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An Integrative Approach to Examining the Trophic Ecology of a Common Benthic Fish in the High Arctic

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An Integrative Approach to Examining the Trophic Ecology of a Common Benthic Fish
in the High Arctic

By
Justin Landry

A Thesis
Submitted to the Faculty of Graduate Studies
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Windsor, Ontario, Canada

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May 24th, 2016

Declaration of Co-Authorship / Previous Publication

I. Co-Authorship Declaration

I hereby declare that this thesis incorporates material that is result of joint research, as follows: Chapter II and III incorporates data collected by coauthors from previous study years at the same study site (Resolute Bay, Nunavut, Canada). The key ideas, primary contributions, experimental designs, data analysis and interpretation, were performed by the author.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from each of the co-author(s) to include the above material(s) in my thesis.

I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work.

II. Declaration of Previous Publication

This thesis includes 1 original paper that has been previously submitted for publication in peer reviewed journals, as follows:

Thesis Chapter	Publication title/full citation	Publication status*
Chapter 2	Landry JJ, Yurkowski DJ, Fisk AT, Hussey NE, Dick T, Crawford RE, Kessel ST (2016) Diet specialization and habitat coupling of a common benthic fish Shorthorn Sculpin (*Myoxocephalus scorpius*) in the high arctic. Mar Ecol Prog Ser.	*Submitted*
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Abstract

Shorthorn Sculpin (*Myoxocephalus scorpius*) are a common fish in the Arctic that congregate in large numbers in nearshore areas during open water periods, yet little is known about their role in arctic food webs relative to other common consumers like Arctic Cod (*Boreogadus saida*). This study made use of stable isotope and stomach content analysis as well as acoustic telemetry to examine prey selection, diet specialization, trophic position/coupling, and movement patterns. The influence of Arctic Cod presence was also examined. Results indicate that Sculpin trophic ecology changes with total length and prey availability. Distinct movement patterns were identified that potentially represent different foraging behaviours. Sculpin changed movement patterns in the presence of high abundances of Cod, and two Cod were found in Sculpin stomachs. However, data suggests that Shorthorn Sculpin trophic ecology and movement patterns are more heavily influenced by other prey and changes in abiotic variables.

Dedication

This thesis is dedicated to family, friends, and coworkers from the lab to the field who encouraged spending time outdoors and learning about the natural world for leisure and for work and making both enjoyable.

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Table of Contents

ix

List of Tables

List of Figures

Chapter I: Introduction

The study of feeding relationships between organisms is an important aspect of ecosystem health and community ecology (MacArthur 1955). Understanding trophic ecology can impact our understanding of system structure and stability which has applications in fields including invasion biology, ecosystem services and conservation biology (Sanders & Suarez 2011, Dunne et al. 2002, Schwartz et al. 2000). Food webs are a way of visualizing community structure and highlighting how different species in a community can directly or indirectly impact each other through predator-prey relationships. These relationships can in turn be represented by trophic positions. Trophic positions (TP) are often used because they are a simple method of illustrating organisms in a food web by way of their functional roles (eg: primary producers at the bottom of the food web, and apex predators at the top (Post 2002)) and also account for omnivory in an organism's diet (Hussey et al. 2014). Studying species' functional roles or niches in a food web can help determine how stable the community is overall and how important different species are to a system (Paine 1969).

Since the 1950s it has been thought that species diversity influenced community stability, with more species creating a more stable ecosystem (MacArthur 1955). However, this idea has undergone several revisions since its inception. McCann (1998) suggested that complexity can generate stability only if there are several weak interactions between organisms, as opposed to a few strong ones. Others have noted that certain functional groups or species have a disproportionate effect on system stability (Menge et al. 1994, Myers et al. 2007). These particular species tend to be consumers in higher TPs that regulate lower level consumers, which in turn ensures that producers

maintain stable populations (Miller et al. 2001). This type of control is known as a top-down effect. Conversely, bottom-up effects occur when community structure is controlled through energy inputs that enter the food web via primary production. Each ecosystem is unique in its structure but it is likely that both top-down and bottom-up effects have impacts on any given system (Hunter & Price 1992). Recent studies have also examined the importance of large mobile consumers that can couple food webs spatially (Rooney et al. 2006, McCann et al. 2005). This coupling allows for a consumer to exploit a diverse range of prey resources available in an environment making it more resilient to changes in prey availability and helps to ensure no single resource is depleted. Trophic coupling would be especially important in systems that have relatively low diversity or significant temporal changes in species abundance (Tamelander et al. 2006). Such conditions would require consumers to be able to switch from one prey item to another depending on availability.

The marine ecosystems of the high Arctic are extremely dynamic with seasonal fluctuations in photoperiod, and ice cover (Walsh 2008). The high Arctic can be distinguished from the low Arctic by changes in environmental characteristics including the decrease in tundra habitat and increase in polar barrens (http://www.britannica.com/place/High-Arctic). These systems support a number of iconic animals such as Polar Bears (*Ursus maritimus*), Beluga Whales (*Delphinapterus leucas*), Narwhals (*Monodon monoceros*), and various seal species which provide food staples for the Inuit communities of the Canadian Arctic. While these organisms dominate the higher TPs, algae, macroinvertebrates, and fishes make up the lower ones. The biomass of these ecosystems are dominated by copepods, amphipods and fishes, which in turn support marine mammals as well as large populations of migrating seabirds (Hobson

et al. 2002). The schooling fish, Arctic Cod (*Boreogadus saida*) are a key species in Arctic food webs because of their high energy content and wide spread distribution, making them an important prey item for marine mammals, birds, and fishes (Hobson & Welch 1992, Hop & Ter 2013). However, there are a number of common Arctic fishes that are not often used in food web assessment such as Sculpin (*Cottidae sp.*).

Shorthorn Sculpin (*Myoxocephalus scorpius*) have a large marine distribution ranging from more temperate waters to the high Arctic (Robins & Ray 1986). These fish share several morphological features with temperate and freshwater Sculpin spp. including: large pectoral fins, large eyes located high on the head, numerous spines and horns on the head and operculum, and the lack of a swim bladder in adults (Fedorov 1986). Due to their morphology, Shorthorn Sculpin are considered to be a benthic species that feed heavily on benthic invertebrates and sometimes fishes (Cui et al. 2012, Kallgren et al. 2014). In contrast, Arctic Cod are considered to be a pelagic or demersal species that form large schools in nearshore areas and feed on pelagic invertebrates such as copepods and amphipods (Matley et al. 2013). Historically, both species have occurred in Lancaster Sound, Barrow Strait and surrounding waters, and large schools of Arctic Cod have been detected in Allen's Bay, Corwallis Island since the 1980s (Welch et al. 1992, Wech et al. 1993).

Despite their abundance, and the fact that Shorthorn Sculpin are easy to capture, little is known about their trophic ecology, particularly in relation to their feeding behaviour and relative importance to arctic food webs. There is little data to suggest that local human populations rely on them commercially or as a food source and Shorthorn Sculpin are unlisted on the IUCN (International Union for Conservation of Nature) Red List. Although they are a readily available prey item for birds and marine mammals, they

seem to be a less favourable compared to other species such as Arctic Cod (Yurkowski et al. 2015, Divoky & Tremblay 2012, Quakenbush & Bryan 2010).

Shorthorn Sculpin success in the high Arctic may be a result of their dietary omnivory. Past studies have showcased a wide array of invertebrate prey and their ability to couple multiple energy pathways, which is somewhat surprising for a benthic fish (Cui et al. 2012, McMeans et al. 2013). In this way Shorthorn Sculpin can act as an important secondary consumer in Arctic food webs, regulating invertebrate populations that in turn feed on phytoplankton and algae. Whether or not Shorthorn Sculpin actively prey on pelagic food sources has yet to be closely examined, and the relationship between Shorthorn Sculpin and Arctic Cod is unknown. It is possible that Shorthorn Sculpin prey on Arctic Cod in order to gain a larger energy payoff per prey item as per the optimal forage strategy (Werner & Hall 1974) and being able to switch between pelagic and benthic prey depending on availability would be an advantageous strategy in Arctic ecosystems because of their dynamic nature. This may in turn promote stability in these food webs by increasing the number of weak interactions between Shorthorn Sculpin and lower level consumers (Polis et al. 1997). The objective of this study was to use a variety of techniques to examine Shorthorn Sculpin trophic ecology in the high Arctic, and determine if it is impacted by the presence or absence of Arctic Cod with respect to predator-prey interactions. A greater understanding of the trophic interactions between these two consumers would be important in our understanding our Arctic food webs dues to how common both species are.

Stable Isotopes and Stomach Contents Analysis (Chapter II)

The analysis of stable isotopes is a common method for studying trophic ecology and animal diets (Peterson & Fry 1987). Naturally occurring isotope ratios of nitrogen (^{14}N, ^{15}N) and carbon (^{12}C, ^{13}C) have been used extensively in constructing food webs, estimating an organism's TP, and studying where organisms are feeding (i.e.: habitat) (Post et al. 2002). These isotopic ratios are usually reported as parts per thousand (‰) in relation to a standard and written as δ^{15}N and δ^{13}C. Nitrogen isotopes can be used to determine the position of an organism in a food web (i.e.: trophic position) because δ^{15}N increases (enrichment of ^{15}N) as trophic position increases (Post 2002). This enrichment is due to isotopic discrimination which leads to the excretion of isotopically light nitrogen, thus, increasing the ratio of ^{15}N to ^{14}N in consumer tissue compared to prey diets (Michener & Kaufman 2007). Carbon isotopic ratios remain relatively unchanged regardless of trophic position, but can be used to infer the habitat where an organism feeds, however this pattern becomes complex with higher consumers that feed on multiple carbon sources (Post 2002). In aquatic systems δ^{13}C vary between nearshore and offshore, benthic and pelagic and lentic and lotic habitats (Michener & Kaufman 2007, France 1995). In benthic habitats δ^{13}C tends to be enriched in ^{13}C because stagnant boundary layers form around cells and limit the rate at which CO_2 diffusion can occur, resulting in the assimilation of heavier carbon isotopes that would normally be discarded (France 1995). In addition to the main mechanisms discussed above, isotopic ratios can also be influenced by other factors including metabolic differences between species, tissue type and life stage (Michener & Kaufman 2007).

Stomach content analysis has long been the main method for examining an organism's diet (Hyslop 1980). This approach is advantageous in that it allows for the identification of specific prey taxa (Baker et al. 2014). However, stomach content

analysis has a host of problems associated with it: contents can be dissolved beyond the point of accurate identification, or the stomachs may be entirely empty upon the time of capture. The use of DNA-based prey identification has shown to be more accurate than visual identification at various temperatures and digestion times, but is costlier (Carreon-Martinez et al. 2011). Because of this, stomach content analysis is often used in conjunction with stable isotope analysis when studying the trophic ecology of organisms (Cocheret de la Morinière et al. 2003). Prey identity can be used to corroborate isotopic results, and conversely isotopes may capture long term dietary trends or account for differential digestion rates that bias gut content analysis towards prey with shells or hard exoskeletons (Whitledge & Rabeni 1997).

Various studies have used stable isotopes to examine Arctic food webs (Hobson & Welch 1992, Hobson et al. 2002, Hobson & Ambrose 1995). While most of these studies include Arctic Cod, many have not sampled Shorthorn Sculpin, though other Sculpin species do appear (Hobson et al. 1992, Hobson & Ambrose 1995). McMeans et al. (2013) found that larger Shorthorn Sculpin (>24 cm) in southern Baffin Island had a trophic position of 4.1 and while a large percentage of the carbon they consumed was benthic in origin, there was still coupling in their diets with pelagic resources of up to 50 %. This data suggests that Shorthorn Sculpin could potentially prey on smaller Arctic Cod, or even compete with them for pelagic resources. Other studies have examined the gut contents of Shorthorn Sculpin in the Arctic but have found a wide array of prey items in different geographic locations. Cui et al. (2012) found that in the Bering Sea Shorthorn Sculpin fed predominantly on crabs and polychaetes, while Kallgren et al. (2014) sampled Shorthorn Sculpin in northern Norway and found large amounts of juvenile fishes in their stomachs. It is unclear whether these differences are due to prey diversity and availability

in each area, or foraging specialization on the part of the Sculpin. This study made use of both stable isotopes and gut content analysis in order to: i) identify taxa that made up Shorthorn Sculpin prey, ii) calculate Shorthorn Sculpin trophic position, iii) examine the proportion of trophic coupling Shorthorn Sculpin exhibit, and iv) study the amount of individual diet specialization to determine if some individuals were more likely to prey on Arctic Cod and pelagic organisms.

Acoustic Telemetry (Chapter III)

In recent years telemetry technology has advanced rapidly allowing for the tracking of many different kinds of animals, for longer periods of time, collecting data on a number of different variables (Hussey et al. 2015, Tucker et al. 2014, Kissling et al. 2014). A common method of aquatic telemetry involves tagging organisms that then transmit positional information to submerged acoustic receivers. Depending on the animal, tags can be attached externally (speared through fins, wrapped around carapace, or glued to epidermis) or implanted internally (typically into the peritoneal cavity in fishes) (Hussey et al. 2015). Acoustic transmitters come in a number of different sizes for different animals and can transmit at different frequencies depending on the model. Receivers are then set to the same frequency as the transmitters they wish to detect. The detection range of the acoustic receivers is influenced by factors such as signal frequency, and environmental conditions (Kessel et al. 2014). Information regarding detections is stored in receivers and downloaded directly from them, which means animal recapture is not an issue after initial tagging. Transmitters (i.e. tags) are most often used to indicate presence/absence or positional data, but can transmit other information such as pressure (i.e. depth), temperature and accelerometry (Espinoza et al. 2015, Landsman et al. 2015).

7

In marine environments receivers are often moored to the seafloor and deployed in arrays that have complete coverage of the study site or at least key areas (Humston et al. 2005) and animals are captured, tagged and monitored within the range of the array. Sentinel tags are often employed in studies to assess changes in signal range and the influence of environment factors on detection over time which can then be used to evaluate array performance (Kessel et al. 2014). Once the archived data is downloaded from a receiver it is processed for future analysis (i.e. the removal of false detections).

Few telemetry studies have focused on Sculpin, and the vast majority of those have used freshwater species in temperate systems. Ovidio et al. (2009) tagged Rhine Sculpin (*Cottus rhenanus*) and found that some individuals moved over 100 m cumulatively in one day and that they were more mobile than stationary day to day. Deboer et al. (2015) tracked the movements of Mottled Sculpin (*Cottus bairdii*) in a newly reconnected habitat to examine post-habitat restoration dispersal. No studies to date have used acoustic telemetry to examine Sculpin feeding ecology, although it has been used with several larger marine predators (Papastamatiou et al. 2010, Huckstadt et al. 2012). Therefore, acoustic telemetry presents a huge opportunity to add to our understanding of Shorthorn Sculpin trophic ecology in the Arctic. In this study tracking data from Shorthorn Sculpin was used to: i) quantify fish movement patterns and how they relate to foraging behaviour, ii) explore any abiotic factors that may influence these movement patterns and iii) observe if the presence of Arctic Cod has an effect on these movement patterns which could indicate a change in Shorthorn Sculpin behaviour.

The first data chapter of this thesis used stable isotope and stomach content analysis to examine Sculpin trophic ecology. Temporal changes in $\delta^{15}N$ and $\delta^{13}C$ can often be used to infer changes in prey selection and individual specialization (Cherel et al.

2007), but can also be the result of ontogenetic shifts in prey selection between different size classes of fish (Cocheret de la Morinière et al. 2003, Kallgren et al. 2014). Therefore, the analyzes in Chapter II will take into account the effects of year to year prey variation (Arctic Cod presence and absence) and Shorthorn Sculpin size (total length). If Shorthorn Sculpin are feeding on Arctic Cod, I hypothesize that their trophic positions will be higher when Arctic Cod are present because they are more enriched in ^{15}N than invertebrates (Hobson et al. 2002). I also predict that Shorthorn Sculpin δ^{13}C will be more negative when Arctic Cod are present because of the pelagic nature of Arctic Cod compared to benthic invertebrate prey, which in turn will also increase the amount of pelagic coupling exhibited by Shorthorn Sculpin. Furthermore, I predict that larger Sculpin will have higher δ^{15}N due to feeding on larger prey items. The second data chapter (III) will use acoustic telemetry to examine Sculpin movement patterns including depth and accelerometry in order to associate different movement patterns with foraging behaviour, and determine if they change in relation to environmental factors and the presence of Arctic Cod. Acoustic telemetry is often used to investigate how environmental variables can effect fish movements (Childs et al. 2008) and this includes feeding and foraging activity (McLean et al. 2014). If Shorthorn Sculpin are feeding on Arctic Cod or picking up on the same feeding event, I hypothesize that movement patterns will change in the presence of Arctic Cod. Both chapters will use different methodology to approach similar questions thereby making hypotheses testing more rigorous through the corroboration of results. The results from this study will broaden our knowledge on Shorthorn Sculpin trophic ecology as well as trophic interactions in the high Arctic.

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Chapter II: Diet Specialization and Habitat Coupling of a Common Benthic Fish,

Shorthorn Sculpin (*Myoxocephalus scorpius*) in the High Arctic

Introduction

Many organisms exhibit varying levels of diet generalization and specialization

both among and within species, which can have important implications for food web

dynamics such as affecting niche width size and stabilizing complex systems (Ceia &

Ramos 2015, Kondoh 2013). Diet specialization can be defined in a number of ways

relating to behaviour or morphological traits, however this study defines dietary

specialization as having a much narrower dietary niche than the total niche width of a

group (Newsome et al. 2009, Bolnick et al. 2002). The total niche width represents the

entire theoretical area created by the consumption of different prey items by a group of

consumers (Newsome et al. 2009). Different feeding strategies within species are

influenced by ontogenetic shifts, prey availability, or dietary specialization (Osenberg et

al. 1992, Croxall et al. 1999, Woo et al. 2008). In complex food webs, larger consumers

tend to feed on a broad range of prey and mobile consumers couple multiple trophic

pathways which is believed to lead to food web stability (Rooney 2006). The ability to

switch between multiple prey items may also be effective in dynamic environments where

prey availability changes seasonally and between years (Tamelander et al. 2006).

However, even within generalist populations individuals, irrespective of age, sex, and

body size may exhibit a high degree of specialization to specific resources (Costa et al.

2015, Bolnick et al. 2003). This specialization may be in response to competitive

exclusion when prey availability is low (Svanback & Bolnick 2007), or may be a way of

exploiting a profitable resource which conspecifics are not feeding on as readily (Costa et al. 2015).

The marine system of the high Arctic is a dynamic environment with extreme seasonal changes in sunlight and periods of ice cover and open water, which drive variation in resource abundance and availability (Walsh 2008). Upper trophic level species in these food webs are dominated by marine mammals and seabirds and potentially Greenland sharks (*Somniosus microcephalus*) (MacNeil et al. 2012) that rely heavily on a variety of fishes and macroinvertebrates (Hobson et al. 2002). One of the most widespread and abundant fish species in this ecosystem is the schooling, pelagic, Arctic Cod (*Boreogadus saida*), which feed heavily on copepods and pelagic zooplankton thus linking lower and higher trophic levels (Hobson & Welch 1992). Arctic Cod are an important prey item for marine mammals, seabirds and other fishes because of their high lipid/energy content (Hop & Gjosaeter 2013). Marine mammals also feed on other fishes, such as Sculpin spp. (*Cottidae*), albeit in lower quantities (Yurkowski et al. 2015). Unlike Arctic Cod, Sculpin spp. are not typically believed to be a preferred prey source for larger predators, however they do contribute significantly to bearded seals' (*Erignuthus burbutus*) diets (Quakenbush & Bryan 2010, Finley & Evans 1983) and are becoming more common in some species' diets due to changing environmental conditions and prey availability (Divoky & Trembaly 2012).

Sculpin are a wide-ranging benthic fish that are found across the Arctic (Johannesen et al. 2012) and Shorthorn Sculpin (*Myxocephalus scorpius*) in particular have a large distribution from temperate waters to the high Arctic (Robins & Ray 1986). The success of this species in the Arctic may be due to a generalist feeding strategy that can incorporate macroinvertebrates and other fishes into their diets (Cui et al. 2012,

Kallgren et al. 2014). Whether or not differences in diets are due to prey availability across geographic locations, or specialization between/within populations and individuals has yet to be explored. Despite the benthic occurrence of Shorthorn Sculpin, individuals can derive up to 50% of their energy intake from pelagic sources (McMeans et al. 2013), suggesting that Shorthorn Sculpin are an important habitat coupler in arctic food webs because they can exploit both benthic and pelagic resources and potentially promote food web stability (Rooney et al. 2006). Similarly, this coupling may be a result of seasonal prey variation or individual specialization with some individuals preferring benthic prey while others feed more on pelagic prey. Studies have found that large schools of Arctic Cod congregate in the high Arctic during summer months where Shorthorn Sculpin are also present (Matley et al. 2013, Kessel et al. 2015). Possibly, Shorthorn Sculpin exploit Arctic Cod like other marine predators such as beluga (*Delphinapterus leucas)*, ringed seals (*Pusa hispida*), and Arctic charr (*Salvelinus alpinus*), when readily available in order to gain a large energy payoff per prey item consumed as per optimal foraging theory (Werner & Hall 1974).

A few studies have used stable isotope analysis (δ^{13}C and δ^{15}N) to examine the trophic ecology of arctic Sculpin spp. (Hosbon & Ambrose 1995, Kallgren et al. 2014, McMeans et al. 2013) but few have used multiple analytical techniques (calculating trophic position, % reliance on phytoplankton and individual specialization) combined with stomach content analysis to explore factors that may influence changes in Sculpin diet and feeding strategies. The objective of this study was two-fold, to use stable isotopes and stomach content analysis to i) examine changes in Shorthorn Sculpin trophic position, trophic coupling, and diet specialization related to Shorthorn Sculpin size (total length), and temporal changes in the environment (interannual variation, sampled in 2012 to

16

2015), and ii) to examine whether the absence or presence of Arctic Cod influenced

Shorthorn Sculpin dietary prey contributions and degree of individual specialization

(Arctic Cod were only present in two of the four sampling years). Stable isotopes were

used to calculate trophic position, % reliance on phytoplankton (α) and individual

specialization and examined along side stomach content analysis. It was hypothesized that

if Shorthorn Sculpin were feeding on Arctic Cod then: i) Shorthorn Sculpin would exhibit

higher trophic positions when Arctic Cod were present than when absent, ii) Shorthorn

Sculpin % reliance on phytoplankton would when Arctic Cod are present due to Arctic

Cod being more pelagic than benthic invertebrates, and iii) that individual specialization

would occur when Arctic Cod presence. Stomach content analysis was used to

corroborate these results and determine which specific taxa Shorthorn Sculpin fed on

when Arctic Cod were present and absent. Establishing a link between these two

important arctic species would further our knowledge of arctic food webs and highlight

the dynamic feeding patterns of benthic fish that is largely unstudied in the Arctic.

Methods

Study Site

Resolute Bay is located on the southern end of Cornwallis Island (74.6829 N, -

94.8509 W, Figure 2.1). The bay is relatively sheltered except to the south where it opens

in to Barrow Strait. It has an average depth of ~ 8 m, with maximum depths of 30 m

occurring near the centre of the bay. The shoreline is mostly composed of glacial shale

mixed with larger rocks, and the substrate consists of silt and rock with scattered patches

of macrophytes. The bay is subject to ice coverage for the majority of the year, with ice

break up usually occurring in July and reforming in October. Due to its location in the

high Arctic, Resolute Bay experiences periods of 24h sunlight during the summer months and no sun during the winter months. The Hamlet of Resolute Bay is located at the northern end of the bay with a population of ~ 200 people. Human activity around and within the bay is noticeable with scattered debris and machinery on the shoreline and locals regularly hunting seals, beluga and Narwhal (*Monodon monoceros*). Schools of Arctic Cod have been observed in Resolute Bay and surrounding waters in multiple years (Matley et al. 2013, Kessel et al. 2015).

Sample Collection

Biological samples were collected during open water periods (August and September) from 2012-2015 following ice break up. Shorthorn Sculpin were collected each year, Arctic Cod were collected in 2012 and 2015 (only years present), and invertebrates were collected each year but primarily in 2015. Shorthorn Sculpin were captured using horizontal gill nets with gradient mesh sizes ($0.5"^2$ to $4"^2$) set in three locations each year (west bay, north bay, east bay). Gill nets were set from 4 to 12 hours depending on year and ice movements within the bay. Arctic Cod were captured by jigging with hook and line. Total length, [L_T] and weight were recorded and all fish were placed in a cooler filled with bay water and transported to the laboratory at Polar Continental Shelf Research Station. Fishes were euthanized by cervical dislocation using a pair of dissection scissors. All fishes were sampled for muscle and liver tissue and Shorthorn Sculpin sex was determined by gonads. Muscle tissue samples were dissected from the left side of each fish posterior to the dorsal fin and ending at the caudal peduncle. Stomachs were removed from the fish, injected with 95% ethanol to preserve contents and stored frozen.

Invertebrate and algae samples were collected using rock scrapes and vertical and horizontal zooplanktons tows. Rock scrapes were carried out during low tides on the western and eastern sides of the bay, and zooplankton tows were conducted from an inflatable Zodiac across the entire bay using a 300 cm net with a mesh size of 363 μm and a mouth diameter of 100 cm. Invertebrates were identified down to the smallest taxonomic group (in most cases genus). All samples were stored in -80°C freezers except during transportation, in which case they were stored on ice and maintained at – 20°C until analyzed.

Stable Isotope Analysis and Stomach Content Analysis

Liver, and muscle tissues from Shorthorn Sculpin and Arctic Cod and whole invertebrates were analyzed for $\delta^{15}N$ and $\delta^{13}C$. All frozen samples were freeze dried for 48 h and then crushed into powder using a mortar and pestle. All samples underwent lipid extraction given that lipid content is depleted in ^{13}C, and consequently lipid removal is required to standardize isotope values (Logan et al. 2008). Lipid extraction involved the addition of 0.8 ml of 2:1 chloroform:methanol to each sample, followed by 24 h in a hot water bath (30°C), centrifugation, the addition of fresh chloroform methanol, a second round of centrifugation, the extraction of chloroform methanol and a 24 h air dry period. Samples were then weighed into tin cups (400-600 μm for muscle and liver tissue, and 600-800 μm for invertebrates). All isotope samples were analyzed using a Thermo Finnigan Delta^{Plus} mass-spectrometer and an elemental analyzer at the Chemical Tracers Lab at the Great Lakes Institute for Environmental Research, University of Windsor. Triplicate samples were analyzed every 10th sample and a measurement of accuracy for $\delta^{15}N$ and $\delta^{13}C$ was recorded. Sample values were compared against known standards

19

(tilapia (internal lab standard, fish muscle), Bovine liver (NIST 1577c)) in order to measure precision and accuracy. Stable isotope values for carbon and nitrogen were reported in parts per thousand (‰) using: $\delta X = [R_{sample}/R_{standard}) - 1] \times 1,000$, where X is ^{13}C or ^{15}N and R equals $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Accuracy and precision readings were 0.09 ‰ $\pm$ 0.16 for $\delta^{15}N$ and -0.04 ‰ $\pm$ 0.08 for $\delta^{13}C$.

Stomachs from each fish were thawed out and dissected. Fish and invertebrates were identified to species and genus, respectively where possible. Prey items were grouped into one of five categories: Amphipod, Decapod, Polychaetae, Fish, and Mollusc.

Data Analysis

In order to examine variation in Shorthorn Sculpin diets, individuals were categorized by year; 2012 and 2015 years when Arctic Cod were present, and 2013 and 2014 when Arctic Cod were absent from the system. Shorthorn Sculpin were further divided by sex (except 2012 when fish were not sexed) and size class given diet can vary by body size (Kallgren et al. 2014, Cardinale 2000). Shorthorn Sculpin were divided into the following size classes: Class one: < 20 cm TL, Class two: 20 – 25 cm TL, and Class 3: > 25 cm TL, based on a previous diet shift observed for this species in the Baltic Sea (Cardinale 2000). A Chi square analysis was used to determine any sampling bias in Shorthorn Sculpin body size between years. Trophic position (TP) for Shorthorn Sculpin, Arctic Cod, and key invertebrates were calculated using $\delta^{15}N$ values (muscle for fishes, and whole bodies for invertebrates) following the scaled method of Hussey et al. (2014):

$$TP = \log(\delta^{15}N_{lim} - \delta^{15}N_{base}) - \log(\delta^{15}N_{lim} - \delta^{15}N_{TP})/K$$

where $\delta^{15}N_{base}$ is a primary consumer at TP 2 (in this case amphipods; *Onisimus sp.,* $\delta^{15}N$ = 8.36), $\delta^{15}N_{TP}$ is the $\delta^{15}N$ value of the organism of interest, and K, and $\delta^{15}N_{lim}$ are constants taken from Hussey et al. (2014).

In order to examine changes in trophic coupling, % reliance on phytoplankton was calculated following the equation of McMeans et al. (2013) which gives a percentage of energy derived from a pelagic source vs. a benthic source:

$$\alpha = (\delta^{13}C_{consumer} - [\Delta^{13}C \times (TP_{consumer} - TP_{baseline})] - \delta^{13}C_{benthic\ source} / \delta^{13}C_{pelgaic\ source} -$$
$$\delta^{13}C_{benthic\ source}) \times 100$$

where $\Delta^{13}C$ was the carbon diet tissue discrimination factor (DTDF, the isotopic ratio transmitted between source and consumer tissues) set to 0.8 for muscle tissue, $TP_{baseline}$ was 2, $TP_{consumer}$ was calculated previously in equation (1), and $\delta^{13}C_{pelgaic\ source}$ and $\delta^{13}C_{benthic\ source}$ were mean $\delta^{13}C$ values taken from *Limacina helicina* and *Onisimus sp.* respectively. A Pearson's correlation analysis was used to examine the relationships between TP, total length and % reliance on phytoplankton. Significant changes in Shorthorn Sculpin trophic position and % reliance on phytoplankton among years, and size classes were calculated via ANOVAs and Tukey post hoc tests. Prey items from Shorthorn Sculpin stomachs were analyzed via percent counts and percent frequency of occurrence (FOi). Chi square tests were used to determine if there were significant differences between the frequency of occurrence of different prey categories among years, by size class and between sexes.

The stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) in muscle and liver tissue were used to examine diet specialization of individual Shorthorn Sculpin. In order to compare muscle and liver samples, $\delta^{13}C$ and $\delta^{15}N$ values were corrected for each tissue using known DTDFs. For liver a DTDF of 0.77 for $\delta^{13}C$, and 1.67 for $\delta^{15}N$, (Caut et al. 2009), and for

muscle a DTDF of 0.8 for $\delta^{13}C$ (McMeans et al 2013) and calculated for $\delta^{15}N$ using $\Delta^{15}N$ = $\beta_0 + \beta_1 \delta^{15}N_{diet}$ (Hussey et al. 2014) where β_0 and β_1 are constants and $\delta^{15}N_{diet}$ is the $\delta^{15}N$ for each muscle sample. The difference in tissue turnover rates between tissues allows for the comparison of diet variability within the same individual over time (ie: muscle represents long term integration of diet values [months], while liver represents short term integration of diet [weeks] (Buchheister & Latour 2010)). Linear mixed-models were used to examine the effect of tissue type, sex and total length on $\delta^{13}C$ and $\delta^{15}N$ values for each year of sampling with fish ID included as a random effect. For each year, size class, and sex a mixed-model variance component analysis in the random effect (fish ID) was used to determine total variability for each group. This was done by summing the intercept variability, representing the between individual component (BIC, reflecting diet variation between individuals in a population) and the residual variability, representing the within individual component (WIC, the variation within an individual's diet over time). The summing of BIC and WIC in turn represents the total isotopic niche width (TINW, Newsome et al. 2009). Individual specialization is represented by WIC/TINW (Newsome et al. 2009) where a value of > 0.5 represents generalist feeding behaviour and a value < 0.5 represents specialized feeding behaviour (Huckstadt et al. 2012). All analyses were done using R (version 3.2.2) using the nlme package (Pinheiro et al. 2015).

Results

Across all four years 156 Shorthorn Sculpin were sampled with the most being sampled in 2013 (n=57) and the least sampled in 2014 (n=26) (Table 2.1). In total 202 Arctic Cod were sampled (2012, n=164, 2015, n=38) with Cod being absent during the sampling time in 2013 and 2014. Amphipods and molluscs were sampled in all 4 years,

the most common amphipods were *Gammarus* and *Onisimus* spp. Pteropods were abundant in 2014 and 2015 and were composed of a single species, *Limicina helicina*, and young of year Sculpin (YOY, < 4 cm, n = 25) were caught in 2015 during invertebrate rock scrapes and zooplankton tows. Table 2.1 summarizes sample size, mean values for total length, $\delta^{15}N$, $\delta^{13}C$, trophic position (TP), and % reliance on phytoplankton (α) for each year and size class of Shorthorn Sculpin, as well as Arctic Cod, juvenile Snailfish (*Liparis* sp.), YOY Sculpin, *Gammarus* spp., Scale worm spp. (*Polynoidae*), *Clione limacina* and *Limacina helicina*. Sampled organism TP from all years were plotted against % reliance on phytoplankton (Figure 2.2). The number of Shorthorn Sculpin sampled in size class one was significantly lower in 2013 than all other years (X^2 = 17.957, p < 0.05). The minimum and maximum size of Shorthorn Sculpin sampled across all years was 12.5 cm and 33.5 cm. Out of all sexed Shorthorn Sculpin, 48 were female and 54 were male. Females (25.98 cm ± 3.7) were significantly larger than males (20.80 cm ± 3.2) (Figure 2.3, t = 7.5524, df = 100).

Trophic Position, Coupling, and Stomach Contents

Shorthorn Sculpin TPs varied significantly among years and size classes (4.1 ± 0.2 to 5.1 ± 0.4, Figure 2.4), and had a significant, positive relationship with total length (r^2 = 0.7, p <0.05). Percent reliance on phytoplankton (α) was not significantly related to total length or TP (r^2 < 10%, p > 0.05). Among years Shorthorn Sculpin had a significantly higher TP in 2013 than in 2012 and within each year TP increased significantly with size class, except in 2014 where there was no significant difference between size classes (Figure 2.4). Female Shorthorn Sculpin had significantly higher TP than males (Female = 4.9 ± 0.4, Male = 4.5 ± 0.3, p < 0.05, Figure 2.3), and all size classes had significantly

higher TP than Arctic Cod (Class one = 4.2 ± 0.3, n = 54, Class two = 4.5 ± 0.3, n = 63, Class three = 5.0 ± 0.3, n = 39, Arctic Cod = 3.98 ± 0.29, n = 200, $p < 0.05$), and sampled invertebrates ($p < 0.05$). Among invertebrates, TP ranged from 1.66 (*Limacina helicin*) to 2.93 (Scale Worm spp.).

Generally, Shorthorn Sculpin TP increased with α (Figure 2.4), however there were no significant differences between α values between size classes (Figure 2.4), and females had significantly higher α than males (Figure 2.3). Between years Shorthorn Sculpin α decreased from 2012 and 2013 to 2014 and 2015 and was significantly lower in 2015 than 2013 (53% ± 0.06, and 60% ± 0.08 respectively, $p < 0.05$). The lowest Shorthorn Sculpin α was 38% and the highest was 77%. The mean Arctic Cod α (66% ± 0.07) was significantly higher than the mean Shorthorn Sculpin α (57% ± 0.08, t = 10.931). Invertebrate % reliance on phytoplankton from all years ranged from 13% (Scale Worm spp. [benthic]) 100 % (*Limacina helicina* [pelagic]).

Stomach contents found that Shorthorn Sculpin preyed heavily on amphipods (FO_i = 0 % to 65 %, *Gammarus* and *Onisimus spp.*) and molluscs (FO_i = 9 % to 58 %) (Table 2.2). Decapod prey consisted of predominantly *Mysid* and *Eualas* shrimp and polychaete prey were entirely composed of Scale Worm spp. An adult Arctic Cod was found in the stomach of a size class three Shorthorn Sculpin (2012), and small Sculpin from YOY up to 15 cm TL were also found in larger Shorthorn Sculpin stomachs from all years, however most fish remains (55 %) were unidentified due to digestion. There was a significantly higher amount of piscivorous prey in the diet of Shorthorn Sculpin in 2012 compared with the other years (FO_i = 10, X^2 = 17.164, $p < 0.05$), while variation in other prey items was not significant. Fish in size class one (< 20 cm) consumed on average more molluscs (FO_i = 34 %), while size class two (20 – 25 cm) consumed the most

amphipods on average (FO_i = 49 %, Table 2.2). Size class three fish (> 25 cm) had more

variation in stomach contents with a decrease in amphipods and molluscs and an increase

in decapod and polychaete prey. Stomach contents of size class three fish also contained a

significantly higher amount of piscivorous prey than size class one (FO_i = 9, X^2 = 4.9934,

p < 0.05). For size class two and three whole fishes were present in stomach contents (47 %

of piscivorous prey): for size class one no whole piscivorous prey were observed. The

majority of piscivorous prey identified consisted of other Sculpin, both Shorthorn and

Fourhorn (*Myoxocephalus quadricornis*). Stomach contents of size class three individuals

also contained large, whole decapods (> 8 cm) most likely *Sclerocrangon boreas*. All

sexed Shorthorn Sculpin with piscivorous prey in their stomach contents were female

barring one individual that was male.

Individual Specialization

Among years, Shorthorn Sculpin collected in 2015 had the largest niche width,

and individuals collected in 2014 had the smallest (TINW = 1.606 and 0.820 respectively).

Between size classes, size class two had the largest niche width, while size class three had

the smallest (TINW = 1.300, and 1.039). Across all years size class one had total intercept

variability (BIC) ranging from 26 – 66 %, class two: 24 – 60 %, and class three: 10 – 75 %

of total observed variability (TINW) (Table 2.3). Diet specialization occurred in all size

classes but varied by year. Size class three fish showed the most dramatic shifts from diet

generalization to diet specialization (Table 2.3). In many cases the intercept variability

accounted for a larger % of variability in TINW than the residual variability for one

isotope ($\delta^{13}C$ or $\delta^{15}N$), however this did not always lead to higher total intercept

variability and therefore did not indicate specialization (IS < 0.5). Nevertheless, when the

intercept variability of δ^{15}N (trophic/diet specialization) accounted for a higher % of variability in TINW than the residual variability this lead to specialization regardless of corresponding intercept and residual variability in δ^{13}C (habitat specialization). When grouped by sex both male and female Shorthorn Sculpin exhibited diet generalization (IS = 0.510, and IS = 0.738 respectively).

Discussion

Trophic Position, pelagic-benthic coupling and diet

This study demonstrated that high arctic Shorthorn Sculpin couple energy from benthic and pelagic sources in the form of invertebrates and fishes, feed across TPs as they grow and demonstrate flexibility in diet between years. These characteristics, in addition to being very abundant in nearshore habitats, provide strong evidence that Shorthorn Sculpin are an important tertiary consumer in Arctic marine ecosystems. Shorthorn Sculpin TPs from this study were on average much higher than those reported from previous studies on arctic Sculpin spp. (TP estimates of 3.6 for Arctic Sculpin (*Myoxocephalus scorpiodes*), 3.4 for Twohorn Sculpin (*Icelus bicornis*) (Hobson & Welch 1992), and 3.3 for Bigeye Sculpin (*Triglops nybelini*) (Hobson & Ambrose 1995)). Shorthorn Sculpin across all size classes from our study fed at higher TP than other Sculpin species in the Arctic due to the incorporation of pisciviorous prey in their diet as the aforementioned Sculpin species have diets consisting of crustaceans and other benthic invertebrates (Fedorov 1986, Coad & Resit 2004). Trophic positions of $4 - 5$ are indicative of a primary piscivores (Hussey et al. 2014) which describes a fish that feeds on other fish that in turn feed on zooplankton. These zooplanktivore fish are represented in Resolute Bay by Arctic Cod, juvenile Sculpin and to a lesser extent juvenile Snailfish

(*Liparis* spp.). Even the larger Shorthorn Sculpin in the smallest size class (< 20 cm) had TP of 4 or greater, and consistent with this, some individuals had the remains of fish in their stomach contents. Trophic position and the amount of piscivorous prey in stomach contents increased with size, this ontogenetic relationship is likely driven by increasing gape size which is correlated to increased length, common in most fish species (Foote & Brown 1998). Increased gape size would allow larger Shorthorn Sculpin to consume larger prey, including fishes and decapods such as Sculptured shrimp (*Sclerocrangon boreas*) that were only found in the largest size class (i.e., 3). Given these relationships the large size of females likely explains their significantly higher TP than males.

Year to year variation in prey availability also influenced Shorthorn Sculpin TP. In 2014 a lack of piscivorous prey found in stomach contents of individuals in size class three occurred along with a shift to an invertebrate-dominated diet and a lower TP, however Shorthorn Sculpin in size class one (i.e. the smallest) had an increase in TP in this year compared with others. The decrease in piscivorous prey in Shorthorn Sculpin stomach contents in 2014 suggested a decrease in Sculpin spp. and fishes in general within Resolute Bay that year. This would in turn mean a lack of piscivorous prey for larger Shorthorn Sculpin.

The trophic coupling observed in Shorthorn Sculpin is characteristic of higher trophic consumers (McCann & Rooney 2009, McMeans et al. 2013): and supports the TP estimates. Previous studies have found Shorthorn Sculpin α values ranging from 74% – 58% which is consistent with our results. All Sculpin preyed on amphipods and polychaetaes that would constitute a more benthic source of energy, while smaller individuals fed on pteropods and larger individuals fed on fishes which would help explain the pelagic sources of energy for all sizes of Sculpin. As well, α calculated from

liver and muscle $\delta^{13}C$ after being corrected for DTDF suggested Shorthorn Sculpin coupled energy sources across all seasons as muscle α (representing a longer time frame) was not significantly different than liver α (liver α = 58% ± 0.09, muscle α = 60% ± 0.07, p > 0.05). Year to year variation in % reliance on phytoplankton was also observed with higher α in 2012 and 2013 and lower α in 2014 and 2015. This agrees with the shift to a diet almost entirely composed of invertebrates observed in 2014, and the lower α in 2015 is likely due to a smaller proportion of pelagic prey such as pteropods and Mysid shrimp that have depleted ^{13}C (Hobson et al. 2002) found in Shorthorn Sculpin stomachs compared to 2013. Similar to TP, α was higher in females than in males and can be attributed to increased consumption of other fishes.

Shorthorn Sculpin stomach contents were similar to those reported in Dick et al. (2009) collected from south Baffin Island that found that amphipods made up the majority of prey items, but variation in prey increased with size: larger fish had a larger diversity of prey items. Cannibalism in *Cottidae* has been observed in different species and often occurs during spawning periods when large numbers of Sculpin are heavily concentrated in the littoral zone (Ruzycki & Wurtsbaugh 1999). The exact timing of spawning varies between location (Luksenburg et al. 2004) and is unknown for Resolute Bay, however several male Shorthorn Sculpin captured during this study exhibited deep red coloration with white spots on the ventral side which is characteristic of spawning fish (Fedorov 1986). This along with the presence of young of year Sculpin in 2012 and 2015 suggests that field work was conducted towards the end of the breeding season. As such, it is likely that larger individuals exploited the high abundance of conspecifics congregating in Resolute Bay as a food source.

Individual Specialization

Diet specialization in Shorthorn Sculpin decreased with size class which is attributed to larger individuals, those greater than 25 cm (size class three) being able to take advantage of a larger size-range of prey. The medium size class (two, 20 – 25 cm) had the largest total isotopic niche width suggesting that individuals in this class represent an "in between" diet strategy composed of both larger and smaller prey items, while Shorthorn Sculpin in the smallest size class (one, < 200 mm) were limited to smaller prey due to smaller gape. However, individual specialization was found in all size classes of Shorthorn Sculpin and varied widely among years. These results suggest that Shorthorn Sculpin diet was driven by prey availability rather than individual feeding strategies. This idea is illustrated by the changes in dietary specialization observed in the largest size class (three) among years. In 2012 this class exhibited slight specialization at a higher TP, while in 2014 they exhibited extreme specialization at a lower TP. Stomach contents from 2012 revealed more piscivorous prey in size class two and three than in 2014, this suggested that fishes were more abundant in 2012 for Shorthorn Sculpin to feed on and thus larger individuals specialized in piscivorous prey which was consistent with isotope data. However, in 2014 Shorthorn Sculpin in size class three exhibited the smallest recorded TINW, the highest amount of IS, and decreased TP compared to other years. This reduction in niche was apparently driven by a decrease in piscivorous prey availability that forced large individuals to feed almost exclusively on invertebrates. Conversely Shorthorn Sculpin in size class one in 2014 exhibited a larger TINW and the largest degree of generalization feeding recorded in their class which supports the idea that smaller individuals were able to exploit a larger diversity and size-range of invertebrate prey. These results, combined with trophic coupling data suggest that

Shorthorn Sculpin are, by nature strong generalists and the occurrence of diet specialization is a result of natural constraints placed on a group. These constraints are identified as either a decrease in prey availability influencing both TINW and IS of different groups of Shorthorn Sculpin, or morphological constraints (gape size) of smaller Shorthorn Sculpin that physical limits the ability to exploit a diverse array of prey items in a system. These results agree with previous studies that have suggested that habitat characteristics (including prey availability) can influence the occurrence of specialization (Newsome et al. 2015).

Effects of Arctic Cod on the diet of Shorthorn Sculpin

Shorthorn Sculpin and Arctic Cod had distinct differences in TP and α although there was some overlap in prey items consumed. Arctic Cod had a lower mean TP based on δ^{15}N than Shorthorn Sculpin of any size class, consistent with stomach contents that showed Shorthorn Sculpin fed on invertebrates and fishes higher in the food web (polynoides TP = 2.81, *Gammarus* spp. TP = 2.38, and Sculpin TP > 2.65: Table 2.1) than prey found in Arctic Cod stomach contents sampled in this study and previous ones (*Limacina helicina* TP = 1.7, *Thermisto* spp. TP = 2.6, and copepods TP = ~ 2.3: Matley et al. 2013, Hobson et al. 2002). As well, Arctic Cod were on average one TP below Shorthorn Sculpin from size class three which made them a possible prey item for larger individuals, however most Shorthorn Sculpin exhibited TP that were too high to be the result of invertebrate prey, but too low to be consistent with feeding on Arctic Cod. Cannibalization of smaller Sculpin likely explains these TP values and corroborates the juvenile Sculpin (< 10 cm) found in Shorthorn Sculpin stomachs.

Arctic Cod α was on average significantly higher than Shorthorn Sculpin (66% vs 57%), consistent with stomach contents that were almost entirely composed of pelagic pteropods (*Limacina helicina*) and pelagic amphipods (*Thermisto* spp.). These results are indicative of a more pelagic feeding strategy compared to Shorthorn Sculpin although there was a small amount of diet overlap between the two species that was most notable in the amounts of pteropods consumed by both.

Shorthorn Sculpin diet specialization had no apparent relation to the presence or absence of Arctic Cod. In 2012, large (class 3) Shorthorn Sculpin likely to prey on Cod exhibited slight specialization, and in 2015 when Cod were also present, the same group exhibited high generalization. Timing of Arctic Cod arrival may have influenced these results as Arctic Cod were not observed or captured in 2015 until the last 5 days of field work (Aug. 31[St]) whereas in 2012 Arctic Cod were sampled as early as July 30th. The presence and absence of piscivorous prey in general likely accounts for the significantly impacted degree of Shorthorn Sculpin specialization exemplified in 2014. Changes in TP, α and specialization were most significant in this year and occurred along with a decrease in piscivorous prey in Shorthorn Sculpin stomach contents. This may reflect a general decrease in fish (in particular Sculpin) abundance in Resolute Bay during this time that affected Shorthorn Sculpin feeding ecology more significantly than the presence/absence of Arcitc Cod.

Overall, these findings show that Shorthorn Sculpin undergo temporal and ontogenetic shifts in trophic ecology due to changes in prey availability and fish size. Sculpin likely reside in the bay to spawn and take advantage of the more productive littoral zone while Juvenile Sculpin remain in Resolute Bay for a period of time after hatching that may be due to increased growth rates afforded by the littoral zone and as a

refuge from predators (Ruzycki & Wurtsbaugh 1999). However, the presence of juvenile and smaller Sculpin seems to have significant impacts on the feeding ecology of Shorthorn Sculpin that exploit conspecifics and other Sculpin spp. as a food source, more so than Arctic Cod. Annual changes in Shorthorn Sculpin TP and diet specialization associated with changes in prey availability, in conjunction with apparent low predation pressure, suggests that Shorthorn Sculpin trophic ecology is regulated more-so by bottom-up effects than top-down effects, with the exception of larger individuals cannibalizing conspecifics (Frederiksen et al. 2006).

Shorthorn Sculpin from all size classes were able to derive energy from both pelagic and benthic sources which has significant implications in determining how benthic species influence food webs. Recent studies suggest that benthic organisms at lower trophic positions contribute a significant proportion of energy to food webs overall and that pelagic and benthic habitats are often treated as isolated systems when a more holistic approach would be more appropriate (Vadeboncoeur et al. 2002, Vander Zanden & Vadeboncoeur 2002). The results from this study support the idea that there is a high degree of connectance between benthic and pelagic habitats not only in lower trophic positions but in secondary/tertiary consumers as well. Benthic energy contributes significantly to the diets of pelagic fishes (Vander Zanden & Vadeboncoeur 2002) and pelagic energy is important in the diets of benthic fishes which has been presented in this study through high percentage of trophic coupling and the identification of pelagic organisms in the diet of a benthic fish. Previous studies have explored this idea in temperate systems, however this study represents one of the few conducted in Arctic systems (McMeans et al. 2013). In either case, results suggest that fishes rely heavily on energy from multiple sources across ecosystems. Future studies should examine the

amount of diet specialization and trophic coupling in different species of benthic fish in

regards to prey availability to examine previous ignored linkages in ecosystems and

species-specific dietary specialization.

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Table 2.1: Sample size, total length, δ^{13}C, δ^{15}N, Trophic Position (TP), and % reliance on phytoplankton (α) (mean $\pm$ 1 SD) for each year and size class of Sculpin and other sampled taxa collected in Resolute Bay, Nunavut. *Multiple individuals used for a single sample.

Taxa	Year	Size Class	Sample size (n)	Total Length (min, max)	δ13C	δ15N	TP	α (%)
Myoxocephalus scorpius	2012	1	15	18.13 ± 1.7 (13.3, 19.8)	-18.27 ± 0.81	14.83 ± 0.44	4.06 ± 0.2	55 ± 0.08
		2	17	21.24 ± 1.2 (20, 23.9)	-18.57 ± 0.46	15.44 ± 0.73	4.36 ± 0.36	61 ± 0.05
		3	4	27.26 ± 3.4 (25.2 ,32.6)	-18.17 ± 0.46	16.35 ± 0.5	4.83 ± 0.28	61 ± 0.06
	2013	1	9	18.3 ± 2.4 (16.9, 19.6)	-18.38 ± 0.61	15.07 ± 0.45	4.17 ± 0.2	57 ± 0.07
		2	23	22.6 ± 1.1 (20.1, 25)	-18.18 ± 0.74	15.95 ± 0.62	4.61 ± 0.33	59 ± 0.09
		3	22	28 ± 2.7 (25.2, 33.5)	-18.27 ± 0.55	16.71 ± 0.62	5.05 ± 0.38	64 ± 0.07
	2014	1	11	17.87 ± 1.9 (14.2, 19.8)	-17.78 ± 0.42	16 ± 0.46	4.64 ± 0.25	56 ± 0.05
		2	9	22.38 ± 1.1 (20.4, 25)	-17.56 ± 0.42	16.05 ± 0.49	4.66 ± 0.28	53 ± 0.04
		3	6	26.12 ± 0.9 (25.5, 27.8)	-18.06 ± 0.77	16.17 ± 0.36	4.72 ± 0.2	58 ± 0.08
	2015	1	19	15.91 ± 2.2 (12.5, 18.9)	-17.76 ± 0.52	15.12 ± 0.71	4.2 ± 0.33	51 ± 0.06
		2	14	22.95 ± 1.3 (20.4, 24.5)	-17.78 ± 0.51	15.87 ± 0.28	4.56 ± 0.14	54 ± 0.05
		3	7	28.37 ± 2.2 (26, 32.1)	-17.6 ± 0.57	16.57 ± 0.46	4.96 ± 0.28	56 ± 0.07
Boregadus saida			202		-19.36 ± 0.68	14.64 ± 0.67	3.98 ± 0.29	66 ± 0.07
Juvenile Liparis sp.			5		-17.37 ± 0.44	13.08 ± 0.42	3.36 ± 0.15	40 ± 0.05
YOY Sculpin			5*		-19.31 ± 0.45	10.88 ± 0.17	2.65 ± 0.05	54 ± 0.04
Polynoidae spp.			3*		-16.51 ± 1.3	11.41 ± 0.38	2.81 ± 0.11	26 ± 0.13
Gammarus spp.			10*		-17.26 ± 0.63	9.87 ± 0.45	2.38 ± 0.12	30 ± 0.06
Limacina helicina			6*		-24.17 ± 0.57	7.02 ± 0.19	1.7 ± 0.04	97 ± 06
Clione limacina			1*		-20.77 ± 0	10.7 ± 0	2.6 ± 0	69 ± 0

Table 2.2: Percent counts and percent frequency of occurrence (FO$_i$) for Sculpin prey items from each year and size class from Resolute Bay Nunavut.

Year	Size Class	Sample size (n)	Amphipod N %, FOi (%)	Polychaetes N %, FOi (%)	Decapods N %, FOi (%)	Fish N %, FOi (%)	Mollusc N %, FOi (%)
2012	1	22	62.8, 32	0,0	17.1, 18	5.70, 9.0	14.3, 9.0
	2	20	54.3, 35	5.60, 10	5.60, 10	13.9, 20	20.0, 20
	3	4	0,0	0,0	0,0	75.0, 75	25.0, 25
2013	1	10	53.1, 60	3.12, 10	9.38, 20	0,0	34.4, 30
	2	23	95.7, 65	1.16, 4	1.94, 17	0.004, 4.0	0.008, 17
	3	24	68.2, 29	19.1, 21	3.82, 17	1.91, 12	7.01, 8.0
2014	1	12	21.3, 33	2.13, 8.0	10.6, 25	0, 0	66.0, 58
	2	12	44.3, 50	9.84, 25	9.84, 33	0, 0	32.8, 42
	3	6	57.4, 33	0, 0	4.25, 17	2.13, 17	36.2, 50
2015	1	45	30.8, 40	7.05, 16	0.006, 20	1.28, 40	60.2, 38
	2	35	49.0, 46	4.00, 8.0	1.00, 3.0	2.00, 6.0	44.0, 31
	3	15	21.9, 33	6.25, 7.0	9.38, 20	6.25, 13	56.2, 33

Table 2.3: Individual specialization for each Sculpin size class within each year collected in Resolute Bay Nunavut. The Between Individual Component (BIC) represents Intercept variation, and the Within Individual Component (WIC) represents Residual variation. Values are shown for both carbon and nitrogen and then totaled to calculate Total Isotopic Niche Width (TINW) and Individual Specialization (IS). Conditional r^2 values are also included for each element. A group is considered to be more specialist than generalist when IS < 0.05 or when the total BIC is greater than total WIC. A value of "0" indicates a value of < 0.0001.

Year	Size Class	C			N			Total			
		BIC Variance	WIC Variance	Conditional r2	BIC Variance	WIC Variance	Conditional r2	BIC Variance	WIC Variance	TINW	IS (WIC/TNW)
2012	1	0.21	0.25	0.45	0.09	0.19	0.62	0.30	0.45	0.75	0.60
	2	0.18	0.06	0.80	0.36	0.40	0.69	0.54	0.46	1.00	0.46
	3	0	0.13	0.72	0.49	0.27	0.87	0.49	0.40	0.89	0.45
2013	1	0.10	0.11	0.62	0.23	0.17	0.68	0.34	0.28	0.62	0.45
	2	0.48	0.15	0.77	0.18	0.30	0.47	0.66	0.44	1.10	0.40
	3	0.18	0.12	0.72	0.12	0.35	0.73	0.30	0.47	0.77	0.61
2014	1	0	0.35	0.03	0.27	0.40	0.71	0.27	0.74	1.01	0.74
	2	0.28	0.32	0.49	0.09	0.23	0.85	0.37	0.56	0.93	0.60
	3	0.18	0.03	0.87	0.12	0.07	0.96	0.31	0.10	0.41	0.25
2015	1	0.41	0.46	0.53	0.68	0.11	0.89	1.09	0.57	1.66	0.34
	2	0.15	0.60	0.39	0.18	0.42	0.55	0.32	1.02	1.34	0.76
	3	0	1.27	0.41	0.17	0.21	0.90	0.17	1.48	1.65	0.90
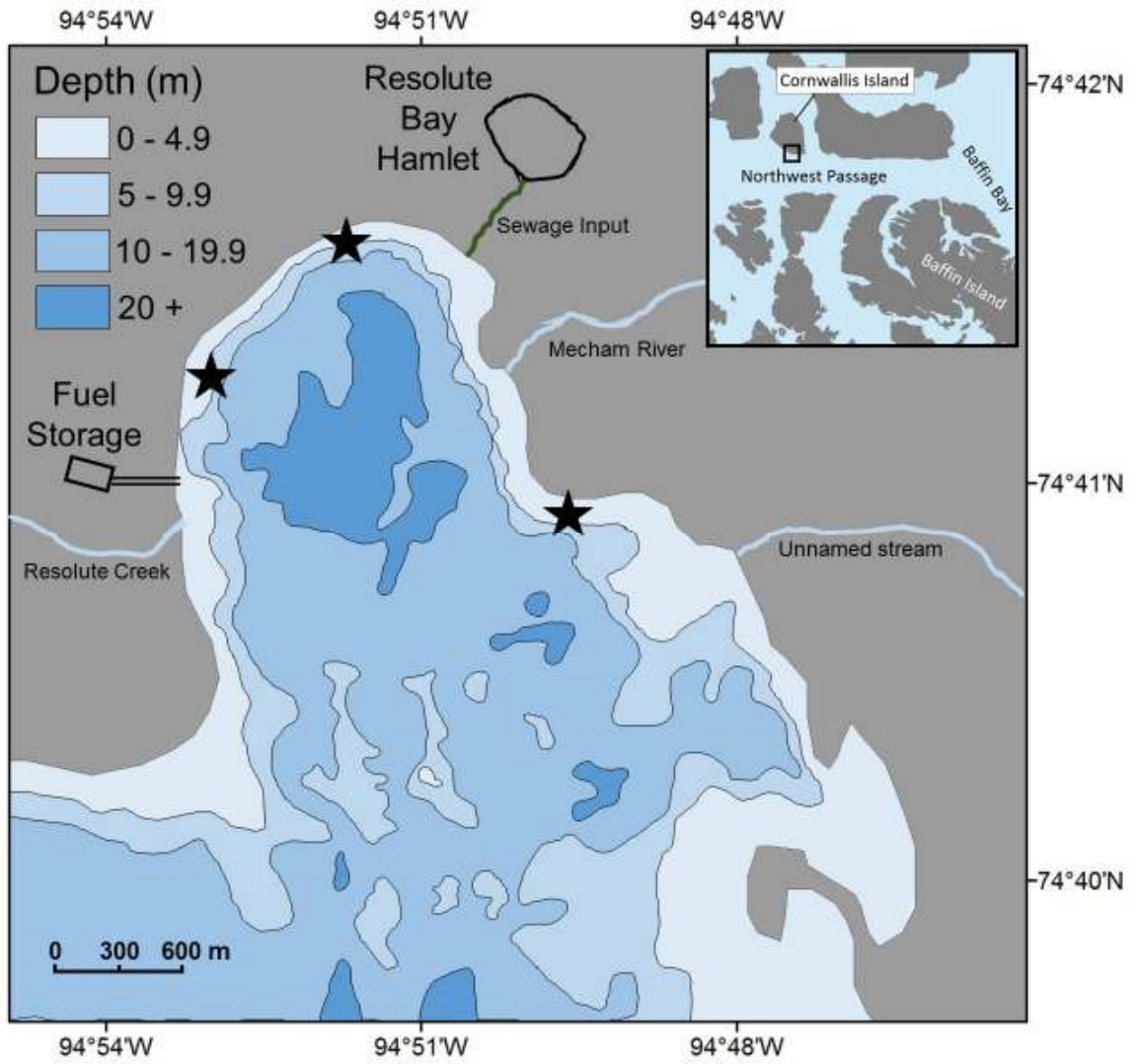
Figure 2.1: Map of study site, Resolute Bay, Nunavut. Sculpin sampling sites within Resolute Bay represented by stars. Inset showing surrounding Arctic waters with Resolute Bay indicated by arrow.
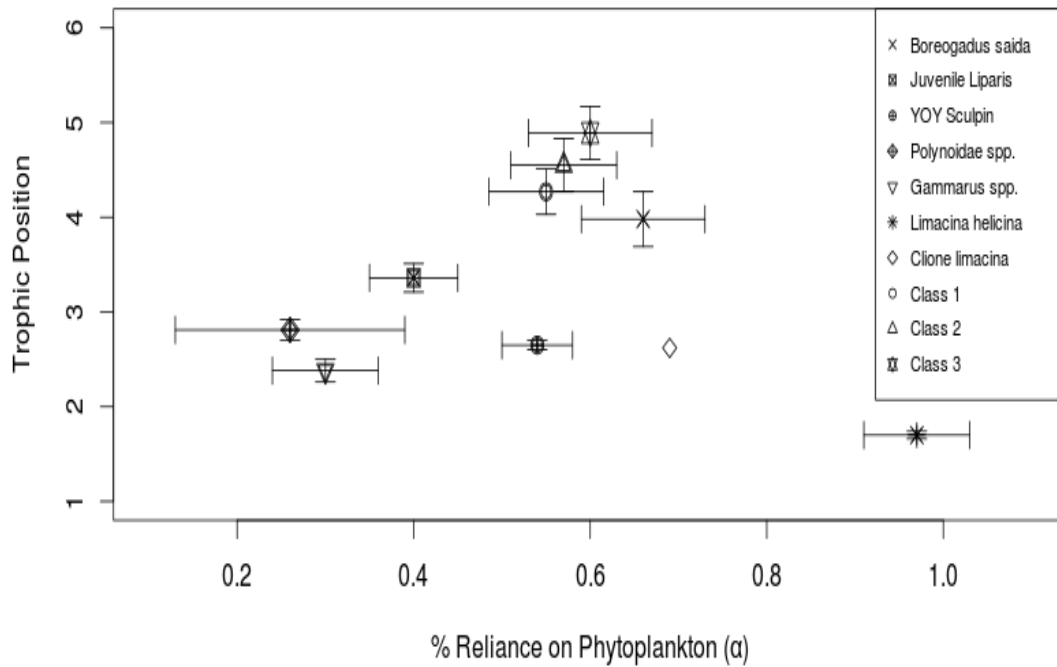
Figure 2.2: Mean trophic position plotted against % reliance on phytoplankton (as a proportion of total, eg: 0.4 = 40 %) with standard deviation for Sculpin size classes (1,2,3) from all years as well as Cod (*Boreogadus saida*), juvenile fish (Snailfish: *Liparis*), YOY Sculpin, and invertebrates collected from all 4 years (see legend). *Clione limacina* consisted of one sample with multiple individuals.
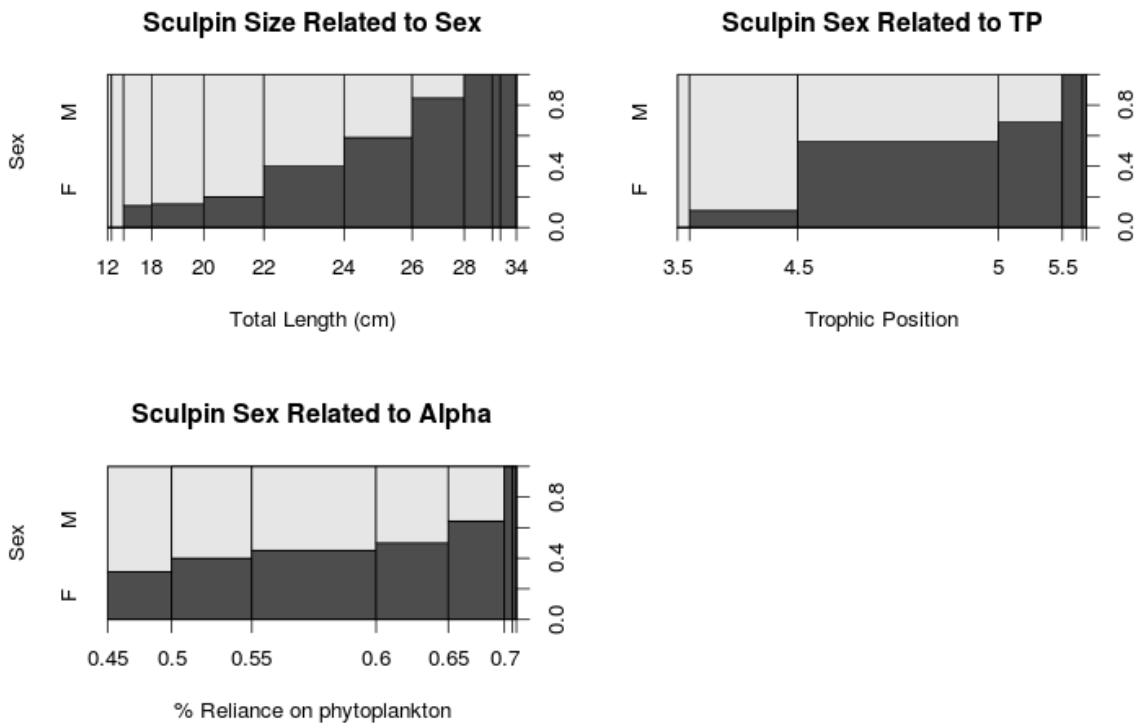
Figure 2.3: Total length, Trophic Position and % reliance on phytoplankton for male and female Sculpin. Males are represented by light grey colouration, females represented by dark grey. Secondary y axis depicts ratios for each metric.
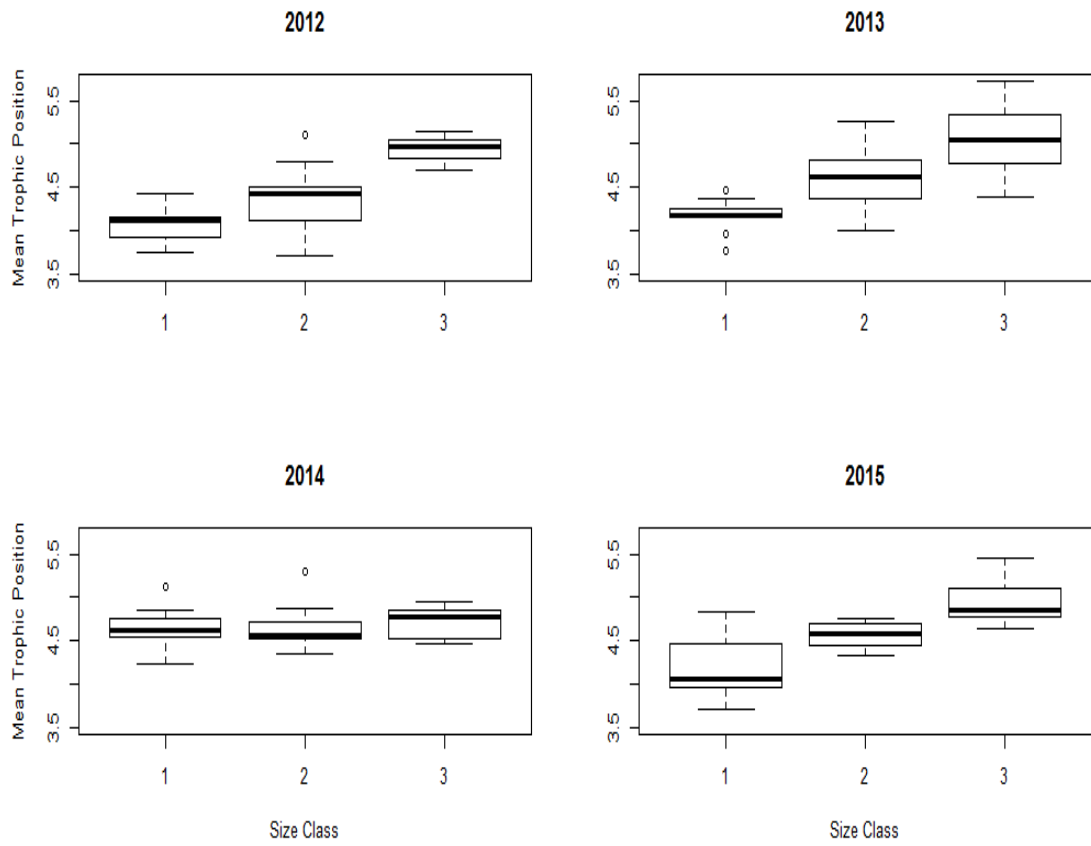
Figure 2.4: Mean Trophic positions with 95% error bars for each Sculpin size class of each year. Open circles represent outliers.
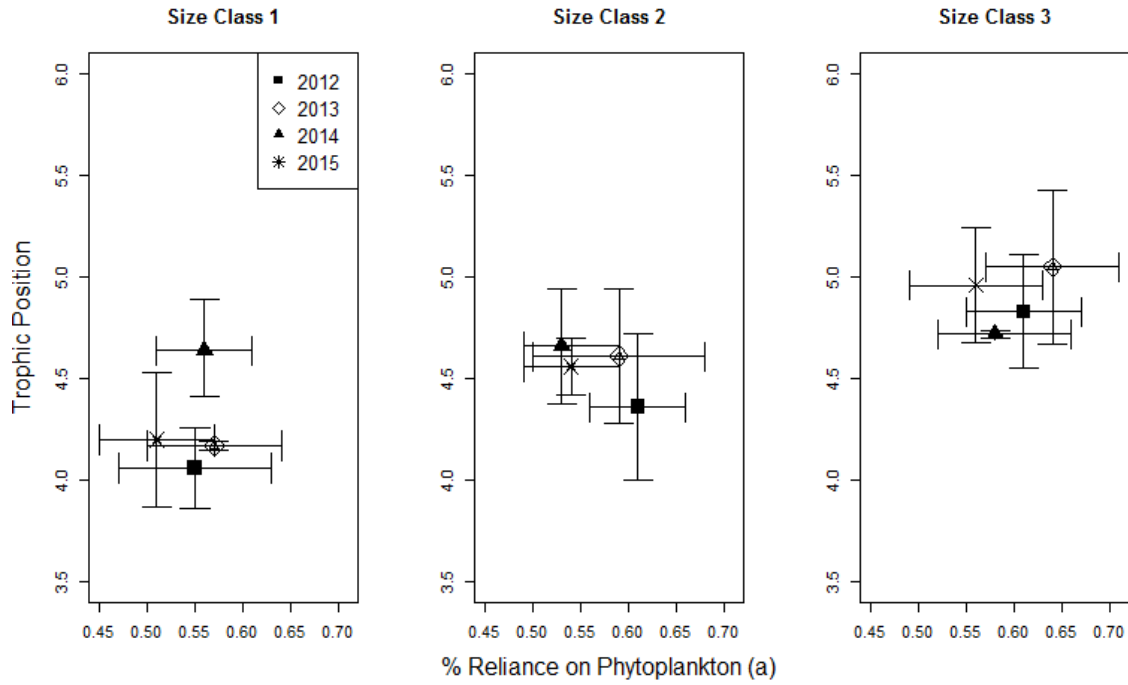
Figure 2.5: Mean Trophic position plotted against % reliance on phytoplankton (α) with standard deviation bars for each Sculpin size class, each shape corresponds to a specific year (see legend).

Chapter III: Movement Patterns and Foraging Behaviour of a Common Benthic Fish

During Open Water Periods in the High Arctic

Introduction

Acoustic telemetry has become more commonly used in assessing aquatic

organism spatial ecology, with advancements in technology allowing for employment on

a wide variety of aquatic organisms ranging in size and global distribution (Hussey et al.

2015). Passive acoustic tracking can be used for the collection of large amounts of data

over long-term periods (up to 10 years) decreasing the relative amount of effort in terms

of field time (Hussey et al. 2015, Heupel et al. 2006). Multiple studies have made use of

the Vemco Positioning System (VPS) which relies on data derived from acoustic tracking

to investigate fine scale movements and habitat use of tagged individuals (Espinoza et al.

2011, Farrugia et al. 2011, Furey et al. 2013, Andrews et al. 2011). Analyzing movement

patterns of aquatic organisms is often used in unison with spatial and temporal

information to discern different types of behaviours associated with foraging and habitat

preference (Cunjak et al. 2005, Brill et al. 2005), and can also be used to examine inter-

species interactions in the form of predator-prey relationships (Meyer et al. 2010,

McMahan et al. 2013). Integrating both habitat preferences and species' interactions can

determine where and when individuals are feeding, and potentially which species they

feed on (Fitzpatrick et al. 2012). Acoustic tracking can also elucidate foraging behaviours

of animals that are understudied, yet potentially significant in the food web of a

community (Vaudo 2011). Many studies that make use of acoustic telemetry to study

trophic ecology have focused on top predators because they are thought to act as food

web stabilizers (Paine 1966) and would therefore be critical to an ecosystem

(Papastamatiou et al. 2010, Heithaus et al. 2002). However, our knowledge of foraging

behaviour and species' interactions of common consumers that can couple multiple

energy pathways is lacking in many ecosystems including the high Arctic. These

consumers are important for the system because they also have the potential to stabilize or

destabilize food webs via predation pressure (McCann et al. 2005).

The marine ecosystems of the high Arctic are dynamic, with large seasonal

changes in light and temperature, which in turn influences the growth and abundance of

primary producers (Walsh 2008). These systems support many marine mammals and sea

bird species which in turn feed on fishes and macroinvertebrates (Hobson et al. 2002).

Arctic Cod (*Boreogadus saida*) are a particularly important fish species in these systems

as they link lower and upper trophic levels and represent a key prey item for larger

consumers due to their abundance, high latitudinal distribution and high energy content

(Hobson & Welch 1992, Hop & Gjosaeter 2013). Another abundant fish species found in

these foods webs is the Shorthorn Sculpin (*Myoxocephalus scorpius*) and although they

do not appear to be as favourable a prey item as Arctic Cod for larger consumers

(Yurkowski et al. 2015, Quakenbush & Bryan 2010) both species' distributions heavily

overlap, especially during open water periods where they congregate in nearshore areas

(Matley et al. 2013). Shorthorn Sculpin are a benthic species of fish that can grow up to

30 cm on average with a wide ranging distribution from temperate to Arctic waters

(Robins & Ray 1986) with diets consisting mainly of benthic invertebrates (Cui et al.

2012). However, some studies have identified juvenile and adult fishes in Shorthorn

Sculpin stomachs (Kallgren et al. 2014, Cardinale et al. 2000, Landry et al. 2016) and

other studies using stable isotope analysis have found that these fish couple benthic and

pelagic energy pathways (McMeans et al. 2013, Landry et al. 2016). One study conducted

on the southern end of Baffin Island found that Arctic Cod made up 1% of prey items

found in the gut contents of Shorthorn Sculpin (Dick et al. 2009), therefore it is possible that Arctic Cod represent an important prey item for Shorthorn Sculpin at higher latitudes.

There are few studies that have made use of telemetry in studying Sculpin movements (Ovidio et al. 2009, Deboer et al. 2015, Broell et al. 2013) and none have used telemetry to examine the foraging ecology of any Sculpin species. Therefore, Shorthorn Sculpin in the Arctic represent an abundant consumer that can be used to test acoustic telemetry to evaluate foraging behaviour based on movement patterns. This approach is non lethal and can be used to collect data that is more temporally sensitive than stable isotope analysis or stomach content analysis which are influenced heavily by isotopic turnover rates (Buchheister & Latour 2010) or what the individual had recently eaten relative to time of capture. Telemetry data from tagged individuals can be used to make inferences regarding when and where they feed and potentially what prey they feeding on over a period of multiple months based on movement patterns. As well, changes in feeding behaviour can be analyzed at a high resolution (by hour) relative to the incorporation of stable isotope signatures from prey items (by week, or month) (Buchheister & Latour 2010). The objective of this study was to use acoustic telemetry to distinguish between movement patterns of Shorthorn Sculpin and identify those associated with foraging, examine how these movement patterns change in relation to environmental variables, and determine if the presence of Arctic Cod influences Shorthorn Sculpin movement patterns and feeding behaviour and could be a potential prey item. It is hypothesized that Shorthorn Sculpin movement patterns will reflect different behaviours that change with relation to changes in abiotic factors, and that the presence of Arctic Cod will elicit foraging behaviour in Shorthorn Sculpin if they are in fact a prey item.

Methods

Study Site

Field work was conducted in Resolute bay from 30 July to 30 August 2012 after ice break up. Resolute bay (74.6829, -94.8509) is located at the south side of Cornwallis Island, Nunavut, Canada and opens at the south end into Barrow Strait (Figure 3.1). The Hamlet of Resolute is located at the north end of the bay with a fuelling station located on the west side of the bay. The surrounding area is composed of gravel, rock and glacial shale with sparse amounts of macrophytes in the intertidal zones. The maximum depth of the bay is ~ 30 m towards the head and near the centre. There is a large underwater shoal that runs parallel and spans the entrance of the bay creating a shallower area around it's perimeter including the entrance of the bay.

Fish Tagging

Shorthorn Sculpin and Arctic Cod were both collected from 26 July to 4 August 2012. Sculpin were caught by gill net (gradient mesh sizes $0.5"^2$ to $4"^2$) set in three locations (west bay, north bay, east bay, Figure 3.1). Arctic Cod were caught by jigging with hook and line from four separate locations in the bay (one from the north end, two from the west end, and one from the mouth, Figure 3.1). After capture the fish were then placed in holding tanks filled with bay water and either transported back to the lab at the Polar Continental Self Project (PCSP) research lab or to a tagging station set up on the shore of the bay (depending on weather conditions). Fish were anaesthetized using MS222 (4 g: 20 l of sea water), and once non-responsive (2 – 5 minutes) fork length (FL), total length (TL) and weight (WT) measurements were taken. Fish were then placed in a

sponge cradle for surgical insertion of the acoustic transmitter (i.e. tag), with continuous

gills irrigation with sea water from a squeeze bottle. A small anterior incision (~ 8 mm)

was made into the peritoneal cavity of the fish, the transmitter was then inserted into the

cavity (Vemco V6 transmitter for Arctic Cod, Vemco V9AP transmitter for Shorthorn

Sculpin) and the incision was then sewn closed using two Vicryl sutures (Ethicon

VCP423, 3-0 FS-2 cutting). All materials including transmitters were sterilized using 10%

betadine prior to surgery. Surgeries ranged from 2 to 4 minutes in duration, and upon

completion fish were placed into recovery tanks and allowed to recuperate for ~ 1 h. All

fish were released en masse back into their original capture sites in the bay, and were

observed swimming away.

Acoustic Telemetry

Data collected between 5 August and 23 October 2012 was used for this study

which included the majority of open water period in Resolute Bay. Both species of tagged

fish were tracked using an acoustic array composed of 59 listening stations (Figure 3.1).

Stations consisted of a rock anchor attached to an ORE Port ME acoustic release in turn

attached to a float to keep the station vertical. Vemco VR2W acoustic receivers (180 kHz

for Arctic Cod, 69 kHz for Shorthorn Sculpin) were attached to a V cup above each float.

Coded transmitters identified presence from tagged fish as well as pressure and

accelerometry (V9AP only) data and transmitted it to listening stations in the bay such

that each individual fish had a unique ID associated with its detections. The listening

stations were deployed at the beginning of the study period and left in the water until the

following summer when they were retrieved and the data was downloaded. Nineteen V9-

sync tags and 17 V6-sync tags were deployed across the array in fixed locations to assess

array performance (for a full description of receiver range testing and detection rates see: Kessel et al. 2015) and to calibrate the locations of listening stations and measure the effects of positioning error. This calibration data was used for Vemco Positioning System (VPS) processing that uses the detections of groups of three or more receivers to triangulate the positions of tagged individuals based on the difference in time it takes for detections to reach each receiver (Lowe 2011).

Identifying Sculpin Movement Patterns

Shorthorn Sculpin detections that had a horizontal positioning error (HPE) of > 37 were removed from the dataset. The HPE represents the radius of estimated circular error related to each VPS position (Espinoza et al. 2011) and this filtering allowed for a relatively small amount of positioning error without decreasing the dataset significantly (22,687 detections in total, 1814 detections filtered and removed). Shorthorn Sculpin trajectories from 5 August to 23 October 2012 were analyzed using the ADEhabitatLT packing (Calenge 2011) in R (version 3.2.4). This package broke up individual trajectories into "bursts" or segments based on time between detections (30 min), for example, if an individual went undetected for more than 30 min the current burst ended and a new one began when they were detected once again. A time frame of 30 min was chosen because it allowed for the creation of a large number of bursts while still maintaining a high enough resolution to capture changes in behaviour between subsequent bursts. Only bursts with 5 or more relocations (detections) were used in the analysis (1158 bursts in total, 373 filtered and removed). In order to distinguish between different movement patterns bursts were characterized using the following variables: sum of total distance, mean turn angle (relative angle), mean bearing (absolute angle), mean

depth (derived from pressure censors in the V9AP tags), mean rate of movement, mean acceleration (taken from V9AP accelerometry data) and Linearity ratio that was calculated by dividing the distance between relocations by the total distance where a value of 1 indicates a more linear or straight path and a value approaching 0 indicates a less linear path (Heupel et al. 2012). A correlation plot was produced using the R package Corrplot (Wei 2012) and variables associated with each burst that had a correlation of > 60% were removed. A within sum of squares analysis was used to help determine the number of clusters that bursts could be grouped into and the package Cluster (Maechler et al. 2002) was used to perform a K means cluster analysis that assigned bursts to identified clusters that represented different movement patterns. A multivariate analysis of variance (MANOVA) was used to distinguish between significant differences in the variables associated with each cluster/movement pattern (significance level $p < 0.05$).

Environmental Variables

Environmental measurements were collected by an oceanographic station (Satlantic STOR-X and a Seabirds Electronics 37-SIP CTD) submerged at the centre of the bay: dissolved oxygen (%), salinity (PSU), and water temperature (°C). Daily sea ice cover (%) in the bay was obtained from the Canadian Ice Services archives (ec.gc.ca/glaces-ice), and daily photo period (h) taken from the time and date archives (time-anddate.com). The proportions of each Shorthorn Sculpin movement pattern for each day of the study period were normalized by removing zeros (where no detections occurred for a particular movement pattern) and ones (where a particular movement pattern had a proportion of 100%). To examine changes in behaviour associated with abiotic changes these movement pattern proportions were then used in a multivaraite

multiple regression against daily changes in environmental variables (photo period (h), ice cover (%), and water temperature (C)).

Affect of Arctic Cod Presence

A previous study had shown that Arctic Cod distribution in Resolute Bay is not uniform during open water periods and that large schools spend the majority of their time in the northern head of the bay (Kessel et al. 2015). It is possible that Arctic Cod presence could influence Shorthorn Sculpin behaviour in this northern area but not in other areas of the bay. To accommodate for this Shorthorn Sculpin movement patterns across the bay were separated into three different zones with movement patterns between zones removed to ensure a larger degree of isolation. Each fish detection was allocated to a zone based on which listening station, or groups of receivers it was detected by (Table 3.2). Zone 1 was located in the northern head of the bay and was associated with high Arctic Cod abundance while zone 2 was on the western opening of the bay and zone 3 on the eastern opening and were designated areas of low Arctic Cod abundance. The relative abundance of both species was calculated in each zone using raw detections for Arctic Cod and VPS for Shorthorn Sculpin by dividing the number of detections per hour by the number of unique individuals detected per hour. To test the effects of Arctic Cod presence on Shorthorn Sculpin movement patterns a binomial regression (1 = movement pattern was displayed, 0 = movement pattern was not displayed) for each movement pattern in each zone was conducted against relative Arctic Cod abundance by the hour.

Results

In total 25 Shorthorn Sculpin were tagged and 17 were used in the analysis of movement patterns (due to 8 having < 3 bursts per individual), and 85 Arctic Cod were tagged and 77 successfully monitored throughout the study period. The TL of Shorthorn Sculpin used in the analysis ranged from 23.0 cm to 36.0 (27.8 ± 0.6, mean ± SE) and the FL of Arctic Cod ranged from 15.0 cm to 26.1 cm (19.1 ± 0.2). Both species were detected everyday over the course of the study period with the exception of Sept. 16, 17, 19, 22, 24, 28, and Oct. 2, 3, 13, 16, 18, and 20 for Shorthorn Sculpin and Oct 2 and 3 for Arctic Cod. Results from detection range testing indicated that the receivers had a minimum effective range of 10 m and a maximum effective range of 130 m during the study period (see: Kessel et al. 2015 for full details).

Sculpin Movement Patterns

Shorthorn Sculpin trajectories were broken down in to a total of 785 bursts, ranging from 7 to 112 per individual. Three unique movement patterns were identified represented by the three different clusters that bursts were grouped into (Figure 3.2). All individuals displayed all three movement patterns over the course of the study however movement pattern two occurred the most often and movement pattern three occurred the least. One or more variables were significantly different between movement patterns (Table 3.1): movement pattern 1 (MP1) had a significantly higher sum of distance (187 ± 74.0 m) and mean rate of movement (0.03 ± 0.03 m s^{-1}) than movement pattern 2 (MP2) (36.9 ± 23.3 m, 0.01 ± 0.01 m s^{-1} respectively) and linearity ratio and mean depth did not differ significantly between MP1 and MP2. Movement pattern 3 (MP3) had a significantly higher sum of distance (784 ± 39.2 m), rate of movement (0.06 ± 0.06 m s^{-1}), occurred in significantly deeper water (16.8 ± 5.22) and had a significantly higher

linearity ratio (0.54 ± 0.34) than both MP1 and MP2. Spatially, MP1 and MP2 predominantly occurred around the edges of Resolute bay in shallower waters, especially in the northern head of the bay and the east and west opening of the bay, whereas MP3 mainly occurred near the centre of the bay in deeper waters (Figure 3.3).

Environmental Variables

The multivariate multiple regression revealed that the proportion of MP2 per day decreased over the course of the study and had a significant positive relation to photo period ($p < 0.001$, $R^2 = 0.47$). Conversely, MP3 increased towards the end of the study period and had a significantly negative relation to photoperiod and a significantly positive relation to ice cover ($p < 0.01$, $R^2 = 0.44$). All movement patterns occurred during daylight and periods of darkness with no differences between patterns, however as the amount of daylight per day decreased the proportion of total Shorthorn Sculpin movement patterns switched from occurring during daylight to occurring during periods of darkness (Figure 3.4).

Effect of Arctic Cod

Zone 1 had the highest number of unique Arctic Cod detected (77) per hour, highest relative Arctic Cod abundance (12.3) and the most hours sampled when both Shorthorn Sculpin and Arctic Cod were present at the same time (494 hrs) compared to the two other zones (Table 3.2). This agrees with the previous study that found Arctic Cod prefer the northern head of Resolute bay during open water periods (Kessel et al. 2015). Sculpin Movement patterns in zones 2 and 3 showed no significant relation to the relative abundance of Arctic Cod, however in zone 1 MP2 increased significantly (z value

= 2.152, p <0.05) and MP1 decreased significantly (z value = -4.294, p <0.001) with an increase in the relative abundance of Arctic Cod per hour.

Discussion

The three Shorthorn Sculpin movement patterns described in this study were similar to those found in McLean et al. 2014 for Atlantic Sturgeon (*Acipenser oxyrhynchu*s) where patterns represented: a searching for prey behaviour, feeding in a prey patch behaviour, and longer in transit movements. The movement patterns found in this study may represent similar behaviours due to movement patterns from both studies sharing several characteristics (higher linearity ratios associated with MP3, a decrease in mean ROM and distance moved between MP1 and MP2). Previous studies examining fish movement patterns have found that feeding behaviour is associated with slower movement speeds and less linear trajectories (Heerhartz & Toft 2015), which supports the idea that MP1 and MP2 from this study represent foraging behaviour as they had a significantly lower linearity ratio and covered less than a quarter of the distance than the third movement pattern. A decrease in swimming speed while foraging is often associated with an individual encountering a suitable prey patch (Coughlin et al. 1992). Mottled Sculpin have been found to associate with patches of high prey abundance (Petty & Grossman 1996) and in the case of Shorthorn Sculpin, MP1 with a higher sum of distance and mean rate of movement may represent individuals covering more ground searching for productive areas, whereas MP2 potentially represents feeding behaviour exhibited when a prey patch is encountered. Although McLean et al. (2014) found the linearity ratio between searching and feeding patterns varied significantly (searching patterns being less linear) in Atlantic Sturgeon there were no significant differences in linearity ratio between

MP1 and MP2 in this study. This could relate to differences in feeding behaviour between the two species. Sturgeon use olfactory cues to locate prey patches, winding back and forth over a patch using their barbells to detect prey (Kasumyan 1999), while Sculpin species rely heavily on their lateral lines to locate prey (Hoekstra & Janssen 1985). Some Sculpin species are considered ambush predators that move less in the presence of prey in order to increase sensitivity of prey movements and orient themselves using neuromast cells (Janssen et al. 1999) and Sculpin have been observed in laboratory studies using quick feeding strikes from sedentary positions to capture prey (Broell et al. 2013). The lack of significant difference between linearity ratios in MP1 and MP2 in Shorthorn Sculpin may be related to a "sit and wait" approach adopted when a prey patch is encountered, using small scale movements to reorient their positions to coincide with prey movements within a patch and then striking when a prey item comes within a certain distance. Movement pattern 3 potentially represents large in transit movements used by individuals when traversing across deeper, less prey-rich portions of the bay due to higher sum of distance, rate of movement, and linearity ratio observed which is consistent with results from McLean et al. (2014).

The vast majority of detections of Shorthorn Sculpin were associated with MP1 and MP2 (10160 in total) compared to detections associated with MP3 (3096). Movement patterns 1 and 2 occurred most often in nearshore areas associated with large numbers of invertebrates and cobble and gravel substrates (field observations, Landry et al. 2016). These types of substrates have been previously linked to surfaces benthic fish readily on (Greenberg 1991). There were three main areas around the perimeter of Resolute Bay where movement patterns 1 and 2 occurred the most (Figure 3.3): the northern, the east and west opening of the bay all of which consisted of shallower areas of 5 to 10 m that

dropped off into areas up to 20 m in depth. These three areas potentially represent foraging "hot spots" as the area located in the north is subject to raw sewage input from the Hamlet of Resolute increasing the local nutrient input and productivity, and the areas near the opening of the bay may be subject to upwelling effects that feed nutrients into the mouth of the bay (Millan-nunez et al. 1982) which in turn attract prey like macroinvertebrates. Field observations in Resolute bay found large numbers of *Gammarus* spp., *Onisimus* spp., and various molluscs in shallow areas, and unpublished data along with other studies (Dick et al. 2009, Landry et al. 2016) has found that amphipods make up the majority of Shorthorn Sculpin prey in the Canadian Arctic. The observed distribution of these prey items heavily overlapped with MP1 and MP2, therefore increased prey abundance may explain the large amount of Shorthorn Sculpin detections in these areas.

Environmental Effects

Shorthorn Sculpin exhibited a higher proportion of MP2 during the start of the study period (August) than towards the end (October) which was related to changes in photoperiod and ice cover. The decrease in MP2 and the increase in MP3 as photoperiod declined and ice cover increased suggests that in Resolute Bay, Shorthorn Sculpin were moving farther distances as time went on. Marine productivity would be in decline as sunlight and temperature decreased (Dalpadado et al. 2014) and ice formation began. Movement pattern 2 decreased sharply at 30 % ice coverage in the bay at the beginning of October and MP3 sharply increased. This same pattern occurred again at the end of October when ice coverage reached ~ 80 %. Many species of arctic amphipods have been found in association with sea ice that affords them protection from predators (Gradinger

& Bluhm 2004). Nearshore ice formation in Resolute Bay may act as a refuge for amphipods from Sculpin predation as they can hide within small cracks and crevices and optical contrast is low between small amphipods and sea ice impairing the use of vision for catching prey (Gradinger & Bluhm 2004) meaning lateral line detection would be the only suitable means for Sculpin to detect prey. The added cover for amphipods and other invertebrate prey along with declines of primary production in the bay may decrease Shorthorn Sculpin feeding efficiency and drive them to deeper waters, cover or cover more area in search of prey which is consistent with an increase in MP3.

Changes in the proportion of movement patterns during this time period may also be related to changes in the densities of conspecifics in the bay. Adult Mottled Sculpin have shown high amounts of territoriality year round (Petty and Grossman 2007) and in Resolute Bay the number of tagged individuals across the study period declined from 25 (beginning of August) to 8 (beginning of October). This decrease in the number of tagged individuals may reflect a population-wide decrease in Shorthorn Sculpin over the course of the study period. If this was the case, any individuals that remained in the bay would be able to expand their home ranges and make movements that cover longer distances. This would also explain the decline in MP2 (which had the smallest sum distance) and the increase in MP3 (highest sum of distance).

At the beginning of August in Resolute Bay there are periods of 24 h daylight, which slowly decline over the course of the month. Studies have shown that fish, including Sculpin species, in sub-Artic to high Arctic areas either desynchronize their circadian rhythms when there is a lack of environmental ques, or undergo temporal niche switching (altering temporal behaviour without altering circadian clock) depending on the time of year (Andreasson 1973, Williams et al. 2015). Patterns of temporal activity and

circadian de/synchronization vary between species, but the activity patterns (number of bursts observed) of Shorthorn Sculpin in this study generally agree with those from a previous study (Andreasson (1973). Individuals appeared to be active at all times during 24 h daylight, however as the proportion of daylight each day decreased Shorthorn Sculpin movement patterns occurred more frequently during darkness indicating a shift in diel behaviour. These observations are similar to those found in Andreasson (1973), where Sculpin activity was observed across all hours of 24 h daylight periods but observed a shift to night-active at the end of September in sub-Artic areas associated with sunset.

Effects of Arctic Cod on Shorthorn Sculpin Movement Patterns

Although Shorthorn Sculpin have been documented feeding on pelagic and demersal fishes (Kallgren et al. 2014, Cardinale et al. 2000) with some evidence that they feed on Arctic Cod (Dick et al. 2009, Landry et al. 2016) the results from this study are inconclusive regarding whether Shorthorn Sculpin actively prey on Arctic Cod in Resolute Bay during open water periods. The change in movements patterns in zone 1 with a decrease MP1 and an increase MP2 may be a result of Arctic Cod presence considering they occurred in much higher abundances and more often than in zones 2 and 3. However, it may also be the result of both species reacting and foraging on the same feeding event or opportunity. Stomach content data from Resolute Bay has shown that both species readily prey on the pelagic mollusc *Limacina helicina* when present during open water periods, and the same dataset has revealed at least two Arctic Cod in the stomachs of Shorthorn Sculpin from Resolute Bay in 2012, although it is unknown whether they were scavenged or actively predated (Landry et al. 2016). It is possible that

58

both scenarios are occurring and that Shorthorn Sculpin will feed on whichever prey items they can catch, as the consumption of a single adult Arctic Cod would have an energy payoff equal to that of many invertebrates (Hop & Gjosaeter 2013), behaviour that would agree with optimal forage theory (Werner & Hall 1974). The schooling behaviour of Arctic Cod may also make them more difficult to catch as large shoals of fish have been shown *in situ* to disrupt the attack sequence of ambush predators (Neill & Cullen 1974). This could hinder Shorthorn Sculpin ability to catch Cod except in rarer instances when individual Cod become separated from the school. If this were the case predation of Arctic Cod would occur less often than the predation of invertebrate prey.

In either case, this study has revealed changes in defined movement patterns associated with higher abundances of Arctic Cod and changes in abiotic variables. There is some evidence to suggest that Shorthorn Sculpin feed on Arctic Cod when present in large numbers in Resolute Bay during open water periods (Landry et al. 2016), or they may be feeding on the same prey resources, or both. The shortcomings in this study with respect to identifying Arctic Cod as a specific prey item may be mitigated in future studies by using acoustic tags that transmit signals more frequently in order to gain a higher resolution in the dataset over short periods of time. This would help identify fast, fine scale movements such as feeding strikes (Broell et al. 2013). The use of Vemco predation tags (currently under development, Halfyard et al. 2016) could also resolve this issue, where suspected prey organisms are tagged with transmitters that can relay when predation events occur and be compared to the movement patterns and behaviour of tagged predators. Using acoustic telemetry and VPS this study derived unique movement patterns of a common mobile consumer in the Arctic, demonstrated how these movement patterns may be linked to foraging ecology and how they are influenced by biotic and

59

abiotic factors. Changes in these movement patterns have implications for the trophic

ecology of Shorthorn Sculpin in relation to prey availability and prey selection.

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Table 3.1: Mean and SD values for variables associate with Shorthorn Sculpin bursts that were significantly different between movement patterns (clusters). Mean ROM (Rate of Movement) was highly correlated to sum distance (> 60%) but was included in the final analysis to observe the values for each movement pattern. Movement Pattern 3 had significantly higher values for all variables than the other two, whereas movement patterns 1 and 2 were only significantly different from each other in sum distance and mean ROM.

Cluster	Sum Distance (m)	Linearity Ratio	Mean ROM (m s^{-1})	Mean Depth (m)
1	187 ± 74.0	0.32 ± 0.33	0.03 ± 0.03	13.0 ± 4.9
2	36.9 ± 23.3	0.29 ± 0.27	0.01 ± 0.01	12.2 ± 4.12
3	784 ± 392	0.5 4± 0.34	0.06 ± 0.06	16.8 ± 5.22

Table 3.2: Total number of hours in which Shorthorn Sculpin were detected in each zone throughout the study period, and total number of hours in which Arctic Cod were also present in the same zone. The maximum and minimum number of unique individuals for any given hour per zone is also recorded. Mean relative abundance for each species with ± SD for the total amount of hours in each zone, relative abundance defined as: number of detections/number of individuals per hour.

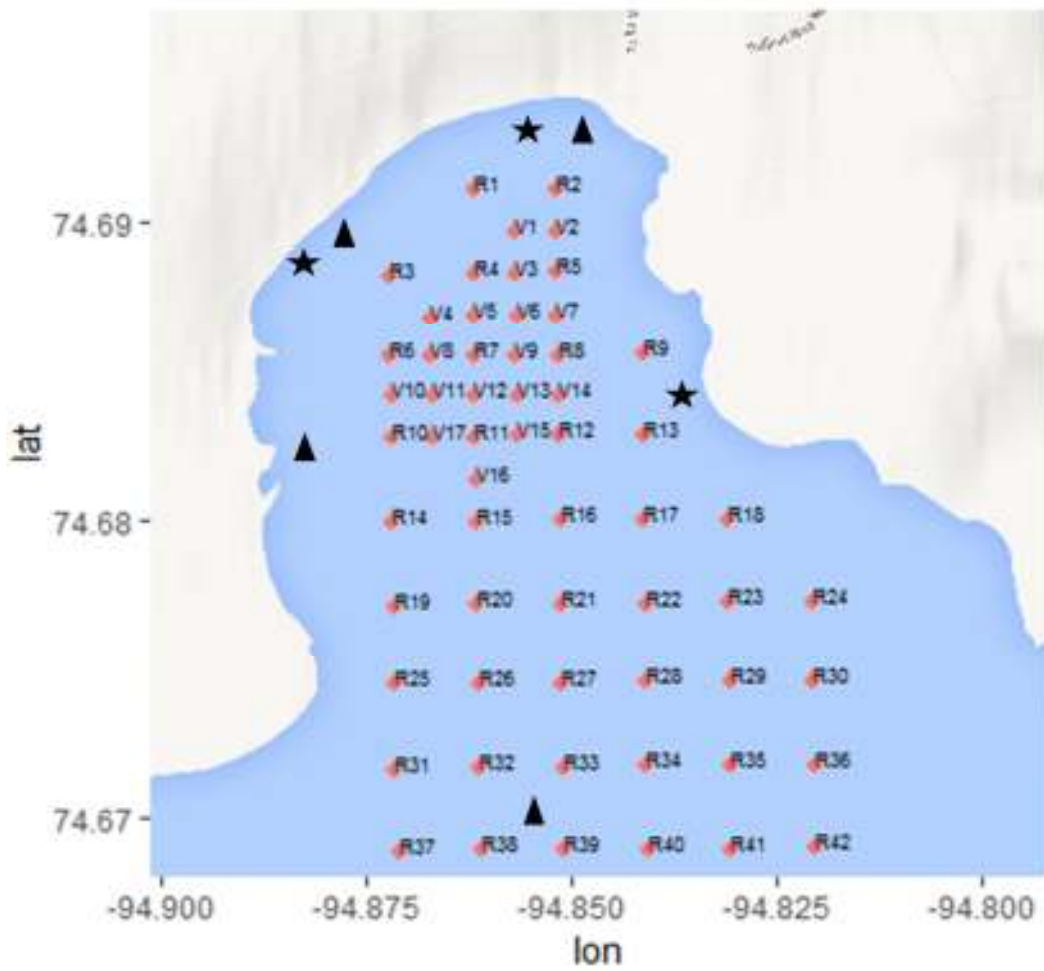| Zone & Associated Stations	Sculpin Present (h)	Both Species Present (h)	Unique Cod (min, max)	Unique Sculpin (min, max)	Relative Abundance Cod	Relative Abundance Sculpin
1 (R1 – R5, VPS1 - VPS3)	503	493	1, 77	1, 4	4.06 ± 2.1	3.62 ± 1.9
2 (R14, R15,R19, R20, R25, R26, R31, R32, R37)	303	68	1, 50	1, 3	3.46 ± 1.9	4.23 ± 2.3
3 (R17, R18, R22, R24, R28, R30, R34, R36)	300	47	1, 49	1, 4	3.28 ± 1.9	4.54 ± 2.5

Figure 3.1: Map of Resolute Bay and named listening stations used in the study. Triangles mark the capture areas of Arctic Cod and stars mark the capture areas of Shorthorn Sculpin.

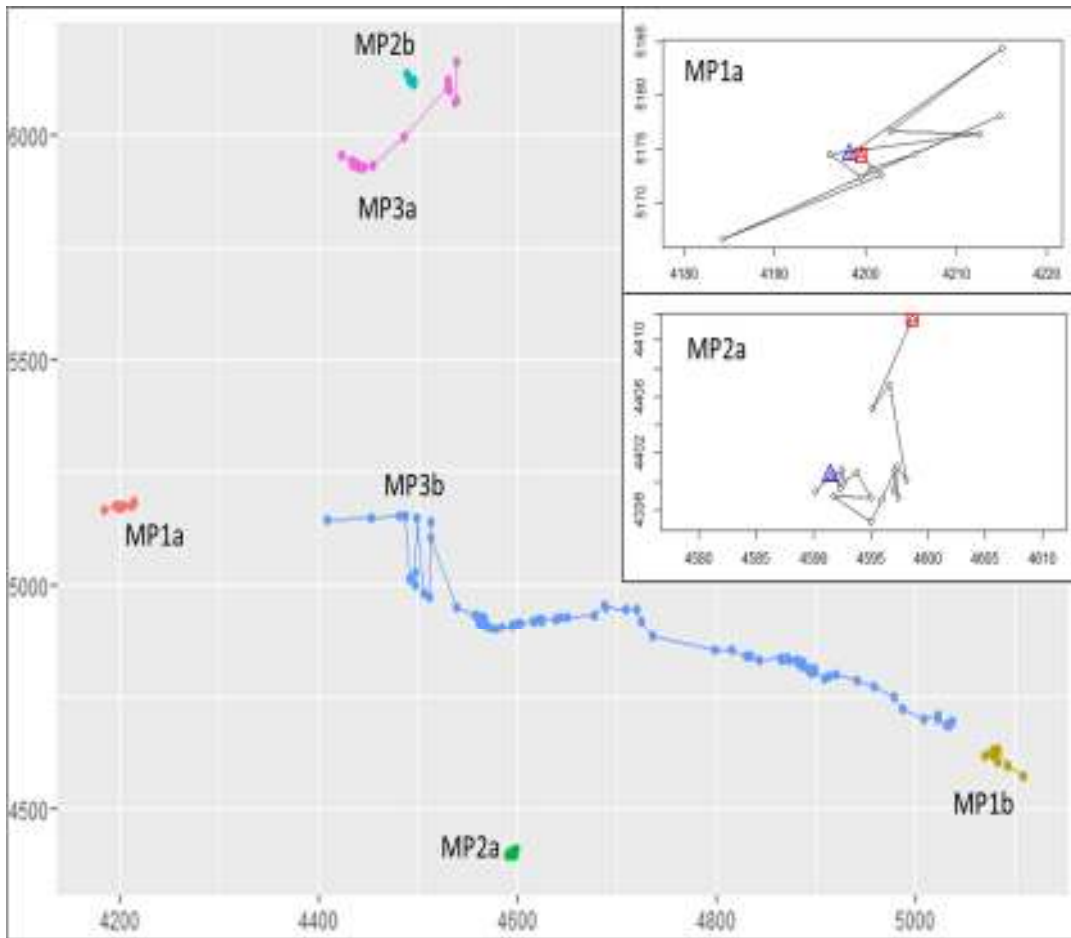Figure 3.2: Examples of the three different clusters/movement patterns described in the study (2 trajectories for each pattern). All movement patterns are compared spatially, to scale with MP1a and MP2a also shown in higher resolution (not to scale) in order to distinguish characteristics of movement patterns 1 and 2. X and y axes represent derived xy coordinates based off of latitude and longitude.
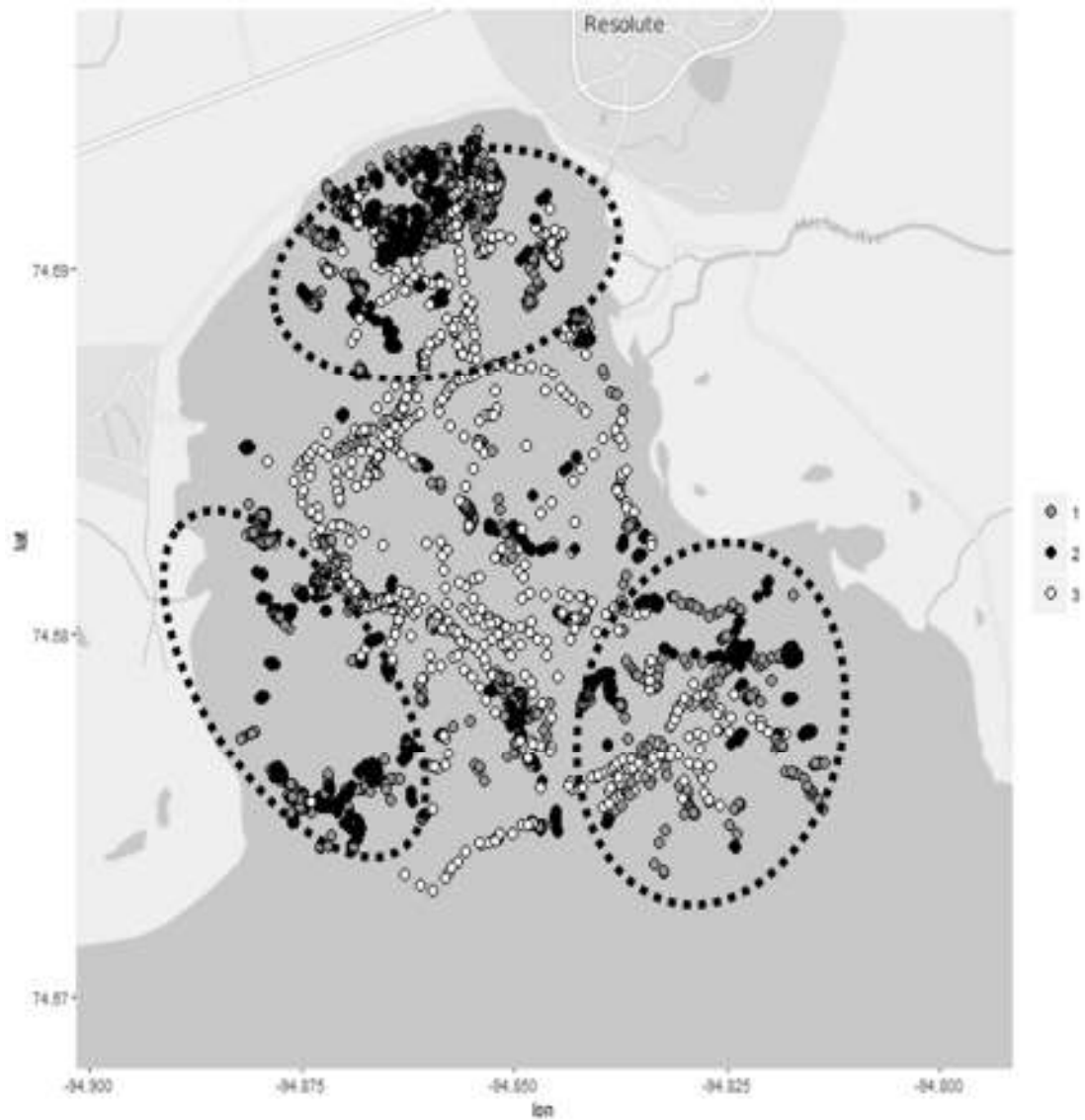
Figure 3.3: Individual relocations that make up different bursts of Shorthorn Sculpin coloured according to movement pattern. Dashed ellipticals represent zones used in the study to analyze Arctic Cod abundance. Zone one is located at the northern end of the Bay, zone two on the south western end, and zone three on the south eastern end.
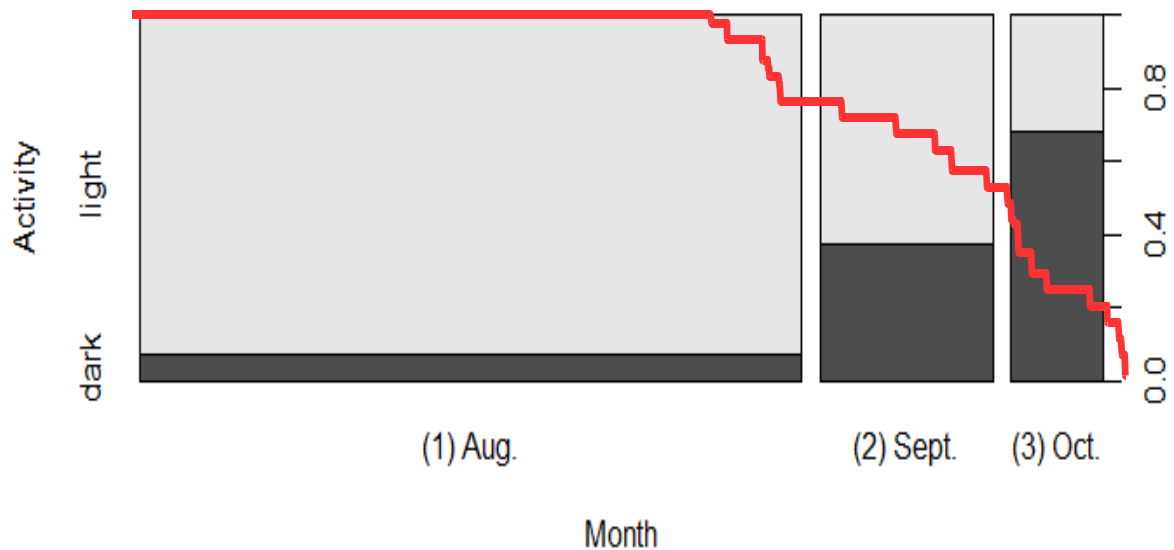
Figure 3.4: Occurrence of all movement patterns as a mean proportion of activity during daylight or darkness for each month during the study period. The solid line indicates the approximate amount of sunlight per day as a proportion of 24 hrs. The size of the box for each month is indicative of the number of data points (Aug = 9467, Sept = 2470, Oct = 1319).

Chapter IV: Conclusion

This study made use of stable isotope and stomach content analysis as well as acoustic telemetry to gain a greater understanding of Shorthorn Sculpin trophic ecology in the high Arctic. This species represents an understudied, common consumer in Arctic food webs that may play an important role in regulating primary consumers and has been shown to couple multiple energy pathways (McMeans et al. 2013, Landry et al. 2016). This gives Shorthorn Sculpin the potential to be an important food web stabilizer in these systems (Rooney et al. 2006). The trophic link between Shorthorn Sculpin and Arctic Cod had not previously been examined which represented a lack of information between two highly abundant aquatic species in the Arctic. As well, this study also represented an opportunity to explore the usefulness of using acoustic telemetry in i) arctic systems and ii) as a method for examining the feeding ecology of an organism, as in both cases studies are lacking compared to more temperate areas (Hussey et al. 2015).

Trophic position, trophic coupling, individual diet specialization and the analysis of unique movement patterns were used to examine the effects of temporal and spatial environmental changes on the general feeding ecology and behaviour of Shorthorn Sculpin. In particular, these parameters were used to determine if Arctic Cod presence and absence could impact Shorthorn Sculpin trophic ecology and if it represented a potential prey item. This study identified trophic relationships between Shorthorn Sculpin and various invertebrate species, conspecifics, and to a degree Arctic Cod. It has also shown the impacts of changes in year to year prey availability and abiotic factors such as ice cover and photo period on the trophic ecology and feeding behaviour of Shorthorn Sculpin. Although there are limitations in the methodologies employed (stable isotopes,

stomach contents analysis, and acoustic telemetry), the findings of this study are more detailed and holistic than if each technique had been used by itself. These findings present information on important linkages in arctic food webs and have implications for species' interactions in a dynamic environment.

The use of different and diverse experimental methodologies to approach a research question has the benefit of corroborating results from each analysis. In this study stable isotope and stomach content analysis found that Shorthorn Sculpin preyed on a variety of invertebrates and to a lesser degree fishes. The spatial distribution of individuals and potential foraging grounds revealed by telemetry data support these results as movement patterns that are more likely to be associated with foraging behaviour occurred in areas associated with identified prey items from stomach contents. The distribution of Shorthorn Sculpin across Resolute Bay and their residency in shallow areas coincides with the less negative $\delta^{13}C$ found, however the use of deeper water, along with pelagic invertebrate and fish prey found in their stomach contents explains how Shorthorn Sculpin were able to derive up to 60 % of their energy from sources with more negative $\delta^{13}C$. Field observations found that Shallow nearshore portions of Resolute Bay were favoured by amphipods, small Sculpin and pteropods which were common prey items of Shorthorn Sculpin. The observed occurrences of these prey items overlap with areas where Shorthorn Sculpin movement patterns likely reflected foraging behaviour (pattern 1 and pattern 2). This also supports $\delta^{15}N$ signatures that suggest an invertebrate diet supplemented with prey items from higher trophic positions (fishes, in particular other Sculpin). The spatial overlap in Arctic Cod and Shorthorn Sculpin positions in the north head of the bay can account for the instances when Arctic Cod were found in Shorthorn Sculpin stomach contents from 2012. The presence of a single species of

pelagic pteropod (*Limacina helicina*) in the stomach contents of both fish species

combined with the fact that Shorthorn Sculpin were observed changing movement

patterns with the increased relative abundance of Arctic Cod suggests that at least in some

areas of the bay both species compete with one another for prey resources. During such

times it is possible that some Shorthorn Sculpin may also attempt to feed on the large

number of Arctic Cod present, however using the current dataset it is unknown whether

the few observed predated Arctic Cod were caught in this way, at random, or scavenged.

Due to the small amount of Arctic Cod found in Shorthorn Sculpin stomach contents it is

concluded that the presence of Arctic Cod is not likely to influence Shorthorn Sculpin

trophic ecology or foraging behaviour as much as other factors previously discussed (i.e.

the presence of other prey items, seasonal changes in abiotic variables).

The results from this study have important implications for Shorthorn Sculpin in

regards to their role within arctic food webs. Shorthorn Sculpin in Resolute Bay are able

to exploit practically every available prey resource including conspecifics which helps

minimize the impact of year to year prey availability and may help keep Shorthorn

Sculpin populations stable in the bay. The ability to predate Arctic Cod is a possibility

though not necessary for Shorthorn Sculpin as they are able to exploit other resources.

However, there is still potential for trophic interactions between the two species through

competition, especially if prey availability declines in localized areas that support large

populations of both fishes. These findings support the findings of previous studies in

which Shorthorn Sculpin were able to couple multiple energy pathways (pelagic and

benthic, McMeans et al. 2013). This in turn supports the idea that this species is an

important consumer in arctic food webs due to its abundance and potential to influence

system stability. Shorthorn Sculpin trophic ecology may promote stability in Arctic

systems due to a high number of weak linkages to lower consumers (McCann 1998, Myers et al. 2007). In this way they can switch between different prey items or groups without depleting one group. This feeding strategy would be crucial at high latitudes where ecosystems have relatively low biodiversity compared to more temperate systems (Roy et al. 1998) and resource availability fluctuates seasonally (Walsh et al. 2008). This approach not only ensures the persistence of consumer populations (Shorthorn Sculpin) by increasing potential prey availability but can also control prey population size and prevent over-grazing of primary producers (Rooney et al. 2006).

Although the scope of this study is limited by sampling location, the results produced here support those found in other studies that were conducted in nearshore areas (Kallgren et al. 2014) and offshore areas (Cardinale 2000). Shorthorn Sculpin prey selection may vary between taxa in different geographical locations however general patterns still persist: i) the incorporation of both invertebrates and fishes in individual diets, ii) size related differences in prey selection and iii) some degree of trophic coupling (Kallgren et al. 2014, Cardinale et al. 2000, McMeans et al. 2013). The use of stable isotope and stomach content analysis in conjunction with acoustic telemetry was beneficial in studying fine scale and longer term changes in foraging behaviour and prey selection, however each technique has its own temporal window. Stable isotopes are a reflection of past trophic interactions (weeks to months, Buckheister & Latour 2010), stomach content analysis represents what an individual had recently been feeding on (days to weeks, Hyslop 1980) and telemetry data is produced only after an individual has been tagged. Therefore, there is lack of data with direct temporal overlap from Shorthorn Sculpin sampled in this study (separate individuals were used for biological sampling and acoustic tagging). However, the application of all of these techniques allowed for an

73

examination of trophic ecology that spanned the entire length of the open water period in Resolute Bay, which extends beyond when field work was conducted. Furthermore, the results from these different techniques support each other. Aside from stomach content analysis, the methodologies employed in this study may not be adequate for examining unique prey species preferred by Shorthorn Sculpin. Both stable isotope analysis and acoustic telemetry rely on a degree of inference, and not direct observation, to reach conclusions regarding which prey items are contributing to the results obtained. As such, it is difficult to identify active predation of Arctic Cod, in the absence of large amounts of direct evidence from Shorthorn Sculpin stomach contents. This could be mitigated in future studies by examining through direct-*in situ* observation the behaviour of Shorthorn Sculpin in the presence of Arctic Cod, by the use of predation tags (currently under development), or using DNA analysis on Shorthorn Sculpin stomach contents to more rigorously identify the presence of Arctic Cod. Future work should also examine potential changes in Shorthorn Sculpin trophic ecology between open water and ice covered periods to examine any changes in habitat preference and prey selection.

In conclusion, this study represents the most thorough examination of Shorthorn Sculpin trophic ecology conducted in the Arctic and in general. It has examined the trophic linkages between this species and others in an understudied system and produced implications for how Shorthorn Sculpin trophic ecology and foraging behaviour may be affected in the future with changes in species distribution and occurrence. In general, this study described how Shorthorn Sculpin fit into Arctic food webs and found them to be able to exploit a wide variety of prey items and couple trophic pathways during open water periods. All of which indicates that they are an important consumer in the high Arctic.

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