 1.3 (0.02, 3.8)	0.1 ± 0.2 (-0.5, 2.1)	3.5 ± 2.6 (-0.1, 11.5)	7.4 ± 2.5 (0.7, 14.9)
n	413	754	2208	5564	7158	23108
I_{ro}	1.22 ± 1.71 (0.00, 2.43)	18.3 ± 29.0 (0, 68.6)	15.0 ± 21.2 (0, 30.0)	52.5 ± 11.8 (44.2, 60.8)	19.3 ± 22.1 (0, 43.5)	10.3 ± 6.4 (2.6, 21.9)
n	2	5	2	2	3	9
I_{rt}	18.3 ± 29.0 (0, 68.6)	15.0 ± 21.2 (0, 30.0)	52.5 ± 11.8 (44.2, 60.8)	19.3 ± 22.1 (0, 43.5)	10.3 ± 6.4 (2.6, 21.9)	27.8 ± 12.4 (6.2, 43.8)
n	5	2	2	3	9	9
I_r	11.6 ± 21.3 (0, 68.6)	17.3 ± 25.3 (0, 68.6)	27.3 ± 26.5 (0, 60.8)	32.6 ± 24.7 (0, 60.8)	11.7 ± 11.5 (0, 43.5)	16.1 ± 14.1 (0, 62.8)
n	11	7	5	5	13	36
R	0.0106	0.0047	-0.0090	-0.0217	0.0031	0.0120
t	576	600	528	816	840	648
C_{24}	3.67	1.89	-3.85	-25.4	0.90	5.93

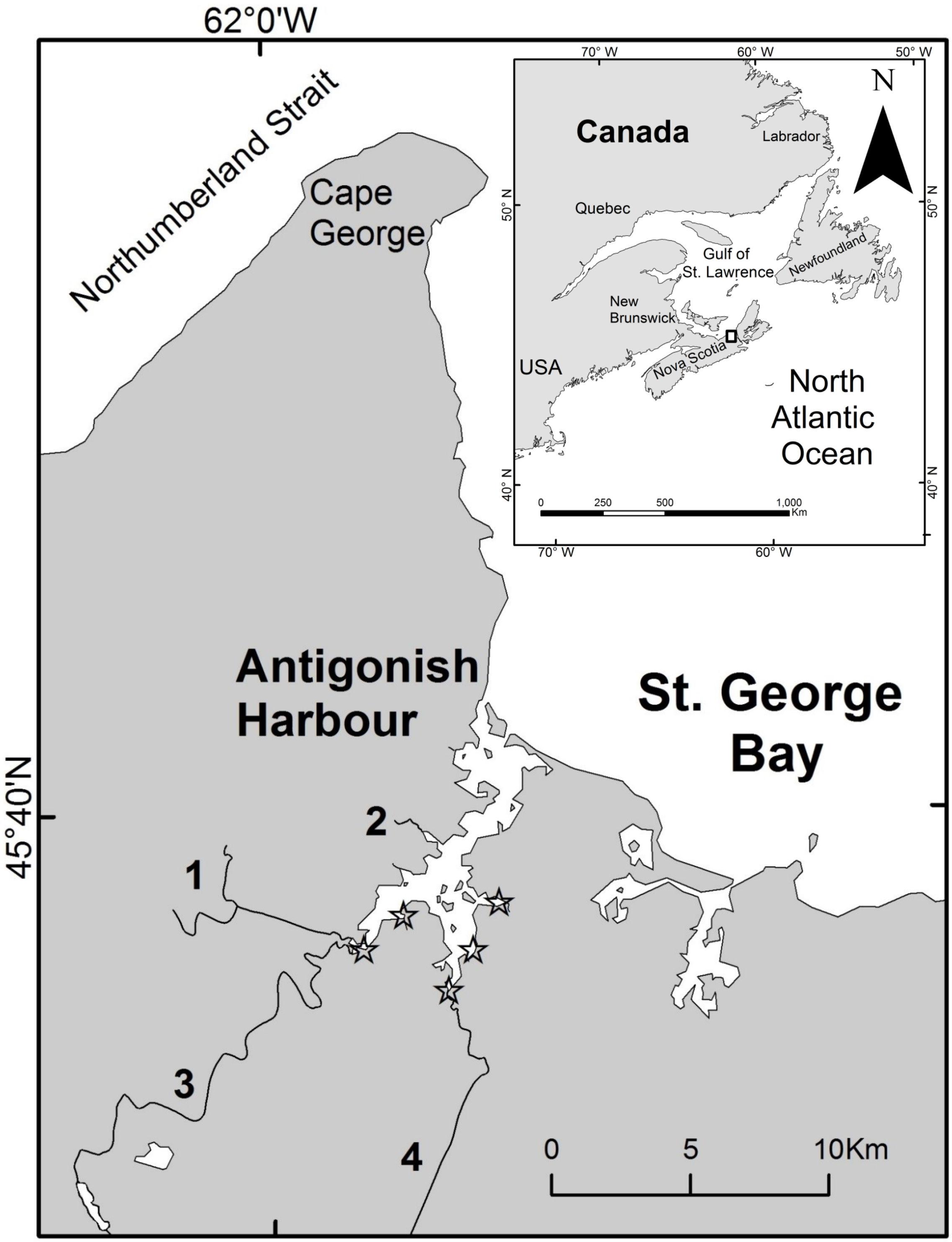


Figure 4.1 - Location of Antigonish Harbour, Nova Scotia, Canada, showing capture sites (stars) of sea-run *S. fontinalis* during late autumn to mid spring from 2010 to 2012. Wrights (1), North (2), West (3) and South (4) rivers.

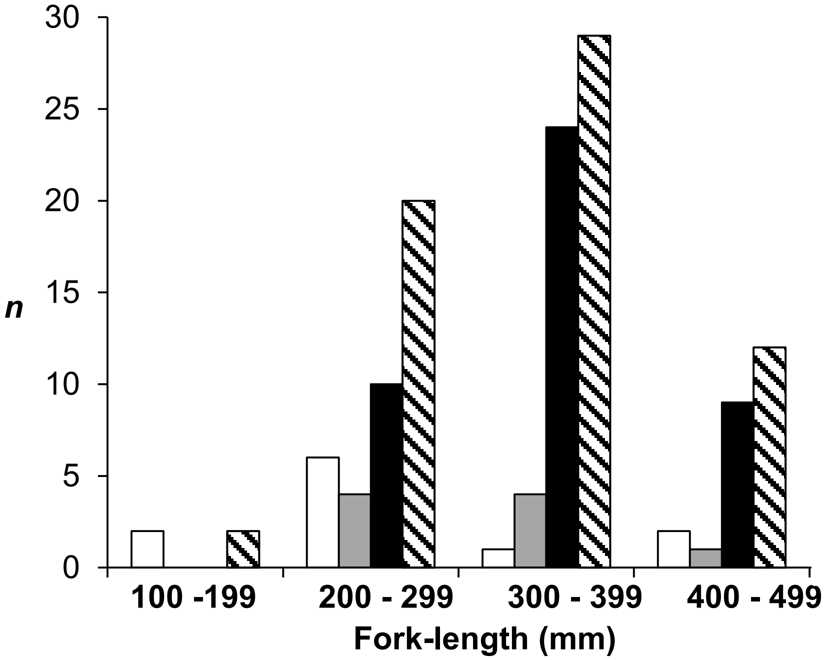


Figure 4.2 - Fork-length (mm) frequency of sea-run *S. fontinalis* captured during autumn (n = 11, open bars), winter (n = 9, shaded bars) and spring (n = 43, solid bars), and all data pooled (n = 63, diagonal bars), from 2010-12 in Antigonish Harbour, Nova Scotia, Canada.

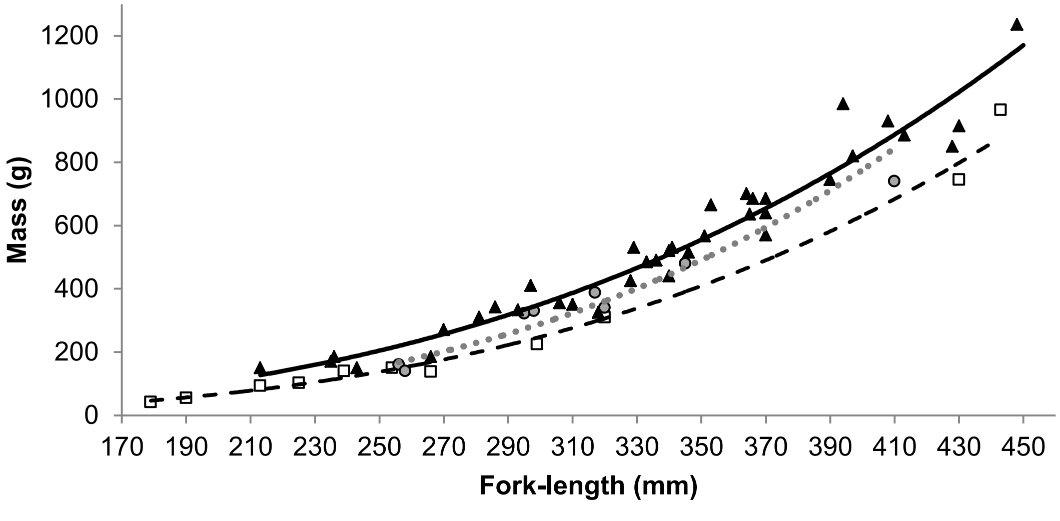


Figure 4.3 - Mass fork-length relationships for sea-run *S. fontinalis* (n = 63) captured 2010-2012 during autumn (19 November – 13 December, open square, dashed line $M = 2\text{E-}06F_L^{3.244}$; $r^2 = 0.9877$; n = 11), winter (7 January – 5 March, grey circle, dotted line; $M = 9\text{E-}07F_L^{3.4275}$; $r^2 = 0.9375$; n = 9) and spring (5 April – 5 May, solid triangle, solid line; $M = 2\text{E-}05F_L^{2.9684}$; $r^2 = 0.9535$; n = 43).

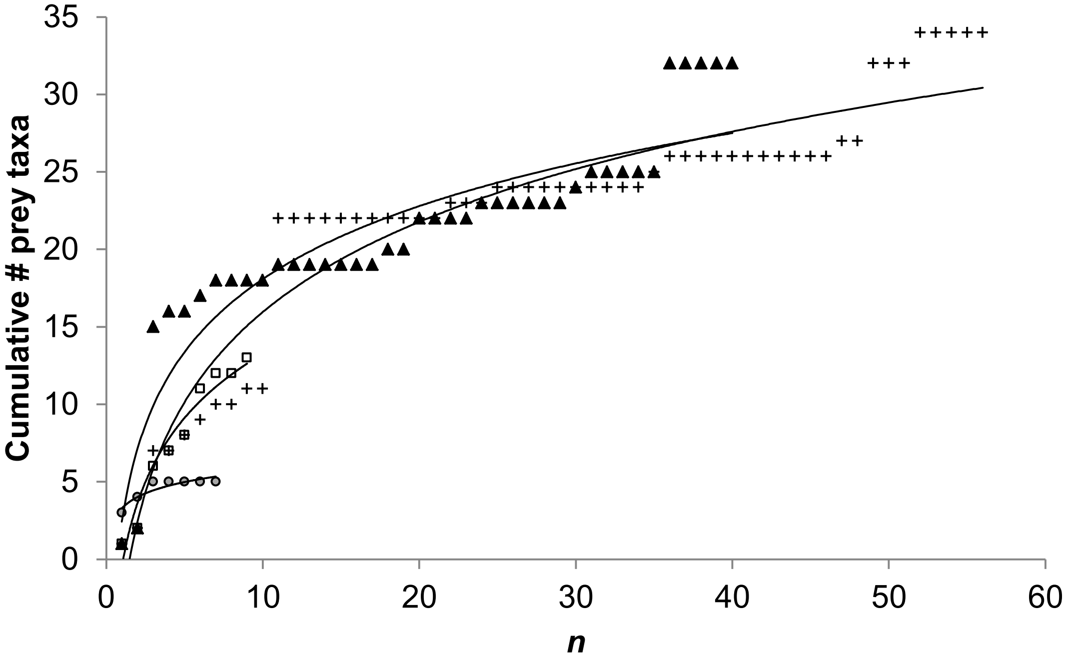
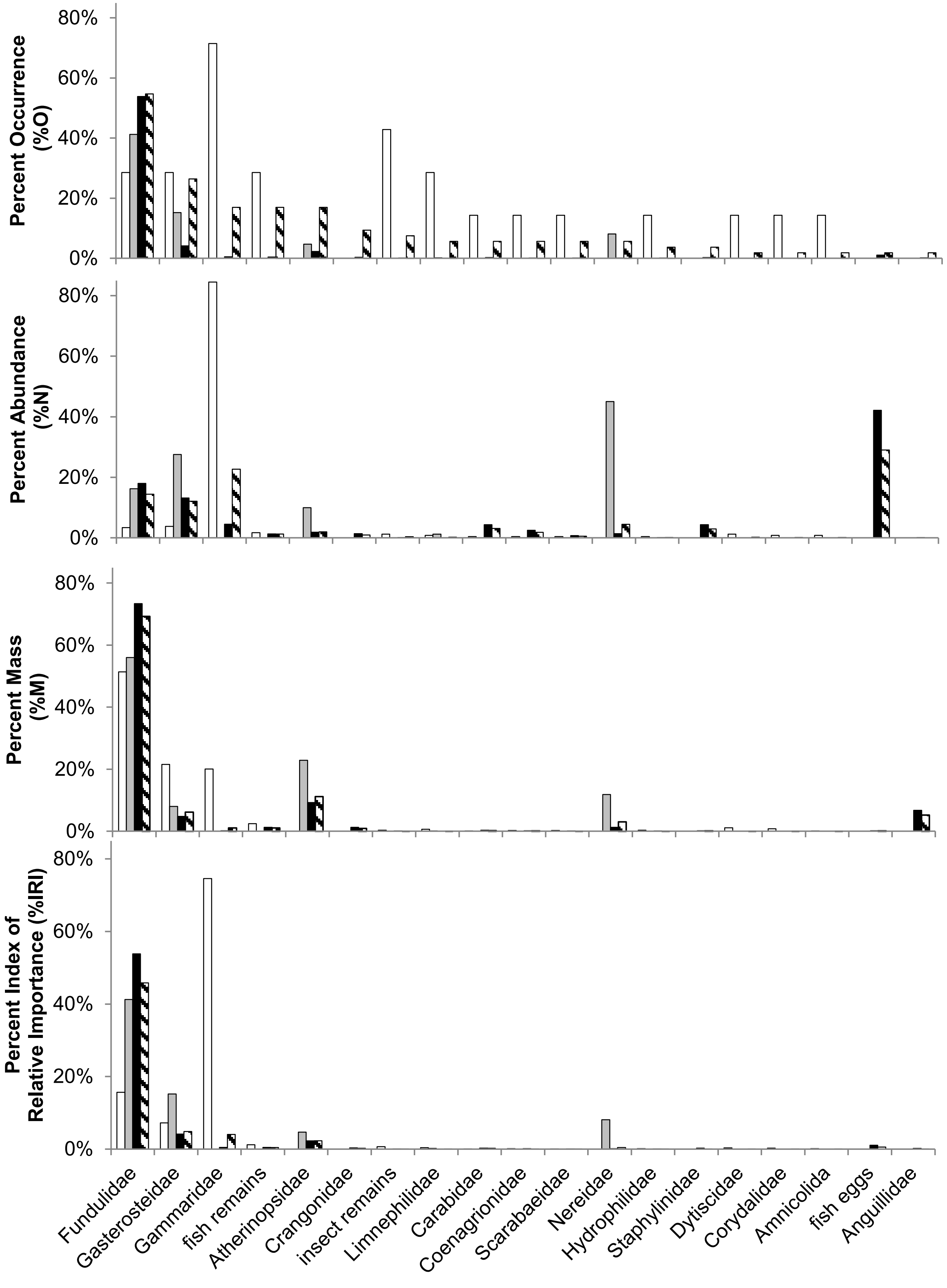


Figure 4.4 **-** Cumulative number of prey taxa for sea-run *S. fontinalis* containing prey during 2010-2012 (*n* = 56, cross), autumn (19 November – 13 December, *n* = 9, open square), winter (7 January – 5 March, *n* = 7, shaded circle) and spring (5 April – 5 May, *n* = 40, solid triangle) with trendline asymptotes showing minimum sample size needed to reach maximum number of taxa.



Percent Occurrence (%O)
80%
60%
40%
20%
0%
Percent Abundance (%N)
80%
60%
40%
20%
0%
Percent Mass (%M)
80%
60%
40%
20%
0%
Percent Index of Relative Importance (%IRI)
80%
60%
40%
20%
0%
Fundulidae
Gasterosteidae
Gammaridae
fish remains
Atherinopsidae
Crangonidae
insect remains
Limnephilidae
Carabidae
Coenagrionidae
Scarabaeidae
Nereidae
Hydrophilidae
Staphylinidae
Dytiscidae
Corydalidae
Amnicolida
fish eggs
Anguillidae

Figure 4.5 **-** Relative occurrence (*%O*), abundance (*%N*), and mass (*%M*) of taxa collected from the stomach contents of sea-run *S. fontinalis* (*n* = 56) captured during autumn (open bars), winter (shaded bars) and spring (solid bars), and all data pooled (diagonal bars), from 2010-12 in Antigonish Harbour, Nova Scotia, Canada. The percent index of relative importance (*%IRI*) of each taxa to trout diet is also presented. Prey taxa with *%O* <10 were not included but the following order **(**Araneae**)** and families: Acrididae, Apidae, Calliphoridae, Chrysomelidae, Cicadellidae, Coccinellidae, Curculionidae, Cydnidae, Elateridae, Formicidae, Leptophlebiidae, Lumbricidae and Pentatomidae, were recovered.

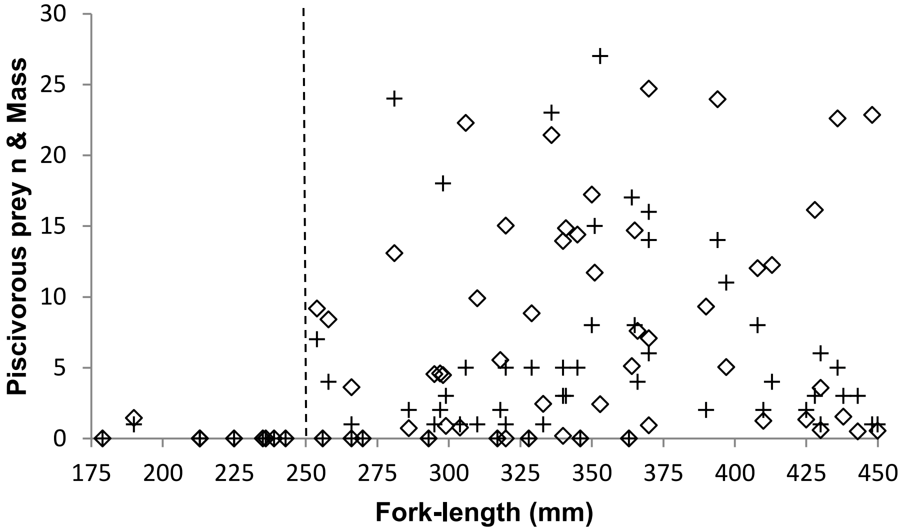


Figure 4.6 - Fork-length (mm) versus piscivory shown by number (cross) and wet mass (g; diamond) of fish consumed by sea-run *S. fontinalis* captured in Antigonish Harbour, Nova Scotia, Canada, from November to May, 2010-12.

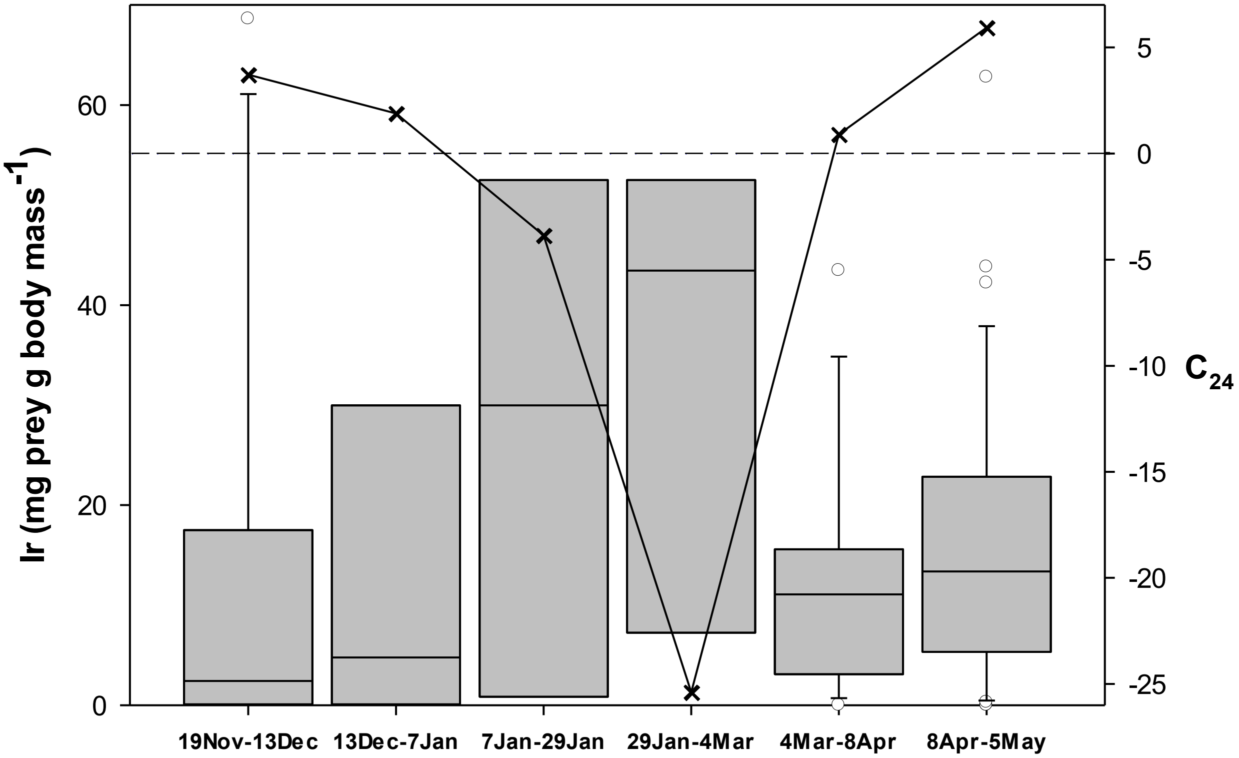


Figure 4.7 - Relationship between stomach fullness indices (*Ir*, mg prey g body mass^{-1}, shaded bars) and daily consumption rates (C_{24}, crosses), calculated for sea-run *S. fontinalis* captured within intervals from 19 November to 5 May, 2010-12, in Antigonish Harbour, Nova Scotia, Canada. Open circles = *Ir* outliers.

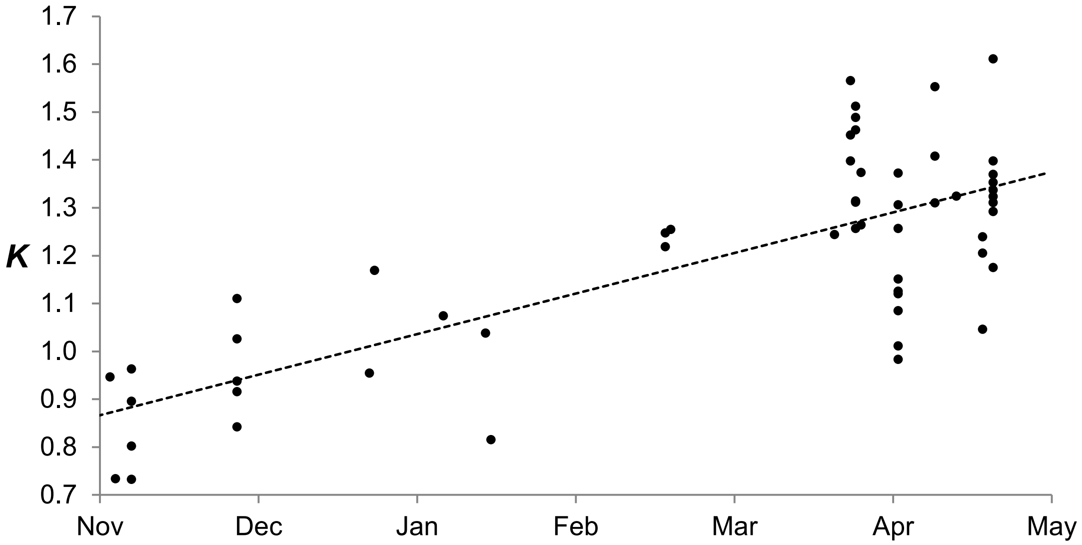


Figure 4.8 **-** Body condition (*K*) of sea-run *S. fontinalis* captured in Antigonish Harbour, Nova Scotia, Canada, from November to May, 2010-12 ($K = 0.0032t - 129.87$, $r^2 = 0.5356$, $n = 63$).

CHAPTER 5

A CRITICAL REVIEW OF MARINE ADAPTABILITY WITHIN THE ANADROMOUS SALMONINAE

5.1. ABSTRACT

Salmoninae adaptability to the marine environment was evaluated based on the following criteria: (1) extent, and (2) duration of migration; (3) horizontal and (4) vertical habitats; and (5) minimum and (6) maximum thermohaline limits experienced. The most-to-least marine adapted genera were *Oncorhynchus*, *Salmo* and *Salvelinus*, agreeing with Rounsefell's anadromy ranking. The lowest and highest thermohaline limits were reached by *O. keta, S. salar, S. alpinus* and *S. malma;* and *O. kisutch, O. keta* and *O. nerka*, respectively. Marine adaptability criteria rearranged Rounsefell's top three species, with *O. keta* and *O. nerka* ranked higher than *O. gorbuscha*, and suggested recently evolved salmonids are adapted to a more marine life history. *Oncorhynchus masou* ranked similar to its sister taxa: *O. mykiss* and *O. clarki*. Lower ranked salmonids usually evolved earlier, adding evidence to a freshwater salmonid ancestor. More research on marine migration is needed on all Salmoninae, especially the lesser studied trout and charr which have shown highly variable life histories compared to salmons.

5.2 INTRODUCTION

In recent years, technology has enabled more detailed studies on anadromous fish marine migration, including behaviour, duration, habitat preferences, routing and survival (Dadswell 2009; Stokesbury *et al*. 2009; Drenner *et al*. 2012; Beardsall *et al*. 2013; McLean *et al*. 2014). In spite of these advances, there has been relatively little research conducted on the marine migration of some salmonids (Dadswell *et al*. 2010). For example, amago *Oncorhynchus rhodurus* Jordan & McGregor 1925 and masu *Oncorhynchus masou* (Brevoort 1856) salmon; brook *Salvelinus fontinalis* Mitchill 1814, bull *Salvelinus confluentus* Suckley 1859, cutthroat *Oncorhynchus clarki* (Walbaum 1792) and lake *Salvelinus namaycush* (Walbaum 1792) trout; and Arctic *Salvelinus alpinus* (L. 1758), dolly varden *Salvelinus malma* (Walbaum 1792) and white-spotted *Salvelinus leucomaenis* (Pallas 1814) charr, appear to be underrepresented in the literature. Recent studies, however, have revealed new information on marine migration of the less-studied *Salvelinus* spp. (Goetz *et al*. 2004; Jensen & Rikardsen 2012; Chapter 3 & 4), and even on the better studied Atlantic salmon *Salmo salar* L. 1758 (Spares *et al*. 2007; Dadswell *et al*. 2010; Chittenden *et al*. 2013; Lacroix 2013) and steelhead trout *Oncorhynchus mykiss* (Walbaum 1792) (Nielsen *et al*. 2011).

Salmonid salinity tolerance has been gauged on preparatory physiology/morphology and saltwater acclimation upon marine exposure (McCormick 1994). Recent tracking has recorded temperature and salinity encountered by marine migrating salmonids (Goetz *et al*. 2004; Jensen & Rikardsen 2012; Lefèvre *et al*. 2012; Chapter 3 & 4), and results cast doubt on the current salinity tolerance hierarchy. Long-distance migratory Salmoninae (*Oncorhynchus* & *Salmo*) have demonstrated salinity tolerance in oceanic environments for months to years (Dadswell *et al*. 2010). Species of the genus *Salvelinus*, however, have been deemed poor osmoregulators in cold water (Saunders *et al*. 1975; Finstad *et al*. 1989). Yet *S. alpinus* has been tracked in water with a maximum salinity of 33 and minimum temperature of 0^{o}C (Jensen & Rikardsen 2008; 2012; Chapter 3) and caught in a salinity of 33 at -1.5^{o}C (Bystriansky *et al*. 2007).

With the marine environment being affected by climate change (Grebmeier *et al*. 2006), it is more likely generalist species may be able to adapt while specialist species may be subject to increasing extinction risk (Townsend *et al*. 2003; Thomas *et al*. 2004). With this in mind, the question is posed: Which Salmoninae species are best adapted to the marine environment? This review examines the most up-to-date marine migration research on Salmoninae species to infer relative inter-specific marine adaptability based on horizontal, vertical and thermohaline habitat limits. Species will be dense ranked most (1) to least (14) adaptable to the marine environment. Although *O. rhodurus, S. leucomaenis* and *S. namaycush* are known to undertake marine migrations (Dunham *et al*. 2008, Swanson *et al*. 2010, Drenner *et al*. 2012), they were excluded due to lack of information.

5.3 DEGREES OF ANADROMY

According to Rounsefell (1958), 'anadromy' is the degree to which freshwater species establish residency at sea, and determined the most to least anadromous Salmoninae genera as *Oncorhynchus*, *Salmo* and *Salvelinus*. Within *Oncorhynchus*, pink salmon *Oncorhynchus gorbuscha* (Walbaum 1792) ranked highest with *O. mykiss* and *O. clarki* ranked lowest. *Oncorhynchus* trout, *Salmo* and *Salvelinus* spp are considered 'optionally anadromous' (Table 5.1; Rounsefell 1958). Based on new information and Rounsefell's criteria, Quinn & Myers (2004) suggested that chum *Oncorhynchus keta* (Walbaum 1792) and sockeye *Oncorhynchus nerka* (Walbaum 1792) salmon ranked higher than *O. gorbuscha* due to their more extensive range and longer duration at sea. Chinook *Oncorhynchus tshawytscha* (Walbaum 1792) was considered less anadromous than coho *Oncorhynchus kisutch* (Walbaum 1792) salmon due to the existence of mature male parr, and iteroparity under experimental conditions. Upon discovering *O. mykiss* undertook a more extensive open-ocean migration, the species was ranked higher than *O. tshawytscha* (Quinn & Myers 2004). Goetz *et al*. (2004) suggested *S. malma* would rank slightly higher than *S. alpinus*. *Salvelinus confluentus* and *S. fontinalis* were also ranked lower then *S. malma*, although *S. confluentus* was classified as *S. malma* at the time of Rounsefell's publication (Goetz *et al*. 2004). *Oncorhynchus masou, O. rhodurus* and *S. leucomaenis* were not included by Rounsefell (Table 5.1).

5.4 MARINE ADAPTABILITY CRITERIA

Rounsefell (1958) based his anadromy hierarchy of Salmoninae on the following criteria: marine migration (1) extent and (2) duration, (3) state of gonad maturation obtained at sea, (4) fresh water or marine spawning, (5) post-spawning mortality, and (6) occurrence of fresh water resident populations. Rounsefell (1958) was assessing anadromy, the ability of Salmoninae species to establish residency at sea, and used freshwater life history characteristics as 'anadromy' indicators. Our review aimed to rank Salmoninae marine adaptability, and focuses on marine migration information. For this reason, modifications of Rounsefell's criteria 1 and 2 were used as marine adaptability criteria. Many species, notably *O. mykiss,* have multiple life history strategies and seasonal runs within a single river whereby some populations enter fresh water with or without fully developed gonads (Quinn 2005). Many species are also intermittent spawners undergoing multiple marine migrations between spawning events, thus migrants may not necessarily channel marine energy gained into fecundity (Gulseth & Nilssen 2001). For these reasons, Rounsefell's criterion 3 was not used in our survey. Although a select few *O. gorbuscha*, *O. keta* and *S. trutta* populations spawn in brackish water (Heard 1991; Salo 1991; Landergren and Vallin 1998; Limburg *et al*. 2001), the vast majority of their populations, like all other salmonids, are freshwater spawners (Rounsefell 1958), thus criterion 4 was not included. Criteria 5 and 6 were excluded, since these criteria didn't address salmonid marine adaptability.

For this review, the degree of a species' marine adaptability was inferred based on the following criteria: (1) extent, and (2) duration of migration; (3) horizontal and (4) vertical habitats; and (5) minimum and (6) maximum thermohaline limits experienced. Migration extent was defined as the maximum straight line distance (SLD) from natal fresh water, where species were ranked highest to lowest in three categories, by traveling ≤10000, 1000 or 100 km, respectively (Table 5.2). Duration was defined as the percentage of time in years a migrant spent in salt water during an average lifespan, with the highest to lowest percentages assigned a corresponding rank from 1 to 14 (Table 5.3). Predominant horizontal and deepest vertical habitats were based on oceanic, neritic and littoral (ranked 1 to 3, Table 5.4); and aphotic (maximum depth, $Z_{\max}$, > 400 m), dysphotic (< 400 m), euphotic (< 150 m) and littoral (< 15 m, ranked 1 to 4, Table 5.5) zones, respectively (Woodward 2012).

To address thermohaline tolerance, species were evaluated based on how close they approached their lethal limits during marine migration. The thermal and salinity limits were estimated based on preferred minimum and maximum temperature and salinity, expressed as a percentage relative to their lower and upper incipient lethal temperature, respectively, at the global mean salinity of 35 (IOC 2010). Minimum thermohaline limit was calculated using $(T_{min} - S)(T_{low} - 35)^{-1}$; where T_{min} is the minimum preferred marine temperature (^{o}C), S is the salinity at T_{min}, and T_{low} is the species' lower incipient lethal temperature (^{o}C, Table 5.6). Maximum thermohaline limit was calculated using $(T_{max} + S)\ (T_{upp} + 35)^{-1}$; where T_{max} is the maximum preferred marine temperature (^{o}C), S is the salinity at T_{max}, and T_{upp} is the species' upper incipient lethal temperature (^{o}C, Table 5.7). Each surveyed species' criteria ranks were summed, with the lowest to highest sums dense ranked 1 to 14, with rank 1 being the most and rank 14 being the least adapted to the marine environment (Table 5.8).

5.5 DOES BODY SIZE MATTER?

Salmonids with larger body size tolerate osmoregulatory stress better than smaller bodied ones (Klemetsen *et al*. 2003). Jensen & Rikardsen (2012) suggested that the decreased surface to volume ratio of larger fish, the changing mechanisms for osmoregulation related to increasing fish size, or both were responsible. As ectotherms, a positive correlation exists between ambient water temperature and enzyme activity responsible for salt ion regulation until a maximum threshold saltwater temperature (>20°C at salinities >30) is reached and enzyme activity decreases. Even small salinity increments near the upper thermal limit often result in osmoregulatory stress or death. For example, *O. kisutch* can tolerate salinities of 28 to 30 at 18°C, but experience 80 to 90% mortality in salinities of 33 to 34 at the same temperature (Pennell & Barton 1996). Low temperatures also decrease the salt exchange enzyme activity, which is countered for in cold-acclimated fishes by increasing enzyme concentrations (McCormick *et al*. 1997). At full-strength saltwater, the minimum lethal temperature is about -0.7°C for *O. kisutch*, *O. tshawytscha, S. salar* and *S. fontinalis* (Balon 1980; Pennell & Barton 1996), with prolonged exposure to temperatures below 3 to 4°C negatively affecting growth and survival (Pennell & Barton 1996; Curry *et al*. 2006). Some species, such as *O. kisutch*, *O. tshawytscha* and *S. salar*, can tolerate a sustained salinity of 21 within their preferred temperature range at any size (Pennell & Barton 1996). Juvenile *O. gorbuscha* inhabit dilute saltwater of shallow coastal waters during their first few weeks of life, and yet 72-hr salinity challenge tests of 0.2 g individuals proved tolerance of 32 and 40 salinities at 11°C and 7°C, respectively (Pennell & Barton 1996; Grant *et al*. 2010).

Although past studies have gauged Salmoninae marine fitness using salinity tolerance based on minimum size of fish undertaking seaward migration (Finstad *et al*. 1989; McCormick 1994), success may also improve with increasing fish size due to decreased predation and increased opportunities of larger-sized prey items (Saloniemi *et al*. 2004). Increasing smolt size may also not consistently confer a survival advantage, as shown by increased survival of larger smolts only when annual marine survival is relatively low (Holtby *et al*. 1990). Considering these conflicting facts and that body size at saltwater entry is a result of freshwater life history, a criterion based on juvenile size was omitted. It should be noted, however, that migration duration (criterion 2) indirectly considers body size at saltwater entry, as species with juveniles entering the sea earlier increase marine residency percentage of life span, and that in turn causes these species to be ranked higher.

5.6 MARINE RESIDENCY

Oncorhynchus keta and *O. gorbuscha* virtually spend their entire lives at sea, 97% and 95%, respectively (Table 5.3), as most individuals enter full-strength saltwater soon after emerging from gravel beds (Heard 1991). The percentage marine life history of these two species could even be 100% as some populations spawn in the intertidal zone (Rounsefell 1958), although the majority spawn in fresh water (Quinn 2005). Iteroparous *Salmo* spp. were assumed to spawn twice during an average life span (Thorstad *et al*. 2011) while *S. alpinus* was assumed to first spawn at 8 yr old (Sprules 1953) and skip marine migrations during spawning years (Hunter 1976). *Salvelinus malma* may spend up to 47% of an average 11 yr life span (Wilson 1997) in salt water given a 5 month long marine migration each year (Armstrong 1974). Stewart *et al*. (2010), however, estimated *S. malma* spend <10% of their life at sea feeding, and this evidence was used for the marine adaptability review. Although marine residency may reflect an anadromous species' adaptability to the marine environment, residency can be controlled by the period the ocean is inhabitable. As no salmonid possess anti-freeze proteins (Enevoldsen *et al*. 2003) and salmonid blood plasma freezes between -0.7 to -1.0°C (Huusko *et al*. 2007), migrants continuously exposed to temperatures approaching the mean saltwater freezing point of -1.9°C (DeVries & Cheng 2005) would be forced to move to warmer water (Dempson & Kristofferson 1987). Although anadromy is more prevalent at higher latitudes due to oligotrophic freshwater systems (Gross *et al*. 1988; Dunham *et al*. 2008), Arctic salmonids tend to have less time with favorable marine conditions, resulting in average marine residencies which generally decrease with increasing latitude (L'Abée-Lund *et al*. 1989).

5.7 HORIZONTAL AND VERTICAL HABITATS

Of the surveyed Salmoninae, more than half were reported to travel >1000 km SLD from natal rivers, including *S. salar*, *S. malma* and all *Oncorhynchus* spp. except *O. clarki* (Table 5.2). *Salvelinus* spp., *S. trutta* and *O. clarki* are predominantly linked to near shore and littoral zones whereas *S. salar* and all other *Oncorhynchus* spp. undertake migration within neritic and oceanic waters (Table 5.4). *Salvelinus malma* has been tagged in Alaska and recaptured in Russia after traversing the Bering Sea (Deccio 1992; Quinn & Myers 2004), yet the majority of individuals remain near shore (Kowalchuk *et al*. 2010). *Salmo salar* kelts were recorded by pop-up satellite archival tags diving to a maximum depth of 950 m (Lacroix 2013). The next two deepest divers: *O. tshawytscha* and *O. keta,* were caught at maximum depths approximately half as deep (Table 5.5), yet these may underestimate actual maximum dive depths due to the limits of trawling depth (Walker *et al*. 2007). These three species were within the aphotic mesopelagic zone

(Woodward 2012), and therefore assigned the same ranking (Table 5.5). There is limited data during winter, but vertical distributions may not change substantially from summer in offshore waters, even if seasonal vertical shifts occur during coastal and shelf migrations. Continuous year-round data on marine vertical distribution is needed for all Salmoninae (Walker *et al*. 2007).

5.8 THERMOHALINE LIMITS

Temperature controls life process of ectothermic organisms, ultimately determining success and survival (McCormick *et al*. 1997). In anadromous Salmoninae, low temperatures encountered by parr and smolts may not only delay smoltification and emigration to sea, but also decrease movement, growth, organ development and osmoregulation rates at sea, thus increasing both juvenile mortality and marine migration duration. Higher temperatures may trigger earlier spring freshets resulting in earlier coastal plankton blooms which may benefit early sea-run emigration or disadvantage later emigrants (Chittenden *et al*. 2009). At sea, warmer water may enhance feeding and maintenance, but too high temperatures (>21^{o}C) may increase respiration and lack of appetite (Straty & Jaenike 1980), and result in lower energy stores of returning migrants (Chittenden *et al*. 2009).

Maximum salinity tolerance of migrants may not be accurately defined solely by field observations of the maximum salinity in which fish have been captured (Kefford *et al*. 2004). Distribution of individuals may be influenced by co-factors, such as food and habitat availability, oxygen concentration, pH and temperature (Bringolf *et al*. 2005). For example, riverine populations of *S. trutta* and *S. alpinus* with unsuitable freshwater overwintering habitat also use estuarine and marine environments, contradicting previous beliefs that they have poor salinity tolerance at low temperatures, and are restricted to overwintering in fresh water (Jensen & Rikardsen 2012).

Long-term exposure to water <0°C has not been documented by tracking studies, yet *S. alpinus* has been captured in full-strength saltwater at -1.5°C (Bystriansky *et al*. 2007). With decreasing temperatures, body fluid viscosity increases, adding pressure within circulatory systems (DeVries & Cheng 2005). Salmonids adapt physiologically by increasing heart and liver size (Huusko *et al*. 2007), and lowering their blood viscosity by decreasing plasma salts, increasing glucose (Huusko *et al*. 2007) and decreasing the number of red blood cells (DeVries & Cheng 2005). Salmonids also often remain inactive in near-freezing temperatures to keep oxygen demand low (DeVries & Cheng 2005). Within cellular membranes, an increase of essential fatty acids (i.e.Omega-3s) enhances flexibility (Metusalach *et al*. 1995), facilitating enzyme function (i.e. Na^+/K^+-ATPase) and decreasing ion leakage (Wu & Fletcher 2000). *Salvelinus alpinus* further reduces leakage by decreasing activity or density of ion channels (Schwarzbaum *et al*. 1991; 1992).

Anthropogenic impacts such as riverine acidification has been suggested to increase marine mortality of *S. salar* post-smolts due to osmotic stress and the resulting increase in estuarine residency for saltwater acclimatization, which may expose post-smolts to higher predation (Halfyard *et al*. 2012; 2013). Salinity is not just an environmental factor to be tolerated by fishes, it may also be critical in navigation of estuaries on route to river mouths or the open ocean (Quinn 2005; Bos &Thiel 2006; Dadswell *et al*. 2010; Thorstad *et al*. 2011; Lefèvre *et al*. 2012; Chapter 3). With increased melting of the polar ice caps resulting in localized dilution, rising sea levels and altered seasonal cycles (Magnuson *et al*. 2000; Livingstone 2001; Robertson *et al*. 2001; Magnuson 2002; Morris *et al*. 2002), salinity gradients may be altered. Salinity tolerance of Salmoninae should be considered on population- or region-specific basis depending on environmental conditions. It may be unwise to generalize by salmonid genera or species as salinity tolerance varies considerably (Rounsefell 1958).

The Salmoninae migrants which ventured closest to their coldest thermohaline limits were *O. keta*, *S. salar*, *S. alpinus* and *S. malma*, as all encountered full saltwater with temperatures ranging from 0°C to -1.5°C (Table 5.6). The highest temperatures at the highest salinities were tolerated by *O. kisutch*, *O. keta* and *O. nerka*, even though the highest temperatures at lower salinities were experienced by *O. clarki* (23.7°C; Table 5.7) and *S. fontinalis* (20.1°C; Chapter 4). Ambient salinity measurements were obtained from conductivity-temperature-depth profiles conducted during tracking, or temporally and spatially similar oceanographic studies; thus cited salinities may not accurately represent actual conditions experienced by migrants. To further research in fish migration relative to environmental conditions or bioprobe oceanography (Cooke *et al*. 2011), development of conductivity/salinity sensor acoustic transmitters or archival tags are necessary to obtain *in situ* data.

5.9 MARINE ADAPTABILITY HIERARCHY

Surveyed species were scored as a percentage of the most 'anadromous' or 'marine adaptable' total score possible for Rounsefell's (1958) or our survey, respectively. Comparison of percentage scores revealed a similar relative rank for Salmoninae genera and species (Fig. 5.1) in spite of our survey's solely marine migration focus, broader scoring categories and additional criteria. This may suggest Rounsefell accurately inferred a degree of 'marine adaptability', even with inclusion of freshwater-based criteria. The major difference between the two surveys was our higher ranking of *O. keta* and *O. nerka* relative to Rounsefell's (1958) top ranked *O.*

gorbuscha, with our results agreeing with Quinn & Myers' (2004) revised anadromy ranking. Within Rounsefell's (1958) lower anadromy ranks, our results switched rank positions of *S. alpinus* and *S. fontinalis*, with the later ranked the least adaptable to the marine environment (Fig.5.1). Although *S. alpinus* and *S. fontinalis* demonstrate a marine migration strategy to remain near shore and fresh water inputs (Curry *et al*. 2006; Morinville & Rasmussen 2006; Rikardsen *et al*. 2007; Chapter 3 & 4), their polar and temperate distribution, respectively, ranked the former higher due to extreme thermohaline adaptations (Jensen & Rikardsen 2012; Chapter 3).

5.10 AN EVOLUTIONARY ANGLE

Based on sequence divergence of mitochondria DNA, separation of the major Salmoninae groups occurred early to mid-Pleistocene (~2.58 – 0.126 Ma), yet colonization of today's zoogeographic limits began within the late Pleistocene during the retreat of ice sheets ~10,000–20,000 years ago. Nuclear microsatellite DNA variation has suggested continuing evolution within salmonid groups (Brunner *et al*. 2001). Members of the genus *Salmo* originated earliest with *S. salar* evolving before *S. trutta*. *Salvelinus* spp. appeared next with *S. fontinalis* evolving earlier than *S. alpinus*, *S. confluentus* and *S. malma* (Fig. 5.2). *Oncorhynchus* spp. are the most recently evolved Salmoninae (Crespi & Fulton 2003). *Oncorhynchus masou*, *O. mykiss* and *O. clarki* evolved earliest as a sister group (Crespi & Fulton 2003), which may account for their similar scoring and lower ranking relative to the other *Oncorhynchus* species. *Oncorhynchus gorbuscha*, *O. keta* and *O. nerka* are the newest species (Crespi & Fulton 2003) and ranked in the top three for this review, suggesting greater adaptability for a marine life history.

Salmo salar may have evolved a longer marine life history due to lack of interspecific salmonid competition or niche availability in the North Atlantic Ocean. In recent years, introduced *O. gorbuscha* and native *S. salar* have been captured in the Greenland and Barents seas, suggesting the genera can co-exist on marine feeding grounds (Rikardsen *et al*. 2008). With the possibility of a link between Atlantic and Pacific Oceans via the Northwest Passage due to climate change (Cressey 2007), there is still a question of whether or not *Oncorhynchus* spp. outcompete *S. salar* on marine feeding grounds. For example, adult *S. salar* are known to migrate predominately within the top 40 m of the water column in the open ocean (Dadswell *et al*. 2010), as do *Oncorhynchus* spp. (Walker *et al*. 2007). Whether or not *S. salar*'s ability to undertake deeper dives (Lacroix 2013) offers a foraging advantage compared to *Oncorhynchus* spp. remains to be seen.

Earlier evolved Salmoninae, such as the lowest ranked *S. fontinalis*, may largely retain fresh water traits, and possess minimal transitional traits associated with adapting from fresh to salt water (Dodson *et al*. 2009). For example, populations of *S. fontinalis* south of the Gulf of Maine resort to solely freshwater residency (Castric & Bernatchez 2003), which may be due to higher freshwater productivity (Gross 1988) or the species' inability to adapt to warmer marine environmental conditions (i.e. osmoregulation at higher temperatures; Pennell & Barton 1996). Year-round acoustic tracking of *S. fontinalis* in the southern Gulf of St. Lawrence found individuals foraged within the estuarine environment from autumn to spring with body temperatures ranging from -0.5 to 20.1°C and returned to fresh water during summer (Chapter 4) where they mostly occupied cool, spring-fed pools (unpublished data Spares *et al*.). This behaviour suggests high estuarine temperatures during summer (mean ± SD, 18.7 ± 3.4°C, n = 231, maximum = 25.8°C; unpublished data Spares *et al*.) were the main influence for individuals to return to fresh water as marine primary productivity was highest during this period (personal observation). Lower body condition upon estuarine re-entry during the autumn also suggested fasting or poor feeding opportunities within fresh water during summer months (Chapter 4), again lending support to temperature shaping anadromous behaviour.

Once considered the same species, *S. confluentus* and *S. malma* (Goetz *et al*. 2004) were similarly ranked, which may relate to genetic similarity (Dodson *et al*. 2009) with *S. malma's* slightly higher rank explained by longer SLD excursions (DeCicco 1992). Although *S. leucomaenis* and *S. namaycush* were excluded in this survey due to lack of marine migration information, both may rank similarly to their sister species, *S. confluentus* and *S. fontinalis*, respectively (Fig. 5.2; Crespi & Fulton 2003).

5.11 CONCLUSIONS

Anthropogenic climate change in marine water acidity, levels, salinity and temperature could alter entire ecosystems and the organisms inhabiting them (Grebmeier *et al*. 2006; Chittenden *et al*. 2009), thus knowledge of niche dimensions and resiliency of marine migrating salmonids is critical. The coldest thermohaline limits were reached by *O. keta, S. salar, S. alpinus* and *S. malma,* and warmest by *O. kisutch, O. keta* and *O. nerka*, suggesting these species would cope best to extreme marine temperatures. Based on this review, the most to least marine adaptable Genera overall were *Oncorhynchus*, *Salmo* and *Salvelinus*, respectively, agreeing with Rounsefell's (1958) anadromy ranking. Our survey rearranged Rounsefell's top three 'anadromy' species as (1) *O. keta,* (2) *O. nerka* and (3) *O. gorbuscha*, agreeing with the alternative ranking proposed by Quinn & Myers (2004). These top three are also the most recently evolved salmonid species, suggesting a long evolutionary history of marine adaptation.

Salmo salar ranked lower than *Oncorhynchus* open ocean migrants, suggesting the possibility of inter-specific competition if a link between Pacific and Atlantic Oceans occurs via the Northwest Passage. Previously unsurveyed species, *O. masou* and *S. confluentus* ranked similarly to genetically related species, *O. mykiss* and *O. clarki*, and *S. malma*, respectively (Crespi & Fulton 2003; Goetz *et al*. 2004; Dodson *et al*. 2009). Lower ranked salmonids, *Salvelinus* ssp., usually evolved earlier, adding evidence to a fresh water salmonid ancestor (Dodson *et al*. 2009).

As the marine climate changes (Grebmeier *et al*. 2006), migratory behaviours of some populations have changed in step; yet there are still many unknowns regarding how environmental factors and ecosystem dynamics influence salmonid marine survival and migratory behaviours (Chittenden *et al*. 2009). This review attempted to summarize known information to date and make broader ecological-evolutionary context predictions. Further marine migration research is needed on all Salmoninae, especially the lesser studied trout and charr species, which have highly variable life histories compared to the salmons (Quinn & Myers 2004; Brenkman *et al*. 2007).

Table 5.1 Rounsefell's (1958) rank of anadromous species of Salmoninae with alternative ranking based on more recent studies (Goetz *et al*. 2004; Quinn & Myers 2004)

Rank	**Common name**	***Genus* sp.**	**Alt Rank**
Obligatory			
1	pink salmon	*Oncorhynchus gorbuscha*	3
2	chum salmon	*Oncorhynchus keta*	1
3	chinook salmon	*Oncorhynchus tshawytscha*	7
Adaptively			
4	coho salmon	*Oncorhynchus kisutch*	4
5	sockeye salmon	*Oncorhynchus nerka*	2
Optionally			
6	Atlantic salmon	*Salmo salar*	5
7	steelhead trout	*Oncorhynchus mykiss*	6
8	brown trout	*Salmo trutta*	8
9	cutthroat trout	*Oncorhynchus clarki*	9
10	dolly varden charr	*Salvelinus malma*	10
11	brook trout	*Salvelinus fontinalis*	11
12	Arctic charr	*Salvelinus alpinus*	12

Table 5.2 Extent of marine migration based on maximum straight line distance (SLD; km) from natal river mouth traveled by surveyed Salmoninae with assigned ranks 1 to 3 corresponding to distances ≤ 10000, 1000 or 100 km, respectively (1 Jensen & Berg 1977; 2 Gibson & Côté 1982; 3 Trotter 1989; 4 DeCicco 1992; 5 Ohkuma *et al*. 1999; 6 Lenormand *et al*. 2004; 7 Quinn & Myers 2004; 8 Brenkman & Corbett 2005; 9 Quinn 2005; 10 Jonsson & Jonsson 2011)

Common name	***Genus* sp.**	**SLD**	**Rank**	**References**
Pacific salmon/trout	*Oncorhynchus*			
pink	*O. gorbuscha*	2821	1	7, 9
chum	*O. keta*	5595	1	7, 9
chinook	*O. tshawytscha*	4557	1	7, 9
coho	*O. kisutch*	2706	1	7, 9
sockeye	*O. nerka*	5597	1	7, 9
steelhead	*O. mykiss*	5370	1	7
cutthroat	*O. clarki*	133	2	3
masu	*O. masou*	1700	1	5
Atlantic salmon/trout	*Salmo*			
Atlantic	*S. salar*	4422	1	2
brown	*S. trutta*	600	2	10
charrs	*Salvelinus*			
dolly varden	*S. malma*	1690	1	4
brook	*S. fontinalis*	100	3	6
Arctic	*S. alpinus*	940	2	1
bull	*S. confluentus*	250	2	8

Table 5.3 Duration of marine migrations of surveyed Salmoninae based on mean saltwater (SW) residency, life span and percentage of SW residency during life span, with assigned ranks (1 to 14) of highest to lowest % SW residency (1 Sprules 1953; 2 Armstrong 1974; 3 Hunter 1976; 4 Randall *et al*. 1987; 5 Pearcy 1992; 6 Wilson 1997; 7 Tamate & Maekawa 2000; 8 Goetz *et al*. 2004; 9 Curry *et al*. 2006; 10 Rikardsen *et al*. 2007; 11 Stewart *et al*. 2010; 12 Jonsson & Jonsson 2011; 13 Thorstad *et al*. 2011; 14 Chapter 3; 15 ADFG 2014; 16 Chapter 4)

Common names	***Genus* sp.**	**SW residency (yrs)**	**Life span (yrs)**	**% SW**	**Rank**	**References**
Pacific salmon/trout	*Oncorhynchus*					
pink	*O. gorbuscha*	1.6	1.7	95%	2	4, 5
chum	*O. keta*	3.0	3.1	97%	1	4, 5
chinook	*O. tshawytscha*	3.3	3.8	87%	3	4, 5
coho	*O. kisutch*	1.0	2.5	40%	6	4, 5
sockeye	*O. nerka*	3.0	4.5	67%	4	4, 5
steelhead	*O. mykiss*	2.2	5.7	39%	8	4, 5
cutthroat	*O. clarki*	1.1	6.0	18%	12	4, 5, 8
masu	*O. masou*	1.0	2.5	40%	6	7
Atlantic salmon/trout	*Salmo*					
Atlantic	*S. salar*	3.2	6.3	50%	5	4, 13
brown	*S. trutta*	1.2	3.8	31%	9	4, 12, 13
charrs	*Salvelinus*					
dolly varden [a]	*S. malma*	5.2	11.0	10%	13	1, 6, 11, 15
brook	*S. fontinalis*	1.2	5.5	21%	10	4, 9, 16
Arctic	*S. alpinus*	1.4	15.0	9%	14	1, 3, 4, 6, 10, 14
bull	*S. confluentus*	1.3	7.0	19%	11	4, 8

[a] estimated to spend <10% life time at sea feeding (Stewart *et al*. 2010)

Table5. 4 Predominant horizontal marine migration habitat occupied by surveyed Salmoninae with assigned ranks (1 to 3) corresponding to oceanic, neritic and littoral zones, respectively (1 Pennell & Barton 1996; 2 Ohkuma *et al*. 1999; 3 Klemetsen *et al*. 2003; 4 Goetz *et al*. 2004; 5 Lenormand *et al*. 2004; 6 Quinn 2005; 7 COSEWIC 2010; 8 Dadswell *et al*. 2010)

Common name	***Genus* sp.**	**Rank**	**References**
Pacific salmon/trout	*Oncorhynchus*		
pink	*O. gorbuscha*	1	6
chum	*O. keta*	1	6
chinook	*O. tshawytscha*	2	6
coho	*O. kisutch*	2	6
sockeye	*O. nerka*	1	6
steelhead	*O. mykiss*	1	6
cutthroat	*O. clarki*	2	6
masu	*O. masou*	2	2
Atlantic salmon/trout	*Salmo*		
Atlantic	*S. salar*	1	8
brown	*S. trutta*	3	1
charrs	*Salvelinus*		
dolly varden	*S. malma*	3	7
brook	*S. fontinalis*	3	5
Arctic	*S. alpinus*	3	3
bull	*S. confluentus*	3	4

Table 5.5 Vertical marine migration habitat of surveyed Salmoninae based on maximum swimming depths (Z_{max}; m) and assigned ranks (1 to 4) corresponding to the following vertical zones, respectively: Aphotic ($Z_{max} > 400$ m), dysphotic (< 400 m), euphotic (< 150 m) and littoral (< 15 m; 1 Ogura & Ishida 1995; 2 Ohkuma *et al*. 1999; 3 Goetz *et al*. 2004; 4 Rikardsen *et al*. 2007; 5 Walker *et al*. 2007; 6 Haque 2008; 7 Nielsen *et al*. 2011; 8 Chapter 3; 9 Lacroix 2013; 10 Spares *et al*. unpublished data)

Common names	***Genus* sp.**	Z_{max}	**Rank**	**References**
Pacific salmon/trout	*Oncorhynchus*			
pink	*O. gorbuscha*	74	3	5
chum	*O. keta*	460	1	5
chinook	*O. tshawytscha*	482	1	5
coho	*O. kisutch*	97	3	5
sockeye	*O. nerka*	240	2	1
steelhead	*O. mykiss*	89	3	7
cutthroat [a]	*O. clarki*	1	4	6
masu [b]	*O. masou*	74	3	2, 5
Atlantic salmon/trout	*Salmo*			
Atlantic	*S. salar*	950	1	9
brown	*S. trutta*	28	3	4
charrs	*Salvelinus*			
dolly varden	*S. malma*	11	4	3
brook	*S. fontinalis*	11	4	10
Arctic	*S. alpinus*	53	3	8
bull	*S. confluentus*	25	3	3

[a] mean depth of tracked cutthroat trout; [b] masu captured co-migrating in North Pacific with 6 Pacific salmon spp., therefore Z_{max} was assumed to be the shallowest swimming cohort

Table 5.6 Minimum temperature (T_{min}; ^{o}C) and corresponding salinity (*S*), lower lethal thermal limit (T_{low}; ^{o}C) and ranked minimum thermohaline limit of marine migrating Salmoninae (1 Brett 1952; 2 Manzer *et al*. 1965; 3 Lake & Walker 1973; 4 Favorite *et al*. 1976; 5 Machidori & Kato 1984; 6 Bell 1991; 7 Staubitz *et al*. 1997; 8 Babaluk *et al*. 2000; 9 Nagasawa 2000; 10 Walker *et al*. 2000; 11 Selong *et al*. 2001; 12 Currie *et al*. 2004; 13 Rikardsen 2004; 14 Azumaya *et al*. 2007; 15 Brystiansky *et al*. 2007; 16 Rikardsen *et al*. 2008; 17 Babaluk *et al*. 2009; 18 Irvine *et al*. 2009; 19 Kuzishchin *et al*. 2009; 20 Signorini & McClain 2009; 21 COSEWIC 2010; 22 Dadswell *et al*. 2010; 23 Elliott & Elliott 2010; 24 Nielsen *et al*. 2011; 25 NOAA 2012b; 26 Lacroix 2013; 27 Chapter 4)

Common names	***Genus sp.***	T_{min}	*S*	T_{low}	**Rank**	**References**
Pacific salmon/trout	*Oncorhynchus*					
pink	*O. gorbuscha*	2.8	34	0.6[a]	4	1, 8, 14, 16, 20, 25
chum	*O. keta*	-1.0	34	0.5	1	1, 10, 14, 18
chinook	*O. tshawytscha*	4.0	34	0.8	6	1, 4, 9
coho	*O. kisutch*	3.7	34	1.7	4	1, 14
sockeye	*O. nerka*	3.3	33	1.0	5	2, 14
steelhead	*O. mykiss*	3.9	34	0.1	7	4, 12, 24
cutthroat	*O. clarki*	8.0	33	0.6	10	4, 6, 25
masu	*O. masou*	6.0	33	0.5	9	4, 5, 19
Atlantic salmon/trout	*Salmo*					
Atlantic	*S. salar*	0.0	36	-0.8	2	22, 23, 26
brown	*S. trutta*	1.3	32	-0.8	8	13, 23
charrs	*Salvelinus*					
dolly varden	*S. malma*	-1.0	32	-0.4[b]	3	21
brook	*S. fontinalis*	-0.5	22	0.1	12	1, 27
Arctic	*S. alpinus*	-1.5	32	-1.0	3	3, 15, 17, 23
bull	*S. confluentus*	7.0	28	5.2	11	7, 11

[a] both *O. gorbuscha* and *O. keta* have Arctic populations (Babaluk *et al*. 2000) with the later tolerating lower temperatures (Brett 1952), thus the lower lethal thermal limit was estimated at 0.6 ^{o}C, slightly higher than *O. keta;* [b] mean of *S. fontinalis* and *S. alpinus*

Table 5.7 Maximum temperature (T_{max}; ^{o}C) and corresponding salinity (*S*), upper lethal thermal limit (T_{upp}; ^{o}C) and ranked maximum thermohaline limit of marine migrating Salmoninae (1 Brett 1952; 2 Favorite *et al*. 1976; 3 Lee & Rinne 1980; 4 Machidori & Kato 1984; 5 Xiong & Royer 1984; 6 Doving *et al*. 1985; 7 Sutterlin & Stevens 1992; 8 Welch *et al*. 1998; 9 Selong *et al*. 2001; 10 Goetz *et al*. 2003; 11 Goetz *et al*. 2004; 12 Wurster *et al*. 2005; 13 Rikardsen *et al*. 2006; 14 Azumaya *et al*. 2007; 15 Hamilton *et al*. 2008; 16 Elliott & Elliott 2010; 17 Fish World 2010; 18 Jonnson & Jonsson 2011; 19 Nielsen *et al*. 2011; 20 NOAA 2012a; 21 Underwood *et al*. 2012; 22 Spares *et al*. unpublished data)

Common names	***Genus* sp.**	T_{max}	S	T_{upp}	**Rank**	**References**
Pacific salmon/trout	*Oncorhynchus*					
pink	*O. gorbuscha*	16.6	34	25.8	6	14, 17
chum	*O. keta*	15.6	34	23.8	2	1, 14, 18
chinook	*O. tshawytscha*	13.4	34	26.2	5	12, 14
coho	*O. kisutch*	15.7	34	23.7	1	9, 14
sockeye	*O. nerka*	13.3	33	24.5	3	8, 9, 14
steelhead	*O. mykiss*	13.0	34	26.2	10	9, 19
cutthroat	*O. clarki*	23.7	29	24.6	4	15, 21
masu	*O. masou*	15.0	32	25.0[a]	9	2, 4,
Atlantic salmon/trout	*Salmo*					
Atlantic	*S. salar*	14.7	34	29.0	11	6, 18
brown	*S. trutta*	16.7	32	26.8	8	13, 16
charrs	*Salvelinus*					
dolly varden	*S. malma*	13.0	32	24.5	12	5, 9, 20
brook	*S. fontinalis*	19.6	28	28.0	13	3, 22
Arctic	*S. alpinus*	15.0	20	23.2	14	7, 16
bull	*S. confluentus*	17.0	28	20.9	7	9, 10, 11

[a] mean of *Oncorhynchus* spp. surveyed

Table 5.8 Rank scores for anadromous Salmoninae based on marine adaptability criteria: (1) extent, and (2) duration of migration; (3) horizontal and (4) vertical habitats; and (5) minimum and (6) maximum thermohaline limits experienced. RA Rounsefell's anadromy rank, RV Quinn & Myers 2004 revised anadromy rank, nr not reviewed

Common names	***Genus* sp.**	**1**	**2**	**3**	**4**	**5**	**6**	**Rank**	**RA**	**RV**
Pacific salmon/trout	*Oncorhynchus*							1	1	1
pink	*O. gorbuscha*	1	2	1	3	4	6	3	1	3
chum	*O. keta*	1	1	1	1	1	2	1	2	1
chinook	*O. tshawytscha*	1	3	2	1	6	5	4	3	7
coho	*O. kisutch*	1	6	2	3	4	1	3	4	4
sockeye	*O. nerka*	1	4	1	2	5	3	2	5	2
steelhead	*O. mykiss*	1	8	1	3	7	10	6	7	6
cutthroat	*O. clarki*	2	12	2	4	10	4	8	9	9
masu	*O. masou*	1	6	2	3	9	9	6	nr	nr
Atlantic salmon/trout	*Salmo*							2	2	2
Atlantic	*S. salar*	1	5	1	1	2	11	5	6	5
brown	*S. trutta*	2	9	3	3	8	8	7	8	8
charrs	*Salvelinus*							3	3	3
dolly varden	*S. malma*	1	13	3	4	3	12	9	10	10
brook	*S. fontinalis*	3	10	3	4	12	13	12	11	11
Arctic	*S. alpinus*	2	14	3	3	3	14	11	12	12
bull	*S. confluentus*	2	11	3	3	11	7	10	nr	nr

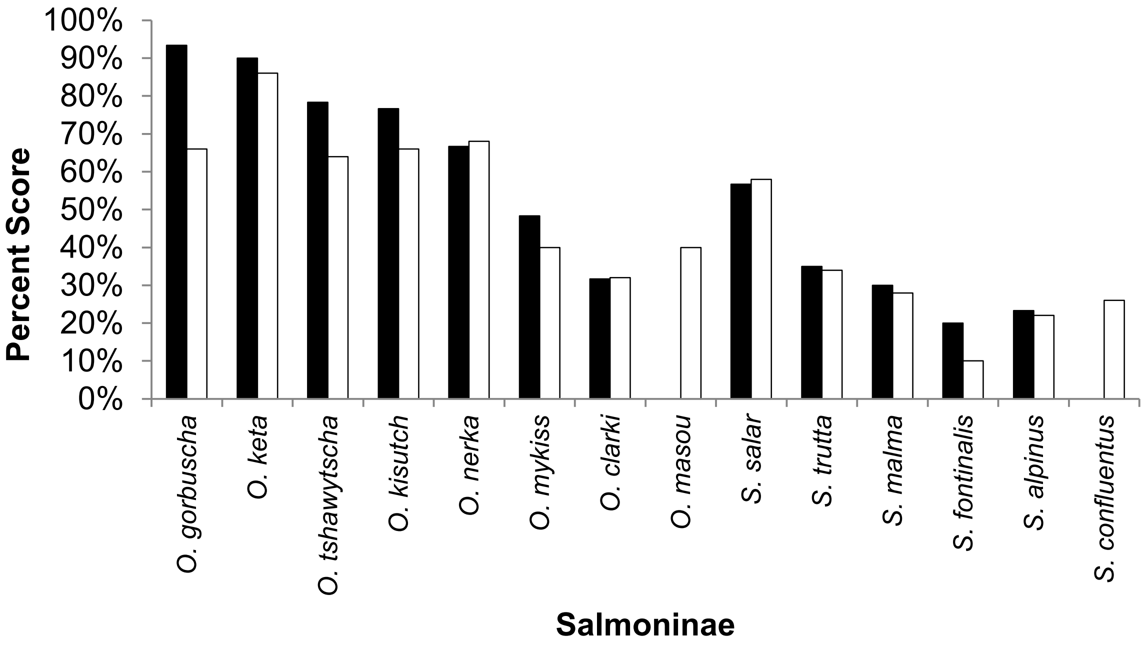


Figure 5.1 - Percentage score of anadromous Salmoninae species surveyed in Rounsefell's (1958) anadromy (solid bar) and this review's marine adaptability (open bar) critique

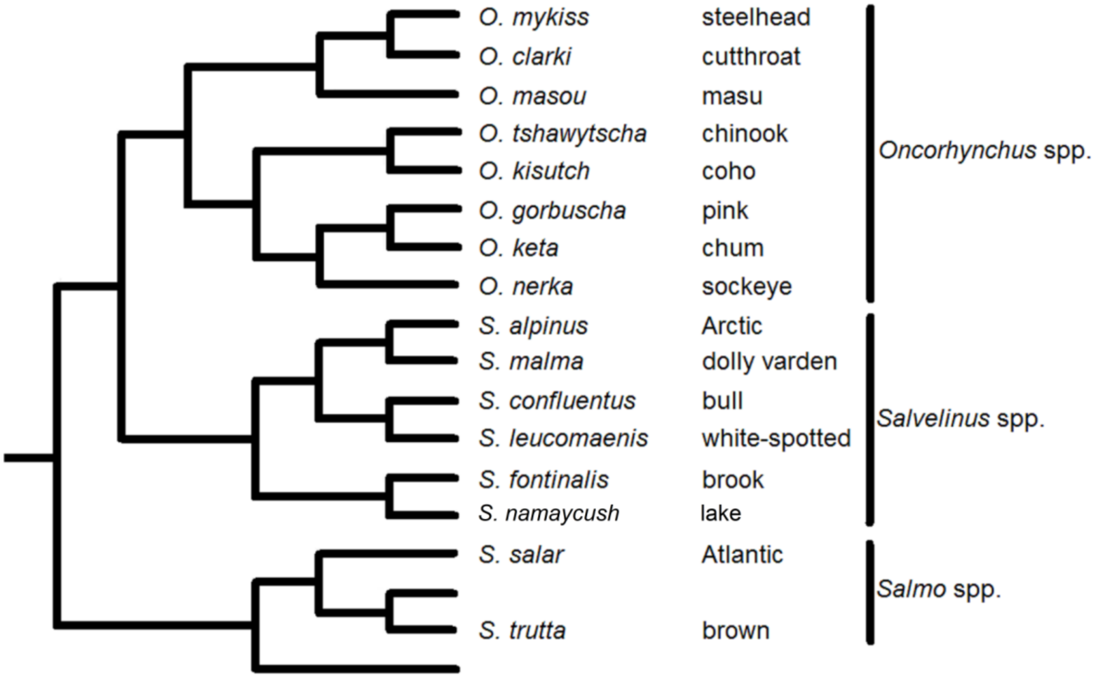


Figure 5.2 - Combined nuclear DNA Bayesian analysis phylogeny for anadromous Salmoninae showing species, common names and Genera (Crespi & Fulton 2003). Phylogeny of *O. rhodurus* not included by Crespi & Fulton (2003).

CHAPTER 6 – DISCUSSION

6.1 MARINE MIGRATION OF *SALVELINUS* SPP.

Objective 1 of this thesis was to describe the marine movements and residency of *S. alpinus* relative to freshwater inputs and immediate estuaries, migration period and tidal phase (**Chapter 2**). As hypothesized, tracked *S. alpinus* remained within three km of shore traveling < 30 km maximum SLD from the major estuary river mouths. Movements were influenced by macrotides, with the lowest mean travel rates occurring during flooding tides which suggested individuals staged before moving into intertidal zones. Migrants were either continuously or intermittent present in estuaries, with 19% of tracked individuals using two major estuaries situated approximately 22 km SLD apart. Increased estuarine residency prior to freshwater re-entry suggested an estuarine transition phase may occur.

Objective 2 described marine feeding behaviours of *S. alpinus* and *S. fontinalis* relative to depth, habitat, season and water temperature (**Chapters 3 & 4**). Marine migrating *S. alpinus* were not restricted to intertidal/upper water column habitats due to higher temperatures, instead used both inter- and sub-tidal zones and tolerated low temperatures at depth. Near-zero temperatures directed both species to behaviourally thermoregulate and osmoregulate by seeking warmer and/or brackish water, respectively. This thesis contains the first account of repetitive diving behavior of *S. alpinus*, whereas abundant prey found at depth likely motivated dives and the temperature gradient between the surface and at depth shaped the short duration and repetitive nature of dive series. Both species were opportunistic feeders, with *S. alpinus* and *S. fontinalis* having staple diets of crustaceans (amphipods and mysids) and fishes (mummichogs and sticklebacks), respectively. Although feeding intensity was expected to decrease with lower temperatures, with percentage of empty stomachs being the highest, and stomach fullness and consumption rates being the lowest; stomach fullness was actually the highest during cold periods, suggesting feeding still occurred and digestion virtually ceased. Both *S. alpinus* and *S. fontinalis* tolerated near-zero temperatures in maximum salinities of 22 and 34, respectively. Once acclimatized to salt water, both species were more than capable of surviving these respective salinities in low temperatures for extended periods of time (hours to days), yet avoided decreasing their body temperature to or below 0^{o}C.

6.1.1 DIVING BEHAVIOUR

The most novel discovery of this thesis was the recorded diving behavior of *S. alpinus*, which was linked to foraging and thermoregulation strategies using stomach content analysis and environmental monitoring, respectively. Although other salmonids have been recorded diving deep soon after saltwater entry and just before freshwater re-entry, many of these recorded behaviours have only been speculated to be related to feeding or orientation (Nielsen *et al*., 2011). Atlantic salmon (*Salmo salar*) kelts have demonstrated near-surface coastal marine migrations which included relatively shallow (Z = 10 - 40 m) daytime dives presumably associated with feeding, and dived deep (Z = 100–1000 m) when crossing ocean channels or shelf edges (Hubley *et al*., 2008; Halttunen *et al*., 2009; Hedger *et al*., 2009; Lacroix, 2013). Only chum salmon (*Oncorhynchus keta*) have been recorded undertaking similar diving patterns as *S. alpinus* within this study, with individual salmon averaging 8.6 'yo-yo' dives per hour lasting 5.1 min each (Tanaka *et al*., 2005; Walker *et al*., 2007). These migrants were presumed to be feeding on prey which had moved deeper during daylight hours (Tanaka *et al*., 2005), yet returns to surface waters with temperature variations of ~10 °C within a single descent or ascent suggested behavioural thermoregulation to minimize metabolic energy cost (Tanaka *et al*., 2000).

Some species, such as steelhead (*Oncorhynchus mykiss*) demonstrated no crepuscular or diel dive patterns and spent most of their marine migration (72-97%) near the surface ($Z < 6$ m; Ruggerone *et al*., 1990; Neilsen et al., 2011). Such variation in vertical niche selection by marine migrating salmonids suggests more behavioural studies are necessary to reveal if behaviours are species specific or shaped by environmental factors.

Diving behaviour recorded on marine migrating pelagics (rays, sharks and tuna) has revealed different diving patterns, with rapid descents followed by oscillatory or stepwise ascents (Block *et al*. 2001; Brunnschweiler *et al*., 2009; Thorrold *et al*., 2014). Diving behavior has been presumed to be prey driven (Thorrold *et al*., 2014), although orienteering behavior may also be the case, as demonstrated by Atlantic bluefin tuna (*Thunnus thynnus*) within the Straits of Gibraltar before entering the Mediterranean Sea (Wilson & Block, 2009) or porbeagle sharks (*Lamna nasus*) following deep water counter-currents below the Gulf Stream to pupping grounds in the Sargasso Sea (Campana *et al*., 2010). Devil rays (*Mobula tarapacana*) dive to forage in extreme environments characterized by high pressure, low dissolved oxygen levels, perpetual darkness and water temperatures $<4^{o}$C (Thorrold *et al*., 2014). These endothermic pelagics, along with billfishes, mackerels and other lamnid sharks, rays and tunas, have evolved a large body volume and *rete mirabile* heat exchangers in organ systems critical for cold water foraging (Block & Finnerty, 1994; Bernal *et al*., 2012). Even though Arctic char do not have endothermic adaptations (Block & Finnerty, 1994), behavioural thermoregulation has enabled them to tolerate extreme temperature changes on par with endotherms (~18-21^{o}C; Thorrold *et al*., 2014). Similar to ectothermic *S. alpinus* in this study, endothermic devil rays still warm-up in surface waters during the day before and after deep dives (Thorrold *et al*., 2014), reinforcing how essential heat recovery arenas are for fishes living in the colder end of their thermal limits.

6.2 SALMONIDAE MARINE ADAPTABILITY

Objective 3 incorporated findings of Chapters 2 to 4 into a critical literature review of marine migration strategies within the family Salmonidae to infer relative inter-specific marine adaptability based on horizontal and vertical niches, and thermohaline limits experienced (**Chapter 5**). Within the review, the questions of how adapted *Salvelinus* spp. are to the marine environment, and how do *S. alpinus* and *S. fontinalis* compare to other Salmonidae species, were addressed. The lowest thermohaline limits were reached by *O. keta, S. salar, S. alpinus* and *S. malma;* suggesting these species would cope best to polar extremes. Based on this review, the most to least marine adaptable Genera overall were *Oncorhynchus*, *Salmo* and *Salvelinus*, respectively. The lower ranked *Salvelinus* spp. usually evolved earlier, adding evidence to a fresh water salmonid ancestor (Dodson *et al*., 2009). A previously unsurveyed *Salvelinus* species, bull trout *S. confluentus*, ranked similarly to evolutionary related species, *S. malma* (Crespi & Fulton, 2003; Goetz *et al*., 2004; Dodson *et al*., 2009).

Inter-specific ranking of fourteen salmonid species placed *S. alpinus* and *S. fontinalis* as the two least marine adapted salmonids. A global warming model for *S. alpinus* agreed that there will be a declining trend in the degree of anadromy for the species, and related the decline to increasing freshwater primary productivity (Finstad & Hein, 2012). This has already been demonstrated by populations located at the species southern distribution (Klemetsen *et al*., 2003). This prediction may also apply to current anadromous *S. fontinalis* populations located nearer the species' southern zoogeography. Other studies have shown increasing sea temperatures may lead to habitat overlap between *S. alpinus* and other salmonids, such as brown trout *S. trutta* (Jensen, 2013), or migratory behaviour changes which affect interactions with other species or trophic levels (Stokesbury *et al.*, 2009; Van der Putten *et al.*, 2010). This research lends evidence to both future possibilities. Recent observations by *S. alpinus* fishers within inner Frobisher Bay have noted increased captures of *S. salar* during summer (pers. obs.), suggesting increased likelihood of inter-specific competition, whereas the more marine adapted *S. salar* may outcompete its northern cousin, *S. alpinus*. New trophic level interactions were also documented with iFB *S. alpinus* preying upon capelin (*Mallotus villosus*), a key prey species which historically migrated throughout the world's boreal oceans during periods of climate change (Rose, 2005). Overall, the best marine advantage of *S. alpinus* is its tolerance of low temperatures (Langeland *et al.*, 1991; Helland *et al.*, 2011), which unfortunately may not hold much water next to climate warming.

6.3 THESIS CONCLUSIONS

6.3.1 MANAGEMENT IMPLICATIONS, CONSERVATION AND FUTURE RESEARCH

With increasing anthropogenic pressures on Salmonidae, more information on marine migration routing, behaviours and feeding grounds is critical for ecosystem management (Stokesbury *et al.*, 2009). Based on this thesis, an effective iFB *S. alpinus* marine management plan should address anthropogenic pressures on adjacent as well as the focal estuary due to inter-estuarine mixing of different populations (Moore *et al.*, 2013; VanGerwen-Toyne *et al.*, 2013). Increased estuarine residency during early and late marine migration, especially nearest river mouths, and staging of migrants within tidal channels during flooding tide should also be taken into consideration when implementing fishery conservation measures. In addition to being excellent feeding grounds, the large intertidal zones of iFB are critical as heat recovery arenas for *S. alpinus* foraging beyond estuaries and/or at depth. Fisheries management must also lobby for environmental protection to ensure the health, productivity and proper thermal functioning of brackish, intertidal ecosystems. This is especially important in the case of the Sylvia Grinnell and Bay of Two Rivers estuaries which are under increasing anthropogenic pressures and pollution due to the 18.1% growth rate of the city of Iqaluit (StatCan, 2006; Gallagher & Dick, 2010). Additional localized anthropogenic impacts to consider may include increased shipping, notably oil tanker traffic, in Iqaluit Harbour, and hydroelectric turbine development on the Armshow River (pers. comm. North/South Consulting Ltd.).

Further foundational marine migration research is needed on all Salmonidae, especially the lesser studied *Salvelinus* trout and char species which have shown highly variable life histories compared to the salmons (Quinn & Myers, 2004; Brenkman *et al*., 2007). This thesis has expanded the known vertical (Z_{max} = 54 m) and minimal thermal (-0.5 ^{o}C) marine habitat for *S. alpinus* and *S. fontinalis*, respectively, further reinforcing the need for more detailed information considering niche selection by fishes may be regional, population or species specific (Jensen, 2013; Thorrold *et al*., 2014).

6.3.2 FINAL CONCLUSIONS

The overall thesis objective to increase detailed knowledge on the marine migration life history strategies of anadromous *Salvelinus* spp. year-round was accomplished. As the marine climate changes (Grebmeier *et al*., 2006), migratory behaviours of some salmonid populations have changed in step; yet there are still many unknowns regarding how environmental factors and ecosystem dynamics influence marine survival and migratory behaviours (Chittenden *et al*., 2009). The plasticity of *Salvelinus* spp. marine migration strategies may have allowed these fishes to exploit extreme environments in evolutionary history. What remains to be seen is if this plasticity, demonstrated in this thesis by wider thermal limits and habitat zones, may offer a crucial survival advantage when faced with rapid climate change.

REFERENCES

A

ADFG (2014) Dolly varden (*Salvelinus malma*) - species profile. Alaska Department of Fish and Game, State of Alaska. http://www.adfg.alaska.gov/index.cfm?adfg=dollyvarden.main. Accessed 13 August 2014

Amundsen, P.A. & Klemetsen, A. (1988). Diet, gastric evacuation rates and food consumption in a stunted population of Arctic char, *Salvelinus alpinus* L., in Takvatn, northern Norway. *Journal of Fish Biology* **33**, 697-709.

Anonymous (2006). Editorial: Ethical justification for the use and treatment of fishes in research. *Journal of Fish Biology* **68**, 1-2. doi:10.1111/j.1095-8649.2006.01035.x

Armstrong, R.H. (1974). Migration of anadromous dolly varden (*Salvelinus malma*) in southeastern Alaska. *Journal of Fisheries Research Board of Canada* **31**, 435-444.

Armstrong, R.H. & Morrow, J.E. (1980). The dolly varden charr, *Salvelinus malma*. In *Charrs: salmonid fishes of the genus Salvelinus* (Balon, E.K., ed), pp 99-140. The Netherlands: Dr. W Junk bv Publishers.

Azumaya, T., Nagasawa, T., Temnykh, O.S. & Khen, G.V. (2007). Regional and seasonal differences in temperature and salinity limitations of Pacific salmon. *North Pacific Anadromous Fish Commission Bulletin* **4**, 179–187.

B

Babaluk, J.A., Reist, J.D., Johnson, J.D. & Johnson, L. (2000). First records of sockeye (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*) from Banks Island and other records of Pacific salmon in Northwest Territories, Canada. *Arctic* **53**, 161-164.

Babaluk, J.A., Reist, J.D., Wastle, R.J., Campbell, J.L. & Halden, N.M. (2009). The anadromous Arctic char of Quttinirpaaq National Park, Ellesmere Island, Canada, as determined by otolith strontium distribution. Poster abstract. In: *Challenges for diadromous fishes in a dynamic global environment* (Haro, A., Smith, K.L., Rulifson, R.A., Moffitt, C.M., Klauda, R.J., Dadswell, M.J., Cunjak, R.A., Cooper, J.E., Beal, K.L. & Avery, T.S., eds), pp 927-928. Bethesda, Maryland: American Fisheries Society Symposium 69.

Balon, E.K. (1980). *Charrs. Salmonid fishes of the genus Salvelinus*. Dr. W. Junk bv Publishers, The Hague

Baran, E. & Warry, F. (2008). *Simple data analysis for biologists*. Phnom Penh, Cambodia: WorldFish Center and the Fisheries Administration.

Barnham, C. & Baxter, A. (2003). Condition factor, K, for salmonid fish. Fisheries Notes, March 1998. http://bamboorods.ca/trout%20condition%20factor.pdf. Accessed 23 September 2014

Beardsall, J.W., McLean, M.F., Cooke, S.J., Wilson, B.C., Dadswell, M.J., Redden, A.R. & Stokesbury, M.J.W. (2013). Consequences of Incidental Otter Trawl Capture on Survival and Physiological Status of Threatened Atlantic Sturgeon *Acipenser oxyrinchus*. *Transactions of the American Fisheries Society* **142**, 1202-1214

Bégout Anras, M.L., Gyselman, E.C., Jorgenson, J.K., Kristofferson, A.H. & Anras, L. (1999). Habitat preferences and residence time for the fresh water to ocean transition stage in Arctic charr. *Journal of the Marine Biological Association of the United Kingdom* **79**, 153-160.

Bell, M.C. (1991). *Fisheries handbook of engineering requirements and biological criteria*. Corps of Engineers, North Pacific Division, Portland, USA

Bernal, D., Carlson, J.K., Goldman, J. & Lowe, C.G. (2012). Energetics, metabolism, and endothermy in sharks and rays. In: *Biology of sharks and their relatives. 2nd ed.* (Carrier, J.C., Musick, J.A. & Heithaus, M.R., eds), pp.211-232, Boca Raton, FL: CRC Press.

Bernatchez, L., Dempson, J.B. & Martin, S. (1998). Microsatellite gene diversity analysis in anadromous arctic char, *Salvelinus alpinus*, from Labrador, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 1264-1272.

Bigelow, H.B. & Welsh, W.W. (1925). *Bulletin US Bureau of Fisheries*. **40**, 1-567.

Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, E.D., Farwell, C.J., Boustany, A., Teo, S.L.H., Seitz, A., Walli, A. & Fudge, D. (2001). Migratory movements, depth preferences, and thermal biology of Atlantic Bluefin tuna. *Science* **293**, 1310-1314.

Block, B.A. & Finnerty, J.R. (1994). Endothermy in fishes: a phylogenetic analysis of constraints, predispositions, and selection pressures. *Environmental Biology of Fishes* **40**, 283–302.

Borror, D.J. & DeLong, D.M. (1954). *An introduction to the study of insects, revised edition.* Toronto, Canada: Holt Reinhart and Winston.

Bos, A.R. & Thiel, R. (2006). Influence of salinity on the migration of postlarval and juvenile flounder *Pleuronectes flesus* L. in a gradient experiment. *Journal of Fish Biology* **68**, 1411–1420

Bottom, D.L., Jones, K.K., Cornwell, T.J., Gray, A. & Simenstad, C.A. (2005). Patterns of chinook salmon migration and residency in the Salmon River estuary (Oregon). *Estuarine, Coastal and Shelf Science* **64**, 79-93.

Brenkman, S.J. & Corbett, S.C. (2005). Extent of anadromy in bull trout and implications for conservation of a threatened species. *North American Journal of Fisheries Management* **25,** 1073-1081

Brenkman, S.J., Corbett, S.C. & Volk, E.C. (2007). Use of otolith chemistry and radiotelemetry to determine age-specific migratory patterns of anadromous Bull trout in the Hoh River, Washington. *Transactions of the American Fisheries Society* **136**, 1-11.

Brett, J.R. (1952). Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. *Journal of the Fisheries Research Board of Canada* **9,** 265-323.

Brett, J.R. (1965). The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *Journal of the Fisheries Research Board of Canada* **22**, 1491-1501.

Brett, J.R. & Higgs, D.A. (1970). Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Oncorhynchus nerka*. *Journal of the Fisheries Research Board of Canada* **27**, 1767-1779.

Bringolf, R.B., Kwak, T.J., Cope, W.G. & Larimore, M.S. (2005). Salinity tolerance of flathead catfish: Implications for dispersal of introduced populations. *Transactions of the American Fisheries Society* **134**, 927-936.

Bromley, J.E.C. & Bleakney, J.S. (1984). *Keys to the flora and fauna of New Minas Basin*. Ottawa, Canada: National Research Council of Canada.

Browne, D.R. & Rasmussen, J.B. (2009). Shifts in the trophic ecology of brook trout resulting from interactions with yellow perch: an intraguild predator–prey interaction. *Transactions of the American Fisheries Society* **138,** 1109–1122. doi: 10.1577/T08-113.1

Brunner, P.C., Douglas, M.R., Osinov, A., Wilson, C.C. & Bernatchez, L. (2001). Holoarctic phylogeography of Arctic charr (*Salvelinus alpinus* L.) inferred from mitochondrial DNA sequences. *Evolution* **55**, 573–586.

Brunnschweiler, J.M., Baensch, H., Pierce, S.J. & Sims, D.W. (2009). Deep-diving behaviour of a whale shark *Rhincodon typus* during long-distance movement in the western Indian Ocean. *Journal of Fish Biology* **74**, 706–714.

Bystriansky, J.S., Frick, N.T., Richards, J.G., Schulte, P.M. & Ballantyne, J.S. (2007). Wild Arctic char (*Salvelinus alpinus*) upregulate gill Na+,K+-ATPase during freshwater migration. *Physiological and Biochemical Zoology* **80**, 270–282.

C

Campana, S.E., Joyce, W. & Fowler, M. (2010). Subtropical pupping ground for a cold-water shark. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 769-773.

Carlander, K.D. (1950). *Handbook of freshwater fishery biology*. Dubuque, Iowa: WM. C. Brown Company.

Castonguay, M., FitzGerald, G.J. & Côté, Y. (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. & Bernatchez, L. (2003). The rise and fall of isolation by distance in the anadromous brook charr (*Salvelinus fontinalis* Mitchill). *Genetics* **163**, 983-996.

Chittenden, C.M., Ådlandsvik, B., Pedersen, O., Righton, D. & Rikardsen, A.H. (2013). Testing a model to track fish migrations in polar regions using pop-up satellite archival tags. *Fisheries Oceanography* **22**, 1-13.

Chittenden, C.M., Beamish, R.J., McKinley, R.S. (2009). A critical review of Pacific salmon marine research relating to climate. *ICES Journal of Marine Science* **66**, 2195–2204.

Claireaux, G. & Audet, C. (1999). Seasonal changes in the hypo-osmoregulatory ability of brook charr: the role of environmental factors. *Journal of Fish Biology* **56**, 347–373.

Collins, A.B., Heupel, M.R. & Motta, P.J. (2007). Residence and movement patterns of cownose rays *Rhinoptera bonasus* within a south-west Florida estuary. *Journal of Fish Biology* **71**, 1159-1178.

Cooke, S.J., Iverson, S.J., Stokesbury, M.J.W., Hinch, S.G., Fisk, A.T., VanderZwaag, D.L., Apostle, R. & Whoriskey, F. (2011). Ocean Tracking Network Canada: A network approach to addressing critical issues in fisheries and resource management with implications for ocean governance. *Fisheries* **36**, 583-592. doi:10.1080/03632415.2011.633464

COSEWIC. (2010). COSEWIC assessment and status report on the dolly varden *Salvelinus malma malma* (western Arctic populations) in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa

Crespi, B.J. & Fulton, M.J. (2003). Molecular systematics of Salmonidae: combined nuclear data yields a robust phylogeny. *Molecular Phylogenetics Evolution* **31**, 658–679. doi:10.1016/j.ympev.2003.08.012

Cressey, D. (2007). Arctic melt opens Northwest passage - Record low for sea-ice retreat. *Nature* **449**, 267. doi:10.1038/449267b

Currie, R.J., Bennett, W.A., Beitinger, T.L. & Cherry, D.S. (2004). Upper and lower temperature tolerances of juvenile freshwater game-fish species exposed to 32 days of cycling temperatures. *Hydrobiologia* **532**, 127–136.

Curry, R.A., Sparks, D. & van de Sande, J. (2002). Spatial and temporal movements of a riverine brook trout population. *Transactions of the American Fisheries Society* **131**, 551-560.

Curry, R., van de Sande, J. & Whoriskey, F. (2006). Temporal and spatial habitats of anadromous brook charr in the Laval River and its estuary. *Environmental Biology of Fishes* **76**, 361-370.

D

Dadswell, M.J. (2006). A review of the status of Atlantic sturgeon in Canada, with comparisons to populations in the United States and Europe. *Fisheries* **31**, 218-229.

Dadswell, M.J. (2009). Ocean migration of diadromous fishes in a changing global environment preamble. In *Challenges for diadromous fishes in a dynamic global environment* (Haro, A., Smith, K., Rulifson, R., Moffitt, C., Klauda, R., Dadswell, M., Cunjak, R., Cooper, J., Beal, K. & Avery, T., eds), pp. 251-253. Bethesda, Maryland: American Fisheries Society Symposium 69.

Dadswell, M.J., Spares, A.D., Reader, J.M. & Stokesbury, M.J.W. (2010). The North Atlantic subpolar gyre and the marine migration of Atlantic salmon *Salmo salar*: the 'Merry-Go-Round' hypothesis. *Journal of Fish Biology* **77**, 435-467.

DeCicco, A.L. (1992). Long-distance movements of anadromous dolly varden between Alaska and the U.S.S.R. *Arctic* **45**, 120-123.

Dempson, J.B. (1993). Salinity tolerance of freshwater acclimated, small-sized Arctic charr, *Salvelinus alpinus* from Northern Labrador. *Journal of Fish Biology* **43**, 451-462.

Dempson, J.B. (1995). Trends in population characteristics of an exploited anadromous arctic charr, *Salvelinus alpinus*, stock in northern Labrador. *Nordic Journal of Freshwater Research* **71,** 197–216.

Dempson, J.B. & Kristofferson, A.H. (1987). Spatial and temporal aspects of the ocean migration of anadromous Arctic char. In *Common Strategies of Anadromous and Catadromous Fishes* (Dadswell, M., Klauda, R., Moffitt, C., Saunders, R., Rulifson, R. & Cooper, J., eds), pp. 340-357. Bethesda, Maryland: American Fisheries Society Symposium 1.

Dempson, J.B., Shears, M. & Bloom, M. (2002). Spatial and temporal variability in the diet of anadromous Arctic charr, *Salvelinus alpinus*, in northern Labrador. *Environmental Biology of Fishes* **64**, 49–62.

DeVries, A.L. & Cheng, C-H.C. (2005). Antifreeze proteins and organismal freezing avoidance in polar fishes. In *The physiology of polar fishes* (Farrell, A.P. & Steffensen, J.F., eds), pp. 155-193. Boston: Elsevier Academic Press.

DFO (Department of Fisheries and Oceans Canada). (2008). Canadian Hydrographical Service – Nautical Chart 7121. Government of Canada, Ottawa

Dick, T.A., Gallagher, C.P. & Yang, A. (2009). Summer habitat use of Arctic char (*Salvelinus alpinus*) in a small Arctic lake, monitored by acoustic telemetry. *Ecology of Freshwater Fishes* **18**, 117-125.

Dodson, J.J., Laroche, J. & Lecomte, F. (2009). Contrasting evolutionary pathways of anadromy in euteleostean fishes. In: *Challenges for diadromous fishes in a dynamic global environment* (Haro, A., Smith, K.L., Rulifson, R.A., Moffitt, C.M., Klauda, R.J., Dadswell, M.J., Cunjak, R.A., Cooper, J.E., Beal, K.L. & Avery, T.S., eds), pp 63-77. Bethesda, Maryland: American Fisheries Society Symposium 69.

Døving, K.B., Westergård, H. & Johnsen, P.B. (1985). Role of olfaction in the behavioural and neuronal responses of Atlantic salmon, *Salmo salar*, to hydrographic stratification. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 1658–1667.

Drenner, S.M., Clark, T.D., Whitney, C.K., Martins, E.G., Cooke, S.J. & Hinch, S.G. (2012). A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. *PLoS ONE* **7**, e31311. doi:10.1371/journal.pone.0031311

Dunham, J., Baxter, C., Fausch, K., Fredenberg, W., Kitano, S., Koizumi, I., Morita, K., Nakamura, T., Rieman, B., Savvaitova, K., Stanford, J., Taylor, E. & Yamamoto, S. (2008) Evolution, ecology, and conservation of dolly varden, white-spotted char, and bull trout. *Fisheries* **33**, 537-550.

Dutil, J.-D. (1986). Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). *Copeia* **1986**, 945-955.

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

Dyck, M.G. & Romberg, S. (2007). Observations of a wild polar bear (*Ursus maritimus*) successfully fishing Arctic charr (*Salvelinus alpinus*) and Fourhorn sculpin (*Myoxocephalus quadricornis*). *Polar Biology* **30**, 1625-1628.

E

Elliott, G.V. & Jenkins, T.M. (1972). Winter food of trout in three high elevation Sierra Nevada 1akes. *California Fish and Game* **58**, 231-237.

Elliott, J. M. (1972). Rates of gastric evacuation in brown trout, *Salmo trutta* L. *Freshwater Biology* **2**, 1-18.

Elliott, J.M. (1991). Rates of gastric evacuation in piscivorous brown trout, *Salmo trutta. Freshwater Biology* **25**, 297-305.

Elliott, J.M. & Elliott, J.A. (2010). Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. *Journal of Fish Biology* **77**, 1793-1817. doi:10.1111/j.1095-8649.2010.02762.x

Enevoldsen, T.L., Heiner, I., DeVries, A.L. & Steffensen, J.F. (2003). Does fish from the Disko Bay area of Greenland possess antifreeze proteins during the summer? *Polar Biology* **26**, 365–370.

F

Favorite, F., Dodimead, A.J. & Nasu, K. (1976). Oceanography of the subarctic Pacific region, 1960-71. *International Pacific Fisheries Commission* **33**, 1-187.

Finstad, A.G. & Hein, C.L. (2012). Migrate or stay: terrestrial primary productivity and climate drive anadromy in Arctic char. *Global Change Biology* **18**, 2487–2497.

Finstad, B., Nilssen, K.J. & Arnesen, A.M. (1989). Seasonal changes in sea-water tolerance of Arctic charr (*Salvelinus alpinus*). *Journal of Comparative Physiology B* **159**, 371–378.

Fish World. (2010). Pink salmon – *Oncorhynchus gorbuscha*. http://underwater-fish.blogspot.ca/2011/10/pink-salmon-oncorhynchus-gorbuscha.html. Assessed 22 August 2014

G

Gallagher, C.P. & Dick, T.A. (2010). Historical and current population characteristics and subsistence harvest of Arctic char from the Sylvia Grinnell River, Nunavut, Canada. *North American Journal of Fisheries Management* **30**, 126–141.

Gaudreault, A., Castonguay, M. & Fitzgerald, G.J. (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. & Côté, Y. (1982). Production de saumonneaux et recaptures de saumons adultes etiquettes a la riviere Matamec, Cote-Nord, Golfe du Saint-Laurent, Quebec. *Naturaliste Canadienne* **109**, 13-25.

Goetz, F., Jeanes, E., Hart, G., Ebel, C., Starkes, J. & Conner, E. (2003). Behaviour of anadromous bull trout in the Puget Sound and Pacific coast of Washington. Oral Presentation. Estuarine Research Federation Conference, Seattle, Washington

Goetz, F., Jeanes, E., Beamer, E., Hart, G., Morello, C., Camby, M., Ebel, C., Conner, E. & Berge, H. (2004). *Bull trout in the nearshore – preliminary draft*. Seattle District: U.S. Army Corps of Engineers.

Grainger, E.H. (1953). On the age, growth, migration, reproductive potential and feeding habits of the Arctic char (*Salvelinus alpinus*) of Frobisher Bay, Baffin Island. *Journal of the Fisheries Research Board of Canada* **10**, 326-370.

Grainger, E. (1975). A marine ecology study in Frobisher Bay, arctic Canada. In: *Energy flow: its biological dimension* (Cameron, T. & Billingsley, L., eds), pp. 261-266, Ottawa: Royal Society of Canada.

Grant, A.M., Gardner, M., Hanson, L.M., Farrell, A.P. & Brauner, C.J. (2010). Early life stage salinity tolerance of wild and hatchery-reared juvenile pink salmon *Oncorhynchus gorbuscha*. *Journal of Fish Biology* **77**, 1282-1292.

Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W., Frey, K.E., Helle, J.H., McLaughlin, F.A. & McNutt, S.L. (2006). A major ecosystem shift in the northern Bering Sea. *Science* **311**, 1461-1464.

Grønvik, S. & Klemetsen, A. (1987). Marine food and diet overlap of co-occurring Arctic charr *Salvelinus alpinus* (L.), Brown trout *Salmo trutta* L. and Atlantic salmon *S. salar* L. off Senja, N. Norway. *Polar Biology* **7**, 173-177.

Gross, M.R., Coleman, R.M. & McDowall, R.M. (1988). Aquatic productivity and the evolution of diadromous fish migration. *Science* **239**, 1291-1293.

Guilbard, F., Munro, J., Dumont, P., Hatin, D. & Fortin, R. (2007). Feeding ecology of Atlantic sturgeon and Lake sturgeon co-occurring in the St. Lawrence estuarine transition zone. In *Anadromous Sturgeons: Habitats, Threats, and Management* (Munro, J., Hatin, D., Hightower, J.E., McKown, K., Sulak, K.J., Kahnle, A.W. & Caron, F., eds), pp. 85-104. American Fisheries Society Symposium 56.

Gulseth, O. & Nilssen, K. (2000). The brief period of spring migration, short marine residence, and high return rate of a northern Svalbard population of Arctic char. *Transaction of the American Fisheries Society* **129**, 782-796.

Gulseth, O. & Nilssen, K. (2001). Life-history traits of charr, *Salvelinus alpinus*, from a high Arctic watercourse on Svalbard. *Arctic* **54**, 1-11.

Gulseth, O., Nilssen, K., Iversen, M. & Finstad, B. (2000). Seawater tolerance in first-time migrants of anadromous Arctic charr (*Salvelinus alpinus*). *Polar Biology* **24**, 270-275.

Gyselman, E.C. (1994). Fidelity of anadromous Arctic char (*Salvelinus alpinus*) to Nauyuk Lake, N.W.T., Canada. *Canadian Journal of Fisheries and Aquatic Sciences* **51,** 1927-1934.

H

Halfyard, E.A., Gibson, A.J.F., Ruzzante, D.E., Stokesbury, M.J.W. & Whoriskey, F.G. (2012). Estuarine survival and migratory behaviour of Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology* **81**, 1626–1645. doi:10.1111/j.1095-8649.2012.03419.x

Halfyard, E.A., Gibson, A.J.F., Stokesbury, M.J.W., Ruzzante, D.E. & Whoriskey, F.G. (2013). Correlates of estuarine survival of Atlantic post-smolts from the southern upland, Nova Scotia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* **70**, 452-460. doi: 10.1139/cjfas-2012-0287

Halttunen, E., Rikardsen, A.H., Davidsen, J.G., Thorstad, E.B. & Dempson, J.B. (2009). Survival, migration speed and swimming depth of Atlantic salmon kelts during sea entry and fjord migration. In: *Tagging and tracking of marine animals with electronic devices. Reviews: Methods and technologies in fish biology and fisheries, vol. 9.* (Nielsen, J.L., Arrizabalaga, H., Fragoso, N., Hobday, A., Lutcavage, M. & Sibert, J., eds), pp 35-50, Dordrecht, the Netherlands: Springer.

Hamilton, S.L., Bravender, B.A., Beggs, C. & Munro, B. (2008). Distribution and abundance of juvenile salmonids and other fish species in the Courtenay River estuary and Baynes Sound, 2001. Canadian Technical Report of Fisheries and Aquatic Sciences 2806, Ottawa

Haque, S.R. (2008). Movement patterns of coastal cutthroat trout *(Oncorhynchus clarki clarki)* in South Puget Sound, Washington 2006-2007. MSc Dissertation, The Evergreen State College

Harden Jones, F.R. (1968). *Fish migration*. London, England: Edward Arnold Ltd.

Harden Jones, F.R. & Scholes, P. (1985). Gas secretion and resorption in the swimbladder of cod *Gadus morhua*. *Journal of Comparative Physiology* **155**, 319–331.

Heard, W.R. (1991). Life history of pink salmon (*Oncorhynchus gorbuscha*). In: *Pacific salmon life histories* (Groot, C. & Margolis, L., eds), pp 319-377. Vancouver: UBC Press.

Hedger, R.D., Hatin, D., Dodson, J.J., Martin, F., Fournier, D., Caron, F. & Whoriskey, F.G. (2009). Migration and swimming depth of Atlantic salmon kelts *Salmo salar* in coastal zone and marine habitats. *Marine Ecology Progress Series* **392,** 179–192. doi:10.3354/meps08227.

Helland, I.P., Finstad, A.G., Forseth, T., Hesthagen, T. & Ugedal, O. (2011). Ice-cover effects on competitive interactions between two fish species. *Journal of Animal Ecology* **80**, 539–547.

Héroux, D. & Magnan, P. (1996). In situ determination of food daily ration in fish: review and field evaluation. *Environmental Biology of Fishes* **46**, 61-74.

Heupel, M.R., Semmens, J.M. & Hobday, A.J. (2006). Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Marine and Freshwater Research* **57**, 1-13.

Hofer, R. (1979). The adaptation of digestive enzymes to temperature, season and diet in roach, *Rutilus rutilus* and rudd, *Scardinus erythrophtalmus*; Proteases. *Journal of Fish Biology* **15**, 373-379.

Holland, K.N., Brill, R.W., Chang, R.K.C., Sibert, J.R. & Fournier, D.A. (1992). Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature* **358**, 410-412. doi:10.1038/358410a0

Holm, M., Holst, J.C., Hansen, L.P., Jacobsen, J.A., O´Maoile´idigh, N. & Moore, A. (2003). Migration and distribution of Atlantic salmon post-smolts in the North Sea and North East Atlantic. In: *Salmon at the Edge* (Mills, D., ed), pp 7-23. Oxford: Blackwell Science Publications.

Holtby, L.B., Andersen, B.C. & Kadowaki, R.K. (1990). Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 2181-2194.

Horne, J.K., Sawada, K., Abe, K., Kreisberg, R.B., Barbee, D.H. & Sadayasu, K. (2009). Swimbladders under pressure: anatomical and acoustic responses by walleye pollock. *ICES Journal of Marine Science* **66**, 1162–1168.

Hubley, P.B., Amiro, P.G., Gibson, A.J.F., Lacroix, G.L. & Redden, A.M. (2008). Survival and behaviour of migrating Atlantic salmon (*Salmo salar* L.) kelts in river, estuarine, and coastal habitat. *ICES Journal of Marine Science* **65**, 1626–1634.

Hunter, J.G. (1976). Arctic char and hydroelectric power in the Sylvia Grinnell River. Fisheries Research Board of Canada Manuscript Report Series 1376, Ottawa

Huusko, A., Greenberg, L., Stickler, M., Linnansaari, T., Nykaanen, M., Vehanen,T., Koljonen, S., Louhi, P. & Alfredsen, K. (2007). Life in the ice lane: The winter ecology of stream salmonids. *River Research and Applications* **23,** 469–491.

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

I

Ibbotson, A.T., Clough, S., Scarlett, P., Ladle, D. & Masters, J. (1996). Piscivorous predation on stocked salmon parr in a chalk stream. Institute of Freshwater Ecology Report RL/T11063g7. Available at http://nora.nerc.ac.uk/14130/1/R-Test_REPORT.pdf (last accessed 14 March 2014).

IOC. (2010). The international thermodynamic equation of seawater - 2010: Calculation and use of thermodynamic properties. Intergovernmental Oceanographic Commission, UNESCO

Irvine, J.R., MacDonald, R.W., Brown, R.J., Godbout, L., Reist, J.D. & Carmack, E.C. (2009). Salmon in the Arctic and how they avoid lethal low temperatures. *North Pacific Anadromous Fish Commission Bulletin* **5**, 39-50.

Isinguzo, I., Gallagher, C. & Dick, T.A. (2002). Feeding ecology of Arctic char *Salvelinus alpinus*. University of Manitoba. Poster presentation.

J

Jákupsstovu, S.H.i. (1988). Exploitation and migration of salmon in Faroese waters. In *Atlantic Salmon: Planning for the Future* (Mills, D. & Piggins, D., eds), pp.458-482. London: Croom Helm.

Jensen, J.L.A. (2013). The seasonal migratory behavior of sympatric anadromous Arctic charr and brown trout. PhD Thesis, University of Tromsø, Tromsø, Norway.

Jensen, J.L.A. & Rikardsen, A.H. (2008). Do northern riverine anadromous Arctic charr *Salvelinus alpinus* and sea trout *Salmo trutta* overwinter in estuarine and marine waters? *Journal of Fish Biology* **73**, 1810–1818.

Jensen, J.L.A. & Rikardsen, A.H. (2012). Archival tags reveal that Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* can use estuarine and marine waters during winter. *Journal of Fish Biology* **81**, 735-749.

Jensen, J.L.A., Rikardsen, A.H., Thorstad, E.B., Suhr, A.H., Davidsen, J.G. & Primicerio, R. (2014). Water temperatures influence the marine area use of *Salvelinus alpinus* and *Salmo trutta. Journal of Fish Biology* **84**, 1640-1653. doi:10.1111/jfb.12366

Jensen, K.W. & Berg, M. (1977). Growth, mortality and migrations of the anadromous char, *Salvelinus alpinus*, L., in the Vardnes River, Troms, Northern Norway. *Institute of Freshwater Research Drottningholm Report* **56**, 70-80.

Jepsen, N., Koed, A., Thorstad, E. & Baras, E. (2002). Surgical implantation of telemetry transmitters in fish: how much have we learned? *Hydrobiologia* **483**, 239-248.

Jobling, S., Johansen, H., Foshaug, I., Burkow & Jørgensen, E. (1998). Lipid dynamics in anadromous Arctic charr, *Salvelinus alpinus* (L.): seasonal variations in lipid storage depots and lipid class composition. *Fish Physiology and Biochemistry* **18**, 225-240.

Johnson, L. (1980). The arctic charr, *Salvelinus alpinus.* In *Charrs, salmonid fishes of the genus Salvelinus* (Balon, E.K., ed), pp. 15-98. The Hague, Netherlands: Dr. **W.** Junk Publishers.

Johnson, L. (1989). The anadromous Arctic charr, *Salvelinus alpinus*, of Nauyuk Lake, N.W.T., Canada. *Physiology and Ecology, Japan* **1**, 201-227.

Jonsson, B. & Jonsson, N. (2011). *Ecology of Atlantic salmon and brown trout – Habitat as a template for life histories.* Springer, New York

Jonsson, N. & Jonsson, B. (2002). Migration of anadromous brown trout in a Norwegian river. *Freshwater Biology* **47**, 1391-1401.

K

Kessel, S.T., Cooke, S.J., Heupel, M.R., Hussey, N.E., Simpfendorfer, C.A., Vagle, S. & Fisk, A.T. (2014). A review of detection range testing in aquatic passive acoustic telemetry studies. *Reviews in Fish Biology and Fisheries* **24**, 199-218.

Klemetsen, A., Amudsen, P.-A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F. & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fishes* **12**, 1-59.

Knip, D.M., Heupel, M.R. & Simpfendorfer, C.A. (2012). To roam or to home: site fidelity in a tropical coastal shark. *Marine Biology* **159**, 1647-1657. doi 10.1007/s00227-012-1950-5

Kowalchuk, M.W., Reist, J.D., Bajno, R. & Sawatzky, C.D. (2010). Population structuring and inter-river movements of northern form dolly varden, *Salvelinus malma malma* (Walbaum 1792), along the north slope of Canada and Alaska. DFO Canada Science Advisory Section Research Document 2010/038, Ottawa

Kuzishchin, K.V., Malyutina, A.M., Gruzdeva, M.A., Savvaitova, K.A. & Pavlov, D.S. (2009). Reproduction ecology of masu salmon *Oncorhynchus masou* in the Kol Basin (Western Kamchatka). *Journal of Ichthyology* **49**, 441-453.

L

L'Abée-Lund, J.H., Jonsson, B., Jensen, A.J., Sættem, L.M., Heggberget, T.G., Johnsen, B.O. & Næsje, T.F. (1989). Latitudinal variation in life-history characteristics of sea-run migrant brown trout *Salmo trutta*. J *Animal Ecology* **58**, 525–542.

Lacroix, G.L. (2013). Population-specific ranges of oceanic migration for adult Atlantic salmon (*Salmo salar*) documented using pop-up satellite archival tags. *Canadian Journal of Fisheries and Aquatic Sciences* **70**, 1011-1030.

Lacroix, G.L. & Voegeli, F.A. (2000). Development of automated monitoring systems for ultrasonic transmitters. In *Advances in Fish Telemetry* (Moore, A. & Russell, I., eds), pp. 37–50. Lowestoft: CEFAS.

Lake, R.A. & Walker, E.R. (1973). Notes on the oceanography of D'Iberville fiord. *Arctic* **26**, 222-229.

Landergren, P. & Vallin, L. (1998). Spawning of sea trout, *Salmo trutta* L., in brackish waters – lost effort or successful strategy? *Fisheries Research* **35**, 229–236.

Langeland, A., L'Abée-Lund, J.H., Jonsson, B. & Jonsson, N. (1991). Resource partitioning and niche shift in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*. *Journal of Animal Ecology* **60**, 895-912.

Larsson, S. (2005). Thermal preference of Arctic charr, *Salvelinus alpinus*, and brown trout*,* *Salmo trutta* – implications for their niche segregation. *Environmental Biology of Fishes* **73**, 89–96.

Larsson, S. & Berglund, I. (2005). The effect of temperature on the energetic growth efficiency of Arctic charr (*Salvelinus alpinus* L.) from four Swedish populations. *Journal of Thermal Biology* **30**, 29–36.

Larsson, S., Forseth, T., Berglund, I., Jensen, A., Näslund, I., Elliott, J. & B. Jonsson. (2005). Thermal adaptation of Arctic charr: experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. *Freshwater Biology* **50**, 353-368.

Lefèvre, M.A., Stokesbury, M.J.W., Whoriskey, F.G. & Dadswell, M.J. (2012). Atlantic salmon post-smolt migration routes in the Gulf of St. Lawrence. *ICES Journal of Marine Science* **69**, 981–990.

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

Lee, R.M. & Rinne, J.N. (1980). Critical thermal maxima of five trout species in the southwestern United States. *Transactions of the American Fisheries Society* **109**, 632-635.

Limburg, K.E., Landergren, P., Westin, L., Elfman, M. & Kristiansson, P. (2001). Flexible modes of anadromy in Baltic sea trout: making the most of marginal spawning streams. *Journal of Fish Biology* **59**, 682–695. doi:10.1006/jfbi.2001.1681

Livingstone, D.M. (2001). Large-scale climatic forcing detected in historical observations of lake ice break-up. *Verhandlungen Internationalen Verein Limnologie* **27**, 2775–2783.

M

Machidori, S. & Kato, F. (1984). Spawning populations and marine life of masu salmon (*Oncorhynchus masou*). *International North Pacific Fish Commission Bulletin* **43**, 1-138.

MacMillan, J. & Madden, R. (2007). Angler effort and harvest of sea-run brook trout from a specially regulated estuary, Nova Scotia, Canada. In *Sustaining wild trout in a changing world; proceedings of Wild Trout IX symposium* (Carline, R.F. & LoSapio, C., eds), pp. 186-193.West Yellowstone, Montana: Wild trout IX Symposium.

Magnuson, J.J. (2002). Signals from ice cover trends and variability. In: *Fisheries in a changing climate* (McGinn, N.A., ed), pp 3-14. Bethesda, Maryland: American Fisheries Society Symposium 32.

Magnuson, J.J., Robertson, D.M., Benson, B.J., Wynne, R.H., Livingstone, D.M., Arai, T., Assel, R.A., Barry, R.G., Card, V., Kuusisto, E., Granin, N.G., Prowse, T.D., Stewart, K.M. & Vuglinski, V.S. (2000). Historical trends in lake and river ice cover in the northern hemisphere. *Science* **289**, 1743–1746.

Manzer, J.I., Ishida, T., Peterson, A.E. & Hanavan, M.G. (1965). Salmon of the North Pacific Ocean. Part 5: Offshore distribution of salmon. International North Pacific Fisheries Commission Bulletin 15.

Marshall, S.A. (2006). *Insects. Their natural history and diversity with a photographic guide to insects of eastern North America*. Richmond Hill, ON: Firefly Books.

Materna, S., Cech, J.Jr & Hopkins, T. (2000). Diel movements of bat rays, *Myliobatis californica*, in Tomales Bay, California: evidence for behavioural thermoregulation? *Environmental Biology of Fishes* **58**, 173–182.

McCart, P.J. (1980). A review of the systematics and ecology of Arctic char, *Salvelinus alpinus*, in the western Arctic. *Canadian Technical Report of Fisheries and Aquatic Sciences* **935**, 1-89.

McCormick, S.D. (1994). Ontogeny and evolution of salinity tolerance in anadromous salmonids: Hormones and heterochrony. *Estuaries* **17**, 26-33.

McCormick, S.D., Shrimpton, J.M. & Zydlewski, J.D. (1997). Temperature effects on osmoregulatory physiology of juvenile anadromous fish. In: *Global warming: Implications for freshwater and marine fish* (Wood, C.M. & McDonald, D.G., eds), pp 279-301. Cambridge: Cambridge University Press.

McLean, M.F., Dadswell, M.J. & Stokesbury, M.J.W. (2012). Feeding ecology of Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus* Mitchill, 1815 on the infauna of the intertidal mudflats of Minas Basin, Bay of Fundy. *Journal of Applied Ichthyology* **29**, 503-509.

McLean, M.F., Simfendorfer, C.A., Heupel, M.R., Dadswell, M.J. & Stokesbury, M.J.W. (2014). Quantifying movement patterns of Atlantic sturgeon (*Acipenser oxyrinchus*) in the Minas Basin, Bay of Fundy, Canada. *Marine Ecology Progress Series* **496**, 59-69.

Metusalach, Brown, J.A., Shahidi, F. (1995). Lipid content and fatty acid composition of Arctic Charr (*Salvelinus alpinus* L.) reared at different stocking densities. *Journal of Food Lipids* **2**, 269-286.

Miller, B.A. & Sadro, S. (2003). Residence time and seasonal movements of juvenile Coho salmon in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon. *Transactions of the American Fisheries Society* **132**, 546–559.

Miller, J.L., Hamon, T., Jones, T. & West, F. (2007). Kokanee exploit large prey in the absence of limnetic predators**.** *American Fisheries Society Symposium* **54,** 73–83.

Montgomery, W.L., McCormick, S.D., Naiman, R.J., Whoriskey, F.G. & Black, G. (1990). Anadromous behavior of brook charr (*Salvelinus fontinalis*) in the Moisie River, Quebec. *Polskie Archiwum Hydriobiologii* **37,** 43–61.

Moore, J-S., Harris, L.N., Tallman, R.F. & Taylor, E.B. (2013). The interplay between dispersal and gene flow in anadromous Arctic char (*Salvelinus alpinus*): implications for potential for local adaptation. *Canadian Journal of Fisheries and Aquatic Sciences* **70,** 1327-1338. dx.doi.org/10.1139/cjfas-2013-0138

Moore, J.W. (1975). Distribution, movements, and mortality of anadromous Arctic char, *Salvelinus alpinus* L., in the Cumberland Sound area of Baffin Island. *Journal of Fish Biology* **7**, 339-348.

Moore, J.W. & Moore, I.A. (1974). Food and growth of arctic char, *Salvelinus alpinus* (L.) in the Cumberland Sound area of Baffin Island. *Journal of Fish Biology* **6**, 79-92.

Morinville, G.R. & Rasmussen, J.B. (2006). Marine feeding patterns of anadromous brook trout (*Salvelinus fontinalis*) inhabiting an estuarine river fjord. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 2011-2027.

Morris, C. & Green, J.M. (2012). Migrations and harvest rates of Arctic charr (*Salvelinus alpinus*) in a marine protected area. *Aquatic Conservation: Marine and Freshwater Ecosystems* **22,** 743–750.

Morris, J.T., Sundareshwar, P.V., Nietch, C.T., Kjerfve, B. & Cahoon, D.R. (2002). Responses of coastal wetlands to rising sea level. *Ecology* **83**, 2869–2877.

Mortensen, A., Ugedal, O. & Lund, F. (2007). Seasonal variation in the temperature preference of Arctic charr (*Salvelinus alpinus*). *Journal of Thermal Biology* **32**, 314–320.

Moyle, P.B. (2002). *Inland fishes of California*. Berkley, CA: University of California Press.

Moyle, P.B. & Cech, J.J. (1996). *Fishes: an introduction of ichthyology. 3rd ed*. New Jersey: Prentice Hall.

N

Nagasawa, K. (2000). Winter zooplankton biomass in the subarctic North Pacifc, with a discussion on the overwintering survival strategy of Pacific salmon (*Oncorhynchus* spp.) *North Pacific Anadromous Fish Commission Bulletin* **2**, 21-32.

Needham, J.G. & Needham, P.R. (1962). *A guide to the study of fresh-water biology*. 5th edn. San Francisco, CA: Holden-Day Inc.

Needler, A.W.H. (1940). A preliminary list of the fishes of Malpeque Bay. *Proceedings of the Nova Scotia Institute of Science* **20**, 33-41.

Nielsen, J.L., Turner, S.M. & Zimmerman, C.E. (2011). Electronic tags and genetics explore variation in migrating steelhead kelts (*Oncorhynchus mykiss*), Ninilchik River, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 1–16.

Nikolsky, G.V. (1963). *The ecology of fishes*. London, England: Academic Press.

NOAA. (2012a). Monthly Mean SST charts (1984-1998), March and October 1984, May and June 1998. National Environmental Satellite, Data, and Information Service. http://www.ospo.noaa.gov/data/sst/mean_mon/October.84.monmean.gif . Accessed 14 August 2012

NOAA. (2012b). Operational 50 km nighttime SST charts for the year 2011, global view, January and August. National Environmental Satellite, Data, and Information Service. http://www.ospo.noaa.gov/Products/ocean/sst/50km_night/2011.html. Accessed 21 October 2012

Northcote, T.G. (1978). Migratory strategies and production in freshwater fishes. In *Ecology of freshwater fish production* (Gerking, S.D., ed), pp. 326-359. Oxford, England: Blackwell Scientific Publications.

Northcote, T.G. (1984). Mechanisms of fish migration in rivers. In *Mechanisms of migration in fishes* (McCleave, J.D., Arnold, G.P., Dodson, J.J., & Neill, W.H., eds), pp. 317-355. New York, New York, USA: Plenum.

Nowak, G.M., Tabor, R.A., Warner, E.J., Fresh, K.L. & Quinn, T.P. (2004). Ontogenetic shifts in habitat and diet of cutthroat trout in Lake Washington, Washington. *North American Journal of Fisheries Management* **24**, 624–635.

O

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. PhD thesis, Memorial University of Newfoundland, St. John's, Newfoundland.

Ogura, M. & Ishida, Y. (1995). Homing behavior and vertical movements of four species of Pacific salmon (*Oncorhynchus* spp.) in the central Bering Sea. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 532-540.

Ohkuma, K., Urawa, S., Ueno, Y. & Davis, N.D. (1999). Easternmost record for ocean distribution of masu salmon (*Oncorhynchus masou*). North Pacific Anadromous Fish Commission Document 422.

Olsen, E.M., Knutsen, H., Simonsen, J.H., Jonsson, B. & Knutsen, J.A. (2006). Seasonal variation in marine growth of sea trout, *Salmo trutta*, in coastal Skagerrak. *Ecology of Freshwater Fishes* **15**, 446–452.

P

Pearcy, W.G. (1992). *Ocean ecology of North Pacific salmonids*. Seattle: University of Washington Press.

Pemberton, R. (1976). Sea trout in North Argyll sea lochs. 2. Diet. *Journal of Fish Biology* **9**, 195-208.

Pennell, W. & Barton, B.A. (1996). *Principles of salmonid culture. Developments in Aquaculture and Fisheries Science 29*. The Netherlands: Elsevier.

Peterson, R.H., Sutterlin, A.M. & Metcalfe, J.L. (1979). Temperature preference of several species of *Salmo* and *Salvelinus* and some of their hybrids. *Journal of the Fisheries Research Board of Canada* **36**, 1137–1140

Pinkas, L., Oliphant, M.S. & Irerson I.L.K. (1971). *Food habits of albacore, bluefin tuna, and bonita in Californian waters*. Fish Bulletin 152: State of California Department of Fish and Game

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

Power, M., Power, G., Caron, F., Doucett, R.R. & Guiguer, K.R.A. (2002). Growth and dietary niche in *Salvelinus alpinus* and *Salvelinus fontinalis* as revealed by stable isotope analysis. *Environmental Biology of Fishes* **64**, 75-85.

Q

Quinn, T.P. (2005). *The behaviour and ecology of Pacific salmon and trout – 1st edition*. Bethesda, Maryland: American Fisheries Society.

Quinn, T.P. & Myers, K.W. (2004). Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisted. *Reviews in Fish Biology and Fisheries* **14**, 421-442.

R

Randall, R.G., Healey, M.C. & Dempson, J.B. (1987). Variability in length of freshwater residence of salmon, trout, and char. In: *Common strategies of anadromous and catadromous fishes* (Dadswell, M., Klauda, R., Moffitt, C., Saunders, R., Rulifson, R. & Cooper, J., eds), pp 27-41. Bethesda, Maryland: American Fisheries Society Symposium 1.

Reddin, A.M., Broome, J., Keyser, F., Stokesbury, M.J.W., Bradford, R., Gibson, J. & Halfyard, E. (2014). Use of animal tracking technology to assess potential risks of tidal turbine interactions with fish. Proceedings of the 2nd International Conference on Environmental Interactions of Marine Renewable Energy Technologies (EIMR2014), Stornoway, Scotland, 28 April – 02 May 2014.

Reddin, D. & Shearer, W. (1987). Sea-surface temperature and distribution of Atlantic salmon (*Salmo salar* L.) in the northwest Atlantic. In: *Common strategies of anadromous and catadromous fishes* (Dadswell, M., Klauda, R., Moffitt, C., Saunders, R., Rulifson, R. & Cooper, J., eds), pp 262-270. Bethesda, Maryland: American Fisheries Society Symposium 1.

Richard, P. (2001). *Marine mammals of Nunavut*. Nunavut: Qikiqtani School Operations.

Richter, H., Lückstädt, C., Focken, U. & Becker, K. (2004). Some mathematical considerations in estimating daily ration in fish using food consumption models. *Ecological Modelling* **171**, 381–393.

Ricker, W.E. (1975). *Computation and interpretation of biological statistics of fish populations. Bulletin 191*. Department of the Environment Fisheries and Marine Service, Ottawa, ON: The Blackburn Press.

Rikardsen, A.H. (2004). Seasonal occurrence of sea lice *Lepeophtheirus salmonis* on sea trout in two north Norwegian fjords. *Journal of Fish Biology* **65**, 711–722.

Rikardsen, A.H., Amundsen, P-A., Knudsen, R. & Sandring, S. (2006). Seasonal marine feeding and body condition of sea trout (*Salmo trutta*) at its northern distribution. *ICES Journal of Marine Science* **63**, 466-475.

Rikardsen, A.H. & Amundsen, P.-A. (2005). Pelagic marine feeding of Arctic charr and sea trout. *Journal of Fish Biology* **66**, 1163-1166.

Rikardsen, A.H. & Dempson, J.B. (2011). 5.2 Post-smolt nearshore feeding. In *Atlantic salmon ecology* (Aas, O., Einum, S., Klemetsen, A., Skurdal, J. eds), pp. 117-118, Oxford, UK: Blackwell Publishing Ltd.

Rikardsen, A.H., Diserud, O.H., Elliott, J.M., Dempson, J.B., Sturlaugsson, J. & Jensen, A.J. (2007). The marine temperature and depth preference of Arctic charr (*Salvelinus alpinus*) and sea trout (*Salmo trutta*), as recorded by data storage tags. *Fisheries Oceanography* **16**, 436-447.

Rikardsen, A.H., Hansen, L.P., Jensen, A.J., Vollen, T. & Finstad, B. (2008). Do Norwegian Atlantic salmon feed in the northern Barents Sea? Tag recoveries from 70-78°N. *Journal of Fish Biology* **72**, 1792-1798.

Robertson, D.M., Wynne, R.H. & Chang, Y.B. (2001). Influences of El Niño on lake and river ice cover in the northern hemisphere from 1990 to 1997. *Verhandlungen Internationalen Verein Limnologie* **27**, 2784–3472.

Rose, G.A. (2005). Caplin (*Mallotus villosus*) distribution and climate: a sea “canary” for marine ecosystem change. *ICES Journal of Marine Science* **62**, 1524-1530.

Rounsefell, G.A. (1958). Anadromy in North American Salmonidae. *US Fish and Wildlife Service Bulletin* **58**, 171-185.

Ruggerone, G.T., Quinn, T.P., McGregor, I.A. & Wilkinson, T.D. (1990). Horizontal and vertical movements of adult steelhead trout, *Oncorhynchus mykiss*, in the Dean and Fisher channels, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* **47,** 1963–1969. doi:10.1139/f90-221.

Ruppert, E.H. & Barnes, R.D. (1994). *Invertebrate Zoology*, 6th edn. Toronto, ON: Saunders College Publishing.

S

Salo, E.O. (1991). Life history of chum salmon, (*Oncorhynchus keta*). In: *Pacific salmon life histories*. (Groot, C. & Margolis, L., eds), pp 231-309, Vancouver: UBC Press.

Saloniemi, I., Jokikokko, E., Kallio-Nyberg, I., Jutila, E. & Pasanen, P. (2004). Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. *ICES Journal of Marine Science* **61**, 782-787.

Sánchez-Hernández, J., Servia, M.J., Vieira-Lanero. R. & Cobo, F. (2012). Ontogenetic dietary shifts in a predatory freshwater fish species: The brown trout as an example of a dynamic fish species. In *New Advances and Contributions to Fish Biology*. (Turker, H. ed), ISBN: 978-953-51-0909-9, InTech, DOI: 10.5772/54133. Available at http://www.intechopen.com/books/new-advances-and-contributions-to-fish-biology/ontogenetic-dietary-shifts-in-predatory-freshwater-fish-species-the-brown-trout-as-an-example-of-a-d (last accessed 13 March 2014).

Sars, G.O. (1890). *An account of the Crustacea of Norway. Vol. I. Amphipoda.* Bergen: ALB Cammermeyer.

Saunders, R.L., Muisse, B.C. & Henderson, E.B. (1975). Mortalities of salmonids cultured at low temperature in sea water. *Aquaculture* **5**, 243-252.

Schwarzbaum, P.J., Weiser, W. & Cossins, A.R. (1992). Species-specific response of membranes and the Na^+/K^+-ATPase pump to temperature changes in the kidney of two species of freshwater fish, roach (*Rutilus rutilus*) and Arctic char (*Salvelinus alpinus*). *Physiological Zoology* **65**, 17-34.

Schwarzbaum, P.J., Weizer, W. & Niederstaetter, H. (1991). Contrasting effects of temperature acclimitation on mechanisms of ionic regulation in a eurythermic and a stenothermic species of freshwater fish (*Rutilus rutilus* and *Salvelinus alpinus*). *Comparative Biochemical Physiology* **98**, 483-489.

Scott, W.B. & Scott, M.G. (1988). *Atlantic fishes of Canada*. Ottawa, ON: Canadian Bulletin of Fisheries and Aquatic Sciences 219.

Selong, J.H., McMahon, T.E., Zale, A.V. & Barrows, F.T. (2001). Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. *Transactions of the American Fisheries Society* **130**, 1026–1037.

Signorini, S.R. & McClain, C.R. (2009). Environmental factors controlling the Barents Sea spring-summer phytoplankton blooms. *Geophysical Research Letters* **36**, L10604. doi:10.1029/2009GL037695.

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

Spares, A.D. & Dadswell, M.J. (2001). Goat Lake, a warm water, estuarine refugia for molluscs on the south shore of Nova Scotia. *Proceedings of the Nova Scotia Institute of Science* **41**, 134-148.

Spares, A.D., Dadswell, M.J., MacMillan, J., Madden, R., O'Dor, R.K. & Stokesbury, M.J.W. (2014). To fast or feed: an alternative life history for anadromous brook trout *Salvelinus fontinalis* overwintering within a harbour. *Journal of Fish Biology* **85**, 621-644. doi:10.1111/jfb.12447

Spares, A.D., Reader, J.W., Stokesbury, M.J.W., McDermott, T., Zikovsky, L., Avery, T. & Dadswell, M.J. (2007). Inferring marine distribution of Canadian and Irish Atlantic salmon (*Salmo salar* L.) in the North Atlantic Ocean from tissue concentrations of bioaccumulated caesium-137. *ICES Journal of Marine Science* **64**, 394-404.

Spares, A.D., Stokesbury, M.J.W., O'Dor, R.K. & Dick, T.A. (2012). Temperature, salinity and prey availability shape the marine migration of Arctic char, *Salvelinus alpinus*, in a macrotidal estuary. *Marine Biology* **159**, 1633-1646.

Sprules, Wm. (1952). The Arctic char of the west coast of Hudson Bay. *Journal of the Fisheries Research Board of Canada* **9**, 1-15.

StatsCan. (2006). Statistics Canada. Population of Iqaluit 2006. www.statcan.gc.ca. Accessed October 15, 2009.

Staubitz, W.W., Bortleson, G.C., Semans, S.D., Tesoriero, A.J. & Black, R.W. (1997). Water-quality assessment of the Puget Sound Basin, Washington—environmental setting and its implications for water quality and aquatic biota. U.S. Geological Survey. Resources Investigations Report 97-4013, Tacoma, Washington

Stewart, D.B., Mochnacz, N.J., Reist, J.D., Carmichael, T.J. & Sawatzky, C.D. (2010). Fish life history and habitat use in the Northwest Territories: Dolly varden (*Salvelinus malma*). Canadian Manuscript Report of Fisheries and Aquatic Sciences 2915, Ottawa

Stokesbury, M.J.W., Dadswell, M.J., Holland, K.N., Jackson, G.D., Bowen, W.D. & O'Dor, R.K. (2009). Tracking diadromous fishes at sea: The electronic future using hybrid acoustic and archival tags. In: *Challenges for diadromous fishes in a dynamic global environment* (Haro, A., Smith, K.L., Rulifson, R.A., Moffitt, C.M., Klauda, R.J., Dadswell, M.J., Cunjak, R.A., Cooper, J.E., Beal, K.L. & Avery, T.S., eds), pp 311-320. Bethesda, Maryland: American Fisheries Society Symposium 69.

Straty, R.R. & Jaenicke, H.W. (1980). Estuarine influence of salinity, temperature and food on the behaviour, growth and dynamics of Bristol Bay sockeye salmon. In: *Salmonid ecosystems of the North Pacific* (McNeil, W.J. & Himsworth, D.C., eds), pp 247-265. Corvallis: Oregon State University Press.

Sturlaugsson, J. & Thorisson, K. (1997). Migration pattern of homing of Atlantic salmon (Salmo salar L.) in coastal waters W- Iceland: recorded by data storage tags. ICES CM 9.

Sutterlin, A. & Stevens, E. (1992). Thermal behaviour of rainbow trout and Arctic char in cages moored in stratified water. *Aquaculture* **102**, 65–75.

Swanson, H.K. & Kidd, K.A. (2009). A preliminary investigation of the effects of anadromous Arctic char on food web structure and nutrient transport in coastal Arctic lakes. In: *Challenges for diadromous fishes in a dynamic global environment* (Haro, A., Smith, K.L., Rulifson, R.A., Moffitt, C.M., Klauda, R.J., Dadswell, M.J., Cunjak, R.A., Cooper, J.E., Beal, K.L. & Avery, T.S., eds), pp 465-483. Bethesda, Maryland: American Fisheries Society Symposium 69.

Swanson, H.K., Kidd, K.A., Babaluk, J.A., Wastle, R.J., Yang, P.P., Halden, N.M. & Reist, J.D. (2012). Anadromy in Arctic populations of lake trout (*Salvelinus namaycush*): otolith microchemistry, stable isotopes, and comparisons with Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 842-853.

Sweka, J.A., Cox, M.K. & Hartman, K.J. (2004). Gastric evacuation rates of brook trout. *Transactions of the American Fisheries Society* **133**, 204-210.

Systat. (2009). Systat statistical software. SYSTAT 13 trial version. http://www.systat.com/. Accessed 12 Nov 2009

Systat. (2013). Systat statistical software. SYSTAT 13 trial version. Available at http://www.systat.com/ (last accessed 20 June 2013).

T

Tamate, T. & Maekawa, K. (2000). Life cycle of masu salmon *(Oncorhynchus masou)* in Shumarinai Lake, northern Hokkaido, Japan. *Eurasian Journal of Forestry Research* **1**, 39-42.

Tanaka, H., Naito, Y., Davis, N.D., Urawa, S., Ueda, H. & Fukuwaka, M. (2005). First record of the at-sea swimming speed of a Pacific salmon during its oceanic migration. *Marine Ecology Progress Series* **291**, 307–312.

Tanaka, H., Takagi, Y. & Naito, Y. (2000). Behavioural thermoregulation of chum salmon during homing migration in coastal waters. *The Journal of Experimental Biology* **203**, 1825-1833.

Teo, S.L.H., Boustany, A., Dewar, H., Stokesbury, M.J.W., Weng, K.C., Beemer, S., Seitz, A.C., Farwell, C.J., Prince, E.D. & Block, B.A. (2007). Annual migrations, diving behavior, and thermal biology of Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds. *Marine Biology* **151**, 1–18.

Thériault, M.H., Courtenay, S.C., Godin, C. & Ritchie, W.B. (2006). Evaluation of the Community Aquatic Monitoring Program (CAMP) to assess the health of four coastal areas within the southern Gulf of St. Lawrence with special reference to the impacts of effluent from seafood processing plants. *Canadian Technical Report of Fisheries and Aquatic Sciences* **2649**: vii + 60 p.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Barend, F.N., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature* **427**, 145-148. doi:10.1038/nature02121

Thorrold, S.R., Afonso, P., Fontes, J., Braun, C.D., Santos, R.S., Skomal, G.B. & Berumen M.L. (2014). Extreme diving behavior in devil rays links surface waters and the deep ocean. *Nature* **5**, 4274. doi: 10.1038/ncomms5274

Thorstad, E.B., Whoriskey, F., Rikardsen, A.H. & Aarestrup, K. (2011). Aquatic nomads: The life and migrations of the Atlantic salmon. In: *Atlantic salmon ecology* (Aas, O., Einum, S., Klemetsen, A. & Skurdal, J., eds), pp 1-32. Oxford: Blackwell Publishing Limited.

Townsend, C.R., Begon, M. & Harper, J.L. (2003) Essentials of Ecology. Blackwell Publishing Limited, Oxford

Trotter, P.C. (1989). Coastal cutthroat trout: A life history compendium. *Transactions of the American Fisheries Society* **118,** 463–473.

Tsukamoto, K., Miller, M.J., Kotake, A., Aoyama, J. & Uchida, K. (2009). The origin of fish migration: The random escapement hypothesis. In: *Challenges for diadromous fishes in a dynamic global environment* (Haro, A., Smith, K.L., Rulifson, R.A., Moffitt, C.M., Klauda, R.J., Dadswell, M.J., Cunjak, R.A., Cooper, J.E., Beal, K.L. & Avery, T.S., eds), pp 45-61. Bethesda, Maryland: American Fisheries Society Symposium 69.

Tudela, S. & Palomera, I. (1995). Diel feeding intensity and daily ration in the anchovy *Engraulis encrasicolus* in the northwest Mediterranean Sea during the spawning period. *Marine Ecology Progress Series* **129**, 55-61.

U

Uchida, K., Kaneko, T., Yamaguchi, A., Ogasawara, T. & Hirano, T. (1997). Reduced hypoosmoregulatory ability and alteration in gill chloride cell distribution in mature chum salmon (*Oncorhynchus keta*) migrating upstream for spawning. *Marine Biology* **129**, 247–253.

Underwood, Z.E., Myrick, C.A. & Rogers, K.B. (2012). Effect of acclimation temperature on the upper thermal tolerance of Colorado River cutthroat trout *Oncorhynchus clarkii pleuriticus*: thermal limits of a North American salmonid. *Journal of Fish Biology* **80**, 2420-2433. doi: 10.1111/j.1095-8649.2012.03287.x.

V

Van der Putten, W.H., Macel. M. & Visser, M.E. (2010). Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B* **365,** 2025-2034.

VanGerwen-Toyne, M., Lewis, C., Tallman, R.F. & Martin, Z. (2013). Information to support the assessment of Arctic char (*Salvelinus alpinus*) in the Sylvia Grinnell River, Nunavut, 2009-2011. DFO Canadian Science Advisory Secretariat Science Response Document 2013/nnn vi+XXp.

VEMCO. (2009). Acoustic tracking and monitoring systems. Halifax, Nova Scotia, Canada. www.vemco.com. Accessed Nov 6, 2009.

Viherluoto, M. (2001). Food selection and feeding behaviour of Baltic Sea mysid shrimps. PhD thesis, University of Helsinki.

W

Walker, R.V., Myers, K.W., Davis, N.D., Aydin, K.Y., Friedland, K.D., Carlson, H.R., Boehlert, G.W., Urawa, S., Ueno, Y. & Anma, G. (2000). Diurnal variation in thermal environment experienced by salmonids in the North Pacific as indicated by data storage tags. *Fisheries Oceanography* **9**, 171–186.

Walker, R.J., Sviridov, V.V., Urawa, S. & Azumaya, T. (2007). Spatio-temporal variation in vertical distributions of Pacific salmon in the ocean. *North Pacific Anadromous Fish Commission Bulletin* **4**, 193–201.

Welch, D.W., Ishida, Y. & Nagasawa, K. (1998). Thermal limits and ocean migrations of sockeye salmon (*Oncorhynchus nerka*): long-term consequences of global warming. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 937-948.

Westerberg, H. (1982). Ultrasonic tracking of Atlantic salmon (*Salmo salar* L.) – II. Swimming depth and temperature stratification. *Report of the Institute of Freshwater Research Drottningholm* **60**, 102–120.

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

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

Wilson, M.F. (1997). Variation in salmonid life histories: patterns and perspectives. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland

Wilson, S.G. & Block, B.A. (2009). Habitat use in Atlantic bluefin tuna *Thunnus thynnus* inferred from diving behaviour. *Endangered Species Research* **10**, 355-367.

Woodward, S.L. (2012). Biomes of the world. Department of Geospatial Science, Radford University. https://php.radford.edu/~swoodwar/biomes/?page_id=408. _Accessed 24 September 2014

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

Wu, Y. & Fletcher, G.L. (2000). Efficacy of antifreeze protein types in protecting liposome membrane integrity depends on phospholipid class. *Biochimica et Biophysica Acta* **1524**, 11–16.

Wurster, C.M., Patterson, W.P., Stewart, D.J., Bowlby, J.N. & Stewart, T.J. (2005). Thermal histories, stress, and metabolic rates of chinook salmon (*Oncorhynchus tshawytscha*) in Lake Ontario: evidence from intra-otolith stable isotope analyses. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 700–713. doi:10.1139/F04-241

X

Xiong, Q. & Royer, T.C. (1984). Coastal temperature and salinity in the northern Gulf of Alaska, 1970-1983. *Journal of Geophysical Research* **89**, 8061-8066.

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Z

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