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Seasonal feeding and movement responses of resident sculpin in the Canadian Arctic

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Seasonal feeding and movement responses of resident sculpin in the Canadian Arctic

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS iii

TABLE OF CONTENTS v

LIST OF TABLES vii

LIST OF FIGURES viii

ABSTRACT x

CHAPTER 1: Introduction 1

1.1 Seasonality and Phenology 1

1.2 Arctic Ecosystems 5

1.3 Tremblay Sound 7

1.4 Sculpin 8

1.5 Thesis Aims 9

1.6 Figures 11

CHAPTER 2: Feeding variability in a seasonal Arctic pulse by marine sculpin 13

2.1 Introduction 13

2.2 Methods 16

2.2.1 Study Site 16

2.2.2 Sampling and Processing 17

2.2.3 Statistical Analyses 18

2.2.3.1 Feeding Intensity *18*

2.2.3.2 Diet Composition *20*

2.3 Results 24

2.3.1 Feeding Intensity 24

2.3.2 Diet Composition 24

2.4 Discussion 26

2.4.1 Conclusion 32

2.5 Tables 33
2.6 Figures 36
2.7 Supplemental Figures 40
CHAPTER 3: Year-round monitoring of Arctic sculpin with passive acoustic telemetry to identify seasonal behavior 42
3.1 Introduction 42
3.2 Methods 45
3.2.1 Study Design and Sampling 45
3.2.2 Seasonality 47
3.2.3 Sequence Analysis 50
3.2.4 Acceleration and Depth 52
3.3 Results 53
3.3.1 Seasonality 53
3.3.2 Sequence Analysis 55
3.3.3 Acceleration and Depth 55
3.4 Discussion 56
3.4.1 Conclusion 63
3.5 Tables 65
3.6 Figures 67
3.7 Supplemental Figures 72
CHAPTER 4: Conclusion 77
4.1 Polar Ecology and Seasonality of Resource Pulses 77
4.2 Insights on Resident Species 81
4.3 Sculpin as Indicator Species 84
LIST OF REFERENCES 88
APPENDIX 109

LIST OF TABLES

Table 2.1 Model selection for estimating relative consumption for diets collected in 2017 33

Table 2.2 Summary of sculpin diet contents using traditional metrics Frequency of Occurrence (FOO), Percent Numeric (PN), and Percent Mass (PM) 34

Table 2.3 Comparisons of sculpin diet communities across all time periods based on centroid distance and dispersion in multivariate space 35

Table 3.1 Specifications for V5, V9, and V9AP transmitters from Innovasea used in this study along with number and burden summaries from releases 65

Table 3.2 Top four model results in the Overall Dynamic Body Activity (ODBA) mixed effects model along with coefficient estimates from full model averaging 66

LIST OF FIGURES

Figure 1.1 Change Paradigm conceptual diagram including exemplar species 11

Figure 1.2 Map of study site—Tremblay Sound, Nunavut, Canada 12

Figure 2.1 Feeding intensity responses over the day of the year from 2017, 2018, and 2019 expressed as (a) binomial empty or not empty and (b) magnitude of consumption relative to body mass 36

Figure 2.2 Graphical assessment of sculpin feeding strategy using Frequency of Occurrence and Prey-Specific Abundance by (a) count and (mass) in 2-week periods 37

Figure 2.3 Levin’s Diet Breadth bootstrap estimates over 2-week periods in 2017 and 2018 sculpin diet communities 38

Figure 2.4 Non-metric multi-dimensional scaling ordination plots for sculpin diet communities in 2017 and 2018 overlayed with (a) year and (b) 2-week time period 39

Figure 2.S1 Prey accumulation curve for all uniquely identifiable diet items across individual sculpin stomachs 40

Figure 2.S2 Sample size of sculpin diets collected in 2017 and 2018 by 2-week time period and fish mass groups 41

Figure 3.1 Map showing the multiple gated array structure within Tremblay Sound used for acoustic telemetry from July 2017-August 2020 67

Figure 3.2 Seasonal activity metrics for sculpin in each observation year. (a) Roaming index, (b) Inter-gate movements, and (c) Residency duration 68

Figure 3.3 Lattice Density home range estimates fit seasonally and across regular isoclines from 50-95% 69

Figure 3.4 Sequence histories of all transmitters indicating the detecting gate............................ 70

Figure 3.5 Histograms summarizing (a) Overall Dynamic Body Activity (ODBA) and (b) absolute depth data from V9AP transmitters in 2019-2020 71

Figure 3.S1 Multi-panel plot showing the impact of variation in Refined Shortest Path point estimation frequency (2 minutes to 1 year) and Lattice Density k step parameter (1-60) 72

Figure 3.S2 Cumulative (a) detection and (b) home range of complete sculpin population throughout the entire 3-year monitoring period 73

Figure 3.S3 Distance matrices across (a) V9, (b) V5, and (c) V9AP transmitter sequences 74

Figure 3.S4 Representative sequences of each transmitter sequence cluster 75

Figure 3.S5 Sculpin depth usage from V9AP transmitters compared to receiver location, expressed as distance from shore and numerical order, and depth 76

ABSTRACT

Environments change across space and time, requiring organisms to adapt behaviorally and/or physiologically. In the Arctic, where productivity varies greatly among seasons, many marine species exploit a resource pulse associated with annual ice melt. Melting sea-ice releases zooplankton on and within the ice into open water causing many consumers to migrate with the receding ice; however, resident species may too rely on the ephemeral prey source. Fourhorn Sculpin (*Myoxocephalus quadricornis*) and Slimy Sculpin (*Cottus cognatus*) are residents of Tremblay Sound, Nunavut Canada which is known as a seasonally productive system in the Arctic. I characterized the seasonal behavior of sculpin by collecting and identifying stomach contents from 175 sculpin during the ice-free periods of 2017-2019. Other individuals were released with acoustic transmitters (n=119) for year-round monitoring of movements throughout Tremblay Sound. Consumption rates were high, with 33% of individuals consuming >5% of their body mass (mean 4.32%; SE 0.25). Diet composition was dominated by amphipods and krill but both traditional and multivariate analyses showed diets shifted and broadened over the short (~6 weeks) ice-free season and between years. Namely, indicator species analysis revealed significant associations with distinct amphipod genera between years (*Gammaracanthus* sp. in 2017, *Onisimus* sp. in 2018). Feeding exploitation corresponded with high rates of activity as several metrics of movement and home range consistently revealed more activity during the ice-free period. Further analyses revealed qualitatively that sculpin showed high site fidelity and were residents within Tremblay Sound year-round, though acceleration and pressure sensors indicate individuals may not be entirely dormant under the ice. Together, showing high levels of activity to feed at high levels while maintaining flexibility in diet composition indicates that sculpin are adapted to exploit ephemeral resources. These physiological and behavioral adaptations are likely important to annual energy budgets and have potential to affect the resilience of sculpin to ongoing climate change in marine Arctic ecosystems.

Keywords: sculpin, resource pulse, Arctic, phenology, generalist, acoustic telemetry, seasonality, movement ecology, climate change, sea-ice

CHAPTER 1: Introduction

Seasonality and Phenology

Seasonal change is experienced by all ecosystems in which conditions cycle semi-annually (Staggemeier et al. 2020). Seasonal changes in abiotic conditions, such as daylength, temperature, or precipitation, can make environments swing between states of productivity (Staggemeier et al. 2020). At transition periods, a great deal of change occurs throughout the ecosystem which can be widely beneficial (Yang et al. 2010) or costly (Landes et al. 2017, 2020). In response, organisms must be adapted to these seasonal changes in conditions. Broadly, organisms can respond to seasonal change through tuning behavior and life history events to those conditions that enable the highest success.

Phenology refers to the timing of cyclical life-history events and their abiotic and biotic causes and consequences (Leith 1974; Visser et al. 2010). Phenological events include leaf bloom and drop (Reich 1995; Richardson et al. 2013) and the timing of migration and reproduction events (Keefer et al. 2009; Anderson et al. 2013). In many situations, rapid swings between seasons result in a sudden change in productivity for organisms to exploit. These resource pulses provide an influx to a system in a short time, infrequently, and peak in magnitude well above background levels (Yang et al. 2008). By coordinating the timing of reproduction (Visser et al. 1998), aggregating populations (Yang et al. 2010), or simply through individual binge-feeding (Furey et al. 2016) organisms are able to benefit from resource pulses well beyond the pulse itself (Moore et al. 2008). Organisms may seek abundant resources to maximize productivity, but mismatches in space and time for a phenological event with preferred conditions can arise (Cushing 1990; Stenseth and Mysterud 2002).

Because phenological events are so diverse and occur globally, they are tied to many different environmental conditions as part of the "rhythm of the seasons" (Morisette et al. 2009). Environmental cues signal the coming conditions to trigger the organismal response, and include daylength, temperature, and water availability (Reich 1995; McNamara et al. 2011; Richardson et al. 2013). Often, multiple environmental cues naturally coincide with each other, such as daylength and temperature, enabling species to use multiple cues for stronger signaling (Visser et al. 2010). However, the synchrony between cues can be disrupted by a change in one that does not occur in the other (McNamara et al. 2011), such as rising temperatures despite stable daylengths due to climate change (Wasmund et al. 2019). Initially, these mismatches were identified by regular interannual variation correlations, such as those between plankton and commercial fish stocks (Cushing 1990) or lemmings and the rest of the tundra food web (Elton 1924; Ims and Fuglei 2005). Increasingly, trophic phenological mismatches have been attributed to climate change—including great tit (*Parus major*) egg laying and caterpillar abundance (Visser et al. 1998) and herbivorous *Daphnia* zooplankton and phytoplankton blooms in aquatic systems (Edwards and Richardson 2004; Winder and Schindler 2004)—and result in whole ecosystem restructuring (Beard et al. 2019). Organisms are capable of adapting their phenology to changing environmental conditions; indeed changes in phenology is an often cited indicator for climate change (see Richardson et al. 2013 and citations therein). Adaptive responses such as this are, however, limited to circumstances in which an event is neither spatially (Cushing 1990) nor temporally (Visser et al. 1998) separated from its cue. Phenological events being successfully paired with suitable conditions is of great consequence for seasonal-adapted organisms.

Organisms may respond to change in their environment in some cross of changing internal conditions and/or the external conditions experienced (cf. Meyers and Bull 2002; Figure 1). The first response of changing external conditions is enacted by migrations, when animals undertake cyclical, directed movements between distinct spatial areas (Bauer and Hoye 2014; Tallman et al. 2019). This includes that of the Arctic tern (*Sterna paradisaea*) which migrates the whole height of the globe to alternate summers in the Arctic and Antarctic (Egevang et al. 2010). Second, changing internal conditions may occur through phenotypic plasticity or the ability to change individual morphological, anatomical, or physiological characteristics to match environmental conditions and best satisfy individual needs (Piersma and van Gils 2011). Examples include Arctic tundra organisms (i.e., Arctic fox (*Vulpes lagopus*), snowshoe hare (*Lepus americanus*), and rock ptarmigan (*Lagopus muta*)) which seasonally thicken and whiten their coat/plumage for the cold, snowy winter and molt to brown in summer (Piersma and van Gils 2011; Zimova et al. 2016). The commonality of these phenotypes across taxa and ecosystems can be difficult to comprehensively capture (Meyers and Bull 2002); however, it has been cited in invertebrates (Lampert 1994), plants (Cook and Johnson 1968), birds (McWilliams and Karasov 2014), reptiles (Secor 2008), fish (Armstrong and Bond 2013), and even in humans (Hill and Olson 2008). Third, an animal may adapt internal and external conditions through coupled migration and plasticity. In some circumstances, organisms relocate to conditions wholly different from those departed and must adapt accordingly. For example, diadromous fishes switch osmoregulatory function due to different demands from fresh- and saltwater habitats (Quinn 2005). Finally, an animal may respond to change by remaining unchanged themselves; simply being robust across a range of environmental conditions (Congdon et al. 1994). Robustness is enabled by characteristics that are canalized, or capable of producing equivalent fitness through a range of environments (Debat and David 2001), and is more frequently observed at northern latitudes (Liefting et al. 2009). Species may fall anywhere on a spectrum of these four broad categorical mechanisms—migration, phenotypic plasticity, flexible migration, and robustness.

Mechanisms of maintaining phenological matching are reflected in the seasonality of an individual's home range and foraging. Home range is the geographic area which an individual utilizes in its regular activity (Burt 1943). Home ranges have been shown to differ across seasons; generally increasing with rising temperatures (Snedden et al. 1999; Lindstrom and Hubert 2004), although not universally (Burrell et al. 2000). This adjustment of home range is driven by new opportunities, either as habitats or food, that arise in the more productive seasons (Snedden et al. 1999; Lindstrom and Hubert 2004). In this way, the home range or movement behavior of an individual is directly linked to its foraging; foraging that can also be seasonal (Swanson et al. 2011). Seasonal foraging is often the result of changing ecosystem productivity providing distinct opportunities to consumers (Yang et al. 2010), including through resource pulses (Yang et al. 2008). These sudden increases of limited resources are absorbed more rapidly and efficiently by aquatic than terrestrial systems, from primary producers through to carnivores (Nowlin et al. 2008). For fish across taxa and niches, heterogeneous feeding is very common (Armstrong and Schindler 2011). Further, exploiting resource pulses is well documented through binge-feeding among many temperate fish taxa including *Salmonidae* (Armstrong and Bond 2013; Furey et al. 2016), *Percidae* (Selgeby 1998), *Centrarchidae* (García-Berthou and Moreno-Amich 2000), and *Cottidae* (Foote and Brown 1998). The ability to respond to variable conditions is most consequential in strongly seasonal environments such as in polar regions.

Arctic Ecosystems

The Arctic is an ideal location to investigate the impacts of seasonal change on animal behavior and the potential consequences of climate change. The Arctic is the northernmost region of the globe which experiences at least two days with neither a sunrise nor sunset (continual daylight, continual night; Berge et al. 2015; AMAP 2017). The climate typical of the Arctic is driven by this dramatic difference in sun exposure, resulting in an annual negative radiation balance, meaning more heat is lost throughout the area than is absorbed (Hinzman et al. 2005). Air temperatures range from averaging 10.5°C to -37.1°C with a combined annual precipitation of less than 100 cm (Environment and Climate Change Canada n.d.). The Arctic is a harsh environment with unique flora and fauna that are highly specialized for the natural seasonal change (Scholander 1955; Elsner 2000). In marine systems of the Arctic, the primary seasonal specialization of organisms is to the cyclical freeze-thaw of large amounts of sea-ice (Bradstreet and Cross 1982). However, organisms are only as successful as their adaptations are suited to the actual conditions they experience (Møller et al. 2008). Therefore, changes to the conditions for which adaptations have been selected threaten species and communities (Gilg et al. 2012; Amélineau et al. 2016; Underwood et al. 2019). The changes throughout much of the Arctic now are growing more severe and less predictable.

Climate change, while a global phenomenon, is affecting the Arctic more than anywhere else. Arctic amplification refers to the observed phenomenon that changes in global climate, particularly due to atmospheric alteration, influence the Arctic region most strongly (Serreze and Barry 2011). In the past 50 years, temperature anomalies in the Arctic have been greater than two times the global average (Serreze and Barry 2011; Overland et al. 2019). Commonly explained as being driven by the albedo effect (Serreze and Barry 2011), there are many factors which contribute to the amplification, including permafrost thawing releasing additional carbon to the atmosphere (Overland et al. 2019), changing cloud cover (Serreze and Barry 2011), and shifting timing of environmental cues and phenological events (Høye et al. 2007; Morisette et al. 2009). As the phenology of the Arctic changes more rapidly than lower latitudes, many migratory species' arrival to the Arctic is increasingly mismatched with its seasonal productivity (Lameris et al. 2017; Beard et al. 2019). While some Arctic-adapted species are struggling, many southern species have been encroaching upon the increasingly temperate conditions (Chen et al. 2011; Campana et al. 2020) and exacerbating the damage (Kortsch et al. 2015). The climate change impacts felt by the Arctic and its inhabitants are not confined to land but operate in marine systems as well.

Within the marine environment, where the dynamics of ice are central to seasonal function for the whole ecosystem (Bradstreet and Cross 1982; Hop et al. 2011; Ramírez et al. 2017), similar consequences of climate change are being observed. Traditionally, marine productivity begins beneath sea-ice with algae and zooplankton that are dependent upon the structure for development (Werner 1997). As ice breaks up and melts, organisms trapped within the ice are released and a bloom of productivity occurs in the open water (Søreide et al. 2010; Hop et al. 2011). As such, associations form between ice and a variety of animals, ranging from predatory amphipods (Gradinger and Bluhm 2004), Arctic cod (*Boreogadus saida*; Gradinger and Bluhm 2004; Fortier et al. 2006), marine mammals (Heide-Jørgensen et al. 2002; Harwood et al. 2012), to seabirds (Amélineau et al. 2016; Ramírez et al. 2017). However, this central feature of marine life in the Arctic has been disappearing at an accelerated rate (Comiso et al. 2008; Park et al. 2016). Ice loss has negatively impacted many animals that rely on the habitat for foraging (Amélineau et al. 2016; Ware et al. 2017). Thus, coastal Arctic systems can serve as useful models to both observing the importance of seasonal sea-ice and assessing the potential consequences of changing sea-ice phenology due to warming waters.

Tremblay Sound

Tremblay Sound (72.35°N, 81.11°W) is an inlet approximately 75 km long x 2 km wide off Eclipse Sound on Baffin Island, Nunavut, Canada (Figure 2). The inlet is largely encompassed by Inuit-owned land of the community at Pond Inlet and remains pristine. The Inuit community has for many years used the site for fishing and hunting due to its high seasonal productivity associated with an annual sea-ice melt. Harvesting efforts are primarily focused on Arctic char (*Salvelinus alpinus*) and narwhal (*Monodon monoceros*) but include other seasonal occupants such as bowhead whales (*Balaena mysticetus*) and ringed seals (*Pusa hispida*) as well as Greenland sharks (*Somniosus microcephalus*) which are of less harvest value. These migratory species are known to follow ice edges and enter the Tremblay system before or during rapid ice-off in late June-July (Heide-Jørgensen et al. 2002, 2012; Harwood et al. 2012; Barkley et al. 2020; Hammer et al. 2021). Tracking ice-off allows these migratory species to exploit a pulse of resources in the marine environment, making their exploitation of and reliance upon the pulse apparent (Bradstreet and Cross 1982; Swanson et al. 2011). Less apparent is the linkage between ephemeral resources, such as those released by ice-melt and the succeeding open-water productivity (Hop et al. 2011), and resident species of Tremblay Sound, such as sculpin that are an abundant fish in this system.

Sculpin

Sculpin (family *Cottidae*) are a diverse, widespread, and abundant group of benthic, resident fishes. As benthic fish, sculpin are adapted to life at the bottom with flattened ventral sides and spiny pectoral fins which splay out for holding position (Adams and Schmetterling 2007; Kane and Higham 2012). Correspondingly, they are known to be opportunistic, ambush predators (Leonardsson et al. 1988) that lie-in-wait with cryptic coloration (Whiteley et al. 2009; Kane and Higham 2012). Their relatively large gape enables them to efficiently consume a diverse diet (Gray et al. 2017). As such, sculpin are thought to be largely immobile (Landry et al. 2019) and remain in the same environment year-round, even beneath sea-ice (Barton et al. 2020). Even relatively rare, transitory movements rarely exceed 1 km continuously (Landry et al. 2019). In more restricted stream systems, the majority of sculpin may move <50 m/year (Breen et al. 2009) exhibiting high site fidelity (Gray et al. 2004). As a clade of highly residential, opportunistic predators, sculpin provide a distinctive and valuable indicator of ecosystem condition.

Sculpin can be found throughout the Arctic in marine environments. As sculpin are generally small fish, they are positioned near the bottom of a relatively simple food web (Kortsch et al. 2015). They can, however, serve as important links to higher trophic levels as well as across habitats (Kortsch et al. 2015; Giraldo et al. 2016). Sculpin are abundant, both in number and biomass (Gray et al. 2017, 2018), constituting a stable prey source across seasons (ct. McMeans et al. 2015) for many larger predators (Dyck and Romberg 2007; Kortsch et al. 2015; Brisson-Curadeau and Elliott 2019). The production of anti-freeze proteins (Yamazaki et al. 2019) can help sculpin withstand polar night conditions without migrating. However, direct monitoring of sculpin activity and foraging has, so far, been limited to the ice-free season

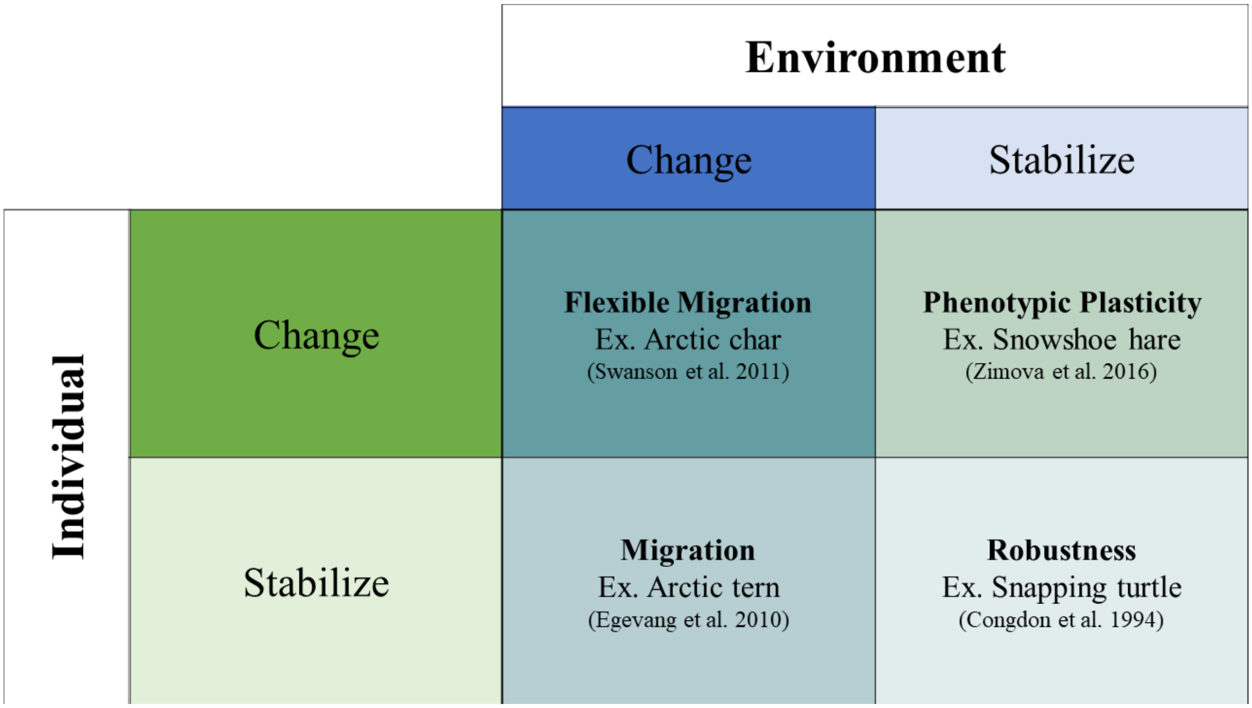
(Landry et al. 2019). As such, the detailed mechanisms by which sculpin, or indeed any resident fishes, can thrive in the highly seasonal Arctic waters is little understood. Sculpin may coordinate the phenology of their reproduction, i.e., in fall-winter (Leonardsson et al. 1988), to ensure offspring development coincides with the summer resource pulse. Further, observations of maturation in summer (Goldberg et al. 1987) may suggest multiple reproductive cohorts, a strategy that has been hypothesized in Arctic cod as a form of bet-hedging to stabilize recruitment over variable summer timings (Fortier et al. 2006). However, this critical link between success and seasonal exploitation has primarily been shown in migratory species such as Arctic cod (Forster et al. 2020) or Arctic char (Swanson et al. 2011). The activity and feeding of sculpin are of central importance to determining the mechanism by which they, as non-migrants, thrive in the Arctic and exploit the seasonal conditions of their marine environment.

Thesis Aims

In this thesis, I aim to characterize the impacts of seasonal change on the feeding and movement behaviors on sculpin in the Arctic. Chapter 2 will explore the feeding habits of sculpin during the resource pulse associated with the annual ice-melt through observations of stomach contents during the ice-free season. Both the intensity and composition of diet will be characterized during this short period of rapidly changing conditions. Chapter 3 will expand the time period of monitoring sculpin behavior through tracking individuals' movements in both the ice-free period, i.e., when diets described in Chapter 2 were collected, and the long, ice-covered Arctic winter. Metrics of activity and space-use in the contrasting seasons will compare the behavioral response of sculpin to the seasonal shift of the coastal marine environment in which they reside. Chapter 4, will connect these two complementary approaches to discuss implications of this research, including the mechanisms by which species exploit seasonality, how different niches rely on ephemeral resources, and the potential sensitivities Arctic ecosystems might experience with progressive climate.

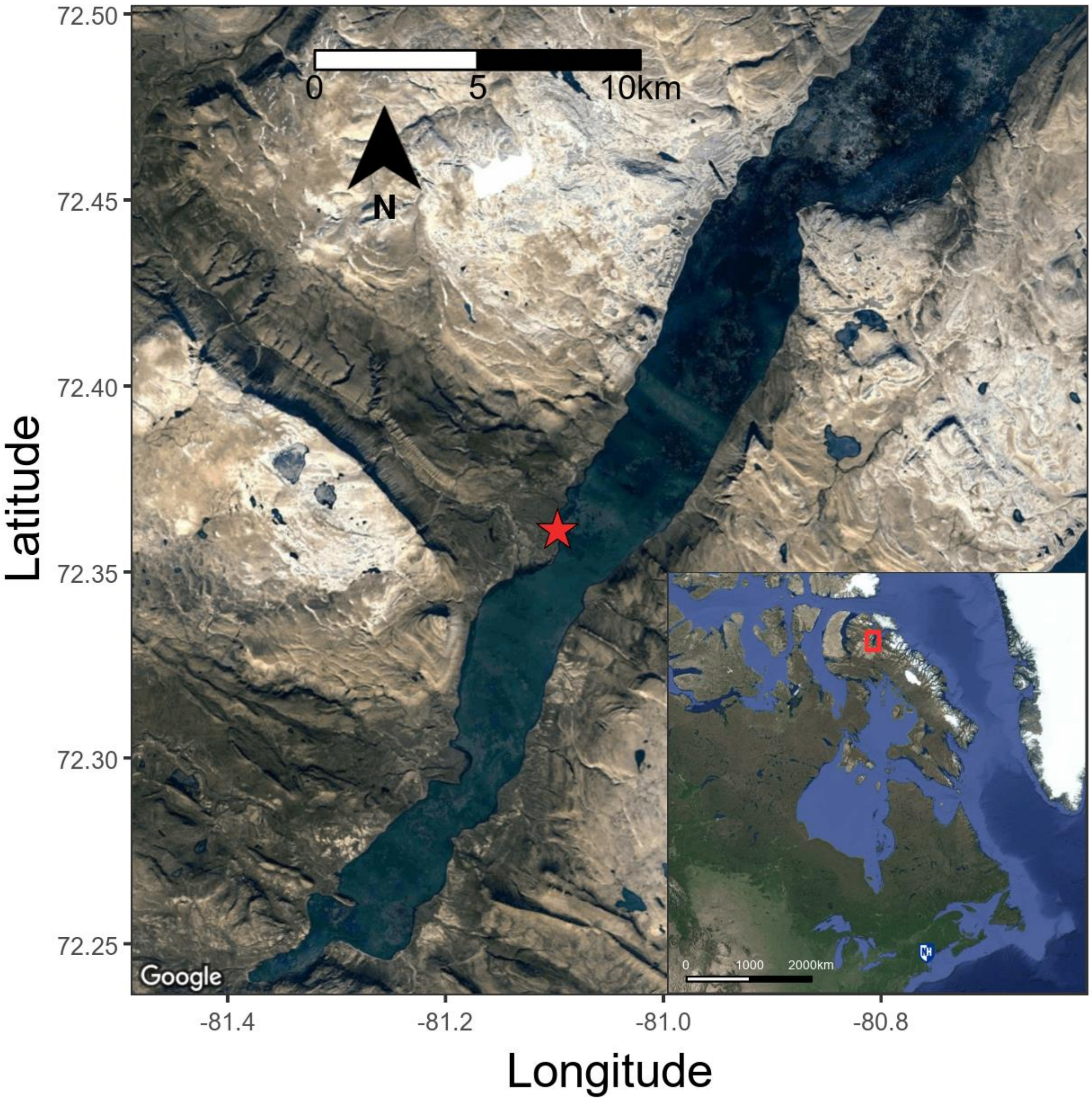
Figures

Figure 1. Conceptual diagram of change paradigm crossing species responses to change through mechanisms of response in external (environment) and internal (individual) conditions. The four categorical responses are named—flexible migration, migration, phenotypic plasticity, and robustness—and cite an exemplar species.



		Environment	
		Change	Stabilize
Individual	Change	**Flexible Migration** Ex. Arctic char (Swanson et al. 2011)	**Phenotypic Plasticity** Ex. Snowshoe hare (Zimova et al. 2016)
	Stabilize	**Migration** Ex. Arctic tern (Egevang et al. 2010)	**Robustness** Ex. Snapping turtle (Congdon et al. 1994)

Figure 2. Map of Tremblay Sound showing its location (red box) on the northern end of Baffin Island. The location of the University of New Hampshire is shown for reference. The location of the campsite is marked with a star. Map source: Google, generated with *ggmap* (Kahle and Wickham 2013) in R (v4.0.2; R Core Team 2020).



CHAPTER 2: Feeding variability in a seasonal Arctic pulse by marine sculpin

Introduction

Organisms encounter change in all environments, at many time scales, from hours to years (Angeler et al. 2013; Rasher et al. 2017), and to varying degrees of consistency and regularity. The variability in conditions results in temporary need for and access to resources, whether those resources are nutrients (Angeler et al. 2013) or predator-excluded foraging habitats enabled by the tides (Rasher et al. 2017). Changes between seasons in the annual cycle are among the most influential. The timing, or phenology, of seasonal changes in productivity of ecosystems can correspond to several environmental cues: temperature, daylength, precipitation, another organism's presence, or some combination of these (McNamara et al. 2011). Organisms exploit the seasonal variations in ecosystem productivity and, thus, use cues to signal the coming environmental conditions (McNamara et al. 2011). However, those cues may become less predictive of conditions with progressive climate change.

Measured primarily by increasing temperatures, climate change has induced a suite of other biome-specific abiotic changes (Hinzman et al. 2005). As conditions change, historical linkages, such as temperature and photoperiod, may become decoupled resulting in mismatches between resources and consumers (Sydeman and Bograd 2009). Whole ecosystems can be disrupted by mismatches between even one trophic linkage (Beard et al. 2019) especially as many linkages rely on those around or below them (Thackeray et al. 2010). It is essential for organisms to be able to respond at rates equal to those of the changing abiotic conditions and to their prey, though producers and primary consumers are known to respond most quickly (Edwards and Richardson 2004) and secondary and higher consumers respond more slowly (Sydeman and Bograd 2009; Thackeray et al. 2010). Additionally, secondary and higher consumers are also often larger-bodied and longer-lived, resulting in appropriate periods of response to occur within the lives of individuals rather than generations. Constraints to individual flexibility are stronger than multi-generational adaptations and better suited for regular, predictable changes (Meyers and Bull 2002; Piersma and van Gils 2011). As such, climate change driven mismatches have threatened (Visser et al. 1998) and continue to threaten (Møller et al. 2008; Visser et al. 2010; Beard et al. 2019) populations of animals around the world. As the rate of change is the cause for threat, areas that experience rapid climate change are most sensitive.

Nowhere is the disruptive nature of climate change more evident than in the Arctic. The climate of the Arctic is highly seasonal in light and temperature, but changing rapidly due to global processes (Jansen et al. 2020; Overland 2020) and local positive feedback (Curry et al. 1995; Polyakov et al. 2020). Temperatures in the Arctic have been increasing over twice the global average, exceeding rates of 1°C/decade for 40 years in some places (Jansen et al. 2020). Compounding the impact of directly increasing temperatures, altered oceanography has led to significant losses in multi-year sea-ice (Serreze et al. 2007) and absolute ice volume (Kwok 2018). For sea-ice that is expected to melt annually, a combination of earlier spring melt and later fall freeze have lengthened the ice-free period in those areas (Barber et al. 2015; Park et al. 2016) and increased open-water area (Comiso et al. 2008). Ecosystem productivity has responded to these direct changes in conditions, most notably in the extended duration of a productive season (Barber et al. 2015; Wasmund et al. 2019). Principle to the marine productivity is the dynamics of ice-cover for algal and zooplankton development.

Ice is central to the base of the marine Arctic ecosystem. Protracted growth seasons for open-water phytoplankton (Wasmund et al. 2019) has shortened the period of growth for algae growing beneath sea-ice (Søreide et al. 2010) and reduced its overall contribution to primary productivity (Castellani et al. 2017). Algal blooms, and their relative timing, are tightly linked to copepod (Søreide et al. 2010) and amphipod life cycles. In particular, ice algae is essential to the diverse class of sympagic (ice-associated) amphipods that spend their adult stages grazing at the underside of ice (Werner 1997; Gradinger and Bluhm 2004, 2010) rather than in open-water or the benthos (Legeżyńska et al. 2012). As such, the composition of and transition between ice algae and sympagic zooplankton to phytoplankton and open-water zooplankton is central to overall productivity during the Arctic summer, even to higher trophic levels (Ramírez et al. 2017). During the short period of ice melt, on the scale of days to weeks, these mixing sources of production result in a sudden pulse of prey for consumers. This pulse is widely understood to be exploited by migratory animals traveling tens (Swanson et al. 2011; Hammer et al. 2021) to thousands (Heide-Jørgensen et al. 2002) of kilometers. However, less studied resident species may similarly exploit ephemeral resources, be indicative of localized environmental change (Barton et al. 2019b), and, as a result, show contrasting resilience with climate change to migratory species (Both et al. 2010). As such, considering the foraging of resident species is also of great importance in monitoring ecosystem function.

Sculpin (family *Cottidae*) are highly residential fishes in temperate and polar waters. These benthic fishes occupy a broad geographic range and habitat types, including the marine Arctic. Sculpin are typically small to moderate in size, mid-trophic, and feed primarily on macroinvertebrates and zooplankton, although little is known specifically about their diet and behavior (but see Moore and Moore 1974; Gray et al. 2017). Corresponding to their sit-and-wait, ambush foraging style (Landry et al. 2019), sculpin generally maintain small home ranges and, in the Arctic, remain beneath extended ice cover year-round (Barton et al. 2020). Long-term dispersal and migrations by sculpin have not been assessed in Arctic environments (Landry et al. 2019); however, studies of Slimy Sculpin (*Cottus cognatus*) in Michigan, USA streams have shown annual displacement did not exceed 500 m with the majority of individuals restricted to just 30 m (Breen et al. 2009). Because of these limited movements and high site fidelity (Gray et al. 2004), sculpin are considered a reflection of the local environmental conditions and may be especially sensitive to changes within that small area (Barton et al. 2019b). Additionally, as a generalist feeder (Gray et al. 2017) that is abundant in nearshore habitats, sculpin can be an effective indicator for environmental stressors such as shifting ice dynamics due to climate change (Barton et al. 2019b). Therefore, sculpin can be an important group to assess the quality of seasonally available resources of an Arctic marine environment.

My broad objective for this study was to evaluate the patterns of feeding by Arctic sculpin during the ice-free season. More specifically, I sought to evaluate their feeding intensity and diet composition. Furthermore, each measure of foraging was assessed for its temporal variability to determine the flexibility of these resident fishes. I hypothesized that (1) consumption levels would be high as sculpin exploit the abundant resources at all times in the ice-free seasons and (2) diet composition would be highly variable as their generalist strategy grants flexibility in matching rapidly changing environmental conditions.

Methods

Study Site

Tremblay Sound (72.35°N, 81.11°W) is located on the northernmost end of Baffin Island, Nunavut, Canada nearest the Inuit community Pond Inlet. The inlet is approximately 150 km^2 (~75 km long x 2 km wide) and exceeds depths of 250 m near the outlet while growing gradually shallower further inland. It is known as a highly productive system that has long been used by Inuit to harvest migratory Arctic char (*Salvelinus alpinus*) and narwhal (*Monodon monoceros*) that are attracted to the annual pulse associated with ice-melt. The inlet is also visited by bowhead whales (*Balaena mysticetus*), ringed seals (*Pusa hispida*), and Greenland sharks (*Somniosus microcephalus*) on a seasonal basis. There are few vertebrate residents of the inlet, with Fourhorn Sculpin (*Myoxocephalus quadricornis*) and Slimy Sculpin being the most visible.

Sampling and Processing

In the summers of 2017-2019, a fyke net was secured in the same place within the sound opening parallel to shore. The net was emptied at each low tide throughout the sampling seasons for each year (21 July – 9 Sept 2017; 30 July – 11 Sept 2018; 11 Aug – 22 Aug 2019) when water depth was below 1 m. At each collection, fish and zooplankton contents were transported to camp for processing and the net was retied for continuous sampling.

Zooplankton collected from the fyke net were filtered from the water using a 500-µm sieve and separated from algae and other debris. Zooplankton were then separated into 9 possible categories by manual inspection with forceps: amphipod, krill, mysid, larval fish, jellyfish, sea angel, copepod, chironomid, and miscellaneous invertebrate. When possible, the number of individuals within each category was counted and the total category mass (to nearest 0.1 g) was taken to estimate contribution to the available prey base.

Sculpin greater than 5 cm total length (TL) were measured for TL (to nearest 0.1 mm) and mass (to nearest 0.1 g). Quotas set by the local Pond Inlet Hunters and Trappers Organization defined the maximum number of individuals that could be sacrificed for dissection while all other individuals were released into the sound after receiving an external tag. Quotas and handling methods were also approved by the University of Windsor (AUPP:#17-12) and

University of New Hampshire (IACUC:#180602). Individuals were sacrificed throughout the sampling season to capture temporal variation in condition and diet as well as across TLs to capture potential ontogenetic shifts in feeding. The combined mass of all stomach contents following their removal from the stomach was measured (to nearest 0.1 g). The contents were then visually sorted into 15 categories: *Gammarus* sp., *Gammaracanthus* sp., *Onisimus* sp., amphipod (for those amphipods that could not be more accurately sorted), krill, mysid, larval fish, jellyfish, sea angel, copepod, chironomid, miscellaneous invertebrate, undigestible material, algae, and digested material. In 2017, this sorting was done on-site whereas in 2018-2019 the contents were frozen at -20°C and sorting was done later. The number of unique individuals were identified and counted as possible and, in 2018 only, each category was massed (to nearest 0.001 g). Collected data were then analyzed for feeding intensity and diet composition.

Statistical Analysis

Feeding Intensity

Feeding intensity was calculated as relative consumption, or the wet mass of the diet contents divided by the wet mass of the fish (g/g). In 2017, however, the wet mass of the diet contents was not measured and relative consumption was instead estimated. A linear model was fit to data from 2018 with relative consumption as the response variable and possible explanatory variables of gut fullness index (1-5) assessed visually with 5 being maximally full and 1 being nearly empty, TL (mm), mass of the fish (g), sex of the fish, and species of the fish (Fourhorn Sculpin or Slimy Sculpin). Using the function *step* in R (v4.0.2, R Core Team 2020), stepwise model selection identified the best model by Akaike's Information Criteria (AIC) scores resulting in the final model:

(1) $C = GFI^2 + TL + Sex + \beta$

where C is relative consumption (g/g), GFI is the gut fullness index (1-5), and TL is total length (mm). This model was significant ($p<0.001$) with an R^2 value of 0.82. Predictions for all individuals in 2017 were made using the function *predict.lm* in R (v4.0.2, R Core Team 2020) and are likely conservative as they are bound by values from 2018 (Figure 1).

A generalized linear model (GLM) framework was used to further analyze factors contributing to variation in relative consumption for years when it was directly measured (2018 and 2019). Explanatory variables included fish mass (g), sex (male, female, unknown), species (Fourhorn or Slimy), year of collection (2018 or 2019) and day of the year of collection. Additional interactions of day of year:year and species:year were included to account for variable sampling between years. As relative consumption had been estimated using these same explanatory factors, 2017 diets were not included in these models. GLMs were constructed with a Gamma distribution using an inverse link function; however, a significant number of empty stomachs resulted in true 0 values. Therefore, diets were additionally analyzed against a binomial distribution to determine factors contributing to empty (0) or not empty (1) stomachs with the same factors as above. Together, this hurdle GLM allowed me to determine variable importance to whether an individual had fed (binomial model) and, given that it had, the magnitude of their consumption (Gamma model; Bolker et al. 2009). All subsets regression was performed using the *dredge* function followed by model averaging of the top models contributing a cumulative 0.95 Akaike weight using the *model.avg* function, both of the package *MuMIn* (Bartoń 2020). Variable importance was then evaluated by the full average z-value (coefficient/standard error) with significance assessed assuming a normal distribution of errors. The same hurdle GLM was used to assess variation over just the day of the year for 2017 diets which were collected over the broadest date range. All analyses were conducted in R (v4.0.2, R Core Team 2020) with $\alpha=0.05$.

Diet Composition

Diet composition was assessed using the three most common metrics, traditionally, for diet items contributing to a population diet: frequency of occurrence (FOO), percent numeric (PN), and percent mass (PM; Garvey and Chipps 2013). FOO is calculated as the percentage of all diets in which the diet item was present; PN is calculated as the mean percentage of the total items in the diet; and PM is calculated as the mean percentage of the mass of the diet (Table 1). Each metric is evaluated independently for each diet category (Table 1) using only those diets for which every diet item was identified (n=158 for FOO), enumerated (n=111 for PN), or massed (n=45 for PM). Sample sizes varied across metrics due to procedural changes between years, i.e., diet contents were not massed in 2017, and inconsistencies in identifiability across diets, i.e., diets with any unidentifiable material could not have percent numeric or mass calculated. Lastly, the Levin's index of niche breadth (B) was calculated using the standardized formula:

$$(2)\quad B = \frac{1}{S-1}\left(\frac{1}{\sum_{i=1}^{S} \%O_i^2} - 1\right)$$

where *S* is the number of prey items and $\%O_i$ is the proportion of the total occurrences for all prey items categorized within prey item *i* (Feiner et al. 2013). Proportion of occurrence was used to maximize sample size as it is an important contributor to estimates of B (Randall and Myers 2001). Mean and standard deviation of B were calculated from bootstrap resampling within 2-week periods spanning the ice-free collection of each year, resulting in 6 time periods. 95% confidence intervals were generated for statistical comparison of niche breadth between periods (Efron and Tibshirani 1986; Randall and Myers 2001).

Feeding strategy of the sculpin population was assessed graphically using a scatterplot of FOO and prey-specific abundance (PSA; Amundsen et al. 1996). PSA is the contribution of a diet category, by PN or PM, except only to those diets that contain diet items of that category.

Prey can then be categorized into four quadrants as, clockwise from the upper left quadrant, Specialized (FOO 0-50, PSA 50-100), Dominant (FOO 50-100, PSA 50-100), Generalized (FOO 50-100, PSA 0-50), and Rare (FOO 0-50, PSA 0-50; Amundsen et al. 1996). The distribution of prey items throughout these quadrants indicates the overall feeding strategy of the population and can be visually compared across time, space, and species. For example, a population with a single Dominant item and the rest as Rare items suggests a population that is dependent upon a single prey item whereas a population with prey scattered throughout the lower half exhibits a very generalized diet with most individuals consuming multiple prey types (Amundsen et al. 1996). The PSA was calculated with both mass and count for those diets where all prey-items are massed (n=30) or enumerated (n=103).

Diets were also analyzed with multivariate techniques allowing each sculpin's whole diet to be treated as a multivariate prey community. Each diet collected was an independent replicate and prey items were treated as species composing that community. Multivariate analyses only used count abundance for prey identification as there are more samples with complete enumeration which span a much broader range of time due to diets not being weighed in 2017. Prey categories for undigestible material and algae were removed from multivariate analyses as they are not representative of true prey items for sculpin. Additionally, digested material was removed as it could not be accurately enumerated nor could it aid in identifying sculpin prey composition. Non-metric multidimensional scaling (NMDS) was used to freely ordinate samples in k dimensions and iteratively adjusted to reduce stress, or disagreement with the true distance matrix calculated using Bray-Curtis distance due to data sparseness (82.28%). This process was automated in R (v4.0.2, R Core Team 2020) with the *metaMDS* function in the *vegan* package (Oksanen et al. 2019) using 250 random starts for k dimensions from 1 to 6. No transformation was made. Final dimensionality for the ordination was chosen using the rules established by McCune and Grace (2002), namely a stress less than 20 but not more than 5 greater than the next higher dimension. The explanatory power of the final ordination was estimated with a coefficient of determination, R^2, from a linear model between the ordination distance matrix and the true distance matrix.

Drivers of variation within the fully multi-dimensional space were analyzed using a permutational multivariate analysis of variance (PERMANOVA). Implemented using the function *adonis* in the *vegan* package (Oksanen et al. 2019), the PERMANOVA serves to attribute dissimilarity among samples to multiple predictor variables, including possible interactions. As *adonis* permutes variable assignment, interpretability is eased by using only categorical response variables. As such, divisions in fish mass were drawn resulting in 4 approximately equally sized groups (Extra-small, Small, Medium, or Large) and day of the year was categorized into 2-week time periods (23 July-5 Aug, 6 Aug-19 Aug, or 20 Aug-6 Sept). Also included within the PERMANOVA model were year (2017 or 2018), sex (Male, Female, or Unknown), and species (Fourhorn or Slimy). Additional interactions of time period:year and species:year were included to account for variable sampling between years. The model was run using 10,000 permutations. Significant variables with 3+ levels, including interactions, were tested *post hoc* using a pairwise PERMANOVA with 1,000 permutations with the function *pairwise.per.manova* in the *RVAideMemoire* package (Hervé 2020).

Significant variables were also assessed *post hoc* with an indicator species analysis (ISA) to identify associations of specific prey items with a group level. The indicator value (IV) for each prey item was calculated in each group level as the product of relative frequency, or the number of samples containing that item, and the relative abundance, or the proportion of its total abundance contributed by that group. IV values range from 0, never found in a group, to 100, present in every sample in a group and only in that group. ISA was performed in R (v4.0.2, R Core Team 2020) using the *multipatt* function from the package *indicspecies* (De Cáceres et al. 2020) with 10,000 permutations.

Finally, sculpin diets were compared to available prey collected in the fyke net to assess potential feeding selectivity. As a fyke net is an imperfect sampling method of zooplankton, prey items were recorded as present-absent at each collection. Fyke net data was then linked with sculpin stomach contents similarly reduced to presence-absence data based on day of collection. Due to time constraints in the field, amphipods were not classified to genus from fyke net samples. Accordingly, the 4 categories within the diet data—*Onisimus* sp., *Gammarus* sp., *Gammaracanthus* sp., and amphipod—were collapsed into a single amphipod category for these analyses. A Mantel Test was performed to calculate the correlation coefficient between the two matrices using the function *mantel* in the R package *vegan* (Oksanen et al. 2019). A significant correlation, from 1,000 permutations, between matrices was assumed to be an indication of non-selective foraging with individuals feeding reflecting available prey whereas a weak correlation may indicate some selectivity. Additionally, as prey may be differentially selected for or against, a Chi-square test of independence was performed for the most frequent prey items—amphipods, krill, fish, and copepods—using the function *chisq.test* in the *stats* package in R (R Core Team 2020). In each test, the null hypothesis of independence suggests sculpin do not show significant selectivity, positive or negative, for that prey item. For items with significant dependence between presence-absence and diet-fyke variables, the effect size was calculated with φ that measures association similar to R^2. All analyses were conducted in R (v4.0.2, R Core Team 2020) with α=0.05.

Results

Feeding Intensity

Among all individuals (n=173), 9.8% of stomachs were empty at the time of collection. The binomial model found the probability of a stomach being empty was not impacted by sex, species, mass, year, nor date of year as well as all interactions (all p>0.648; Figure 1a). For non-empty stomachs, relative consumption ranged from 0.3-12.1% of fish body mass with a median of 3.57% (Figure 1b). Relative consumption did not significantly vary with sex, species, mass, year, and day of year nor any interactions (all p>0.675), though the intercept was significant (p<0.001). For 2017 diets, the wider range of dates was non-significant in both the binomial and gamma models (p=0.178 and p=0.346, respectively).

Diet Composition

Traditional diet metrics (FOO, PN, and PM) revealed that amphipods were of most importance to sculpin diet (Table 2). Amphipod prey were present in the majority of diets (71.5%) and contributed the most numerically (mean=55.5%; SE=4.3%) and by mass (mean=57.3%; SE=8.6%). Of secondary importance were krill that were found in nearly 40% of stomachs and represented ~25% of identifiable diet contents (Table 2). Other minor diet items found in >10% of diets included copepods and larval fish (Table 2). In total, 26 unique prey items were identified, with prey accumulation curves suggesting they constitute most of the available forage (Figure S1).

Ordinating diet items by frequency and prey-specific abundance indicated that the majority of items occur in few (<50%) diets and contribute little (<50%) to those diets in which they are present (Figure 2). Such clustering of diet items in the lower-left quadrant, where prey may be considered rare or of little importance alone, is indicative of generalized feeding (Amundsen et al. 1996). Diets were broad throughout the ice-free period with at least 11 prey categories being identified during each 2-week period. Evenness in the prey-specific abundance increased over the ice-free season as the standard deviation of PSA decreased from 31.2 to 25.8 corresponding to a loss of dominant prey items late in the season (Figure 2c,f). The increased contribution of prey types late in the season was further shown using Levin's niche breadth (Figure 3). Though increasing over the ice-free season in both years, the broadening of diet was shown to be significant only in 2017 by non-overlapping 95% CIs (Figure 3).

NMDS successfully reduced the diet community to two dimensions. The resulting ordination resulted in an acceptable stress level (13.8) which did not exhibit a dramatic reduction by adding a third dimension. The coefficient of determination for the two synthetic axes, based on the correlation of reduced and full dimensional distance matrices, was 0.453 (Figure 4). Variation in ordination space was driven by variation in the timing of a fish's diet collection more than by characteristics of the fish itself. In the PERMANOVA, both the year ($p<0.001$; Figure 4a) and time period ($p<0.001$; Figure 4b) during which a sample was collected were significant. Differences were driven by significantly higher dispersion, i.e., distance from points to group centroid, in 2017 than 2018 (0.607 vs 0.511; $p<0.001$) and a shift in space, i.e., distance between group centroids, of 0.455. Each 2-week time period was significantly different through pairwise comparisons (all $p<0.041$). Differences were again due to a combined change in dispersion ($p<0.001$) and space (Table 3). Additional variation was attributable to sculpin size classes ($p=0.001$), though a three-way interaction with time period and year suggests the explanatory power is an artifact of unequal sampling within size classes over time (Figure S2). No other characteristics of the fish contributed significantly to diet composition, nor did they interact with time variables. All variables analyzed together were estimated to determine 26.7% of the variation in diet composition with 16.2% coming from time period and year. ISA revealed group differences were most strongly associated with changing amphipod consumption, notably associations of unidentified Amphipods (A=0.766, p<0.001) and *Gammaracanthus* sp. (A=0.452, p=0.044) with 2017 and *Onisimus* sp. (A=0.759, p<0.001) with 2018 (Figure 4a). Similarly, the earliest time period was significantly associated with unidentified Amphipods (A=0.835, p<0.001) and *Gammaracanthus* sp. (A=0.433, p=0.014), the middle time period was associated with Mysids (A=0.435, p=0.013), and the latest time period was associated with *Onisimus* sp. (A=0.476, p=0.028) and larval fish (A=0.465, p=0.007; Figure 4b).

Comparisons with fyke net contents indicated an overall weak correlation between sculpin diets and prey availability. By a Mantel Test, the diet and fyke net matrices were weakly correlated (r=-0.107) and non-significant (p=0.997). More closely, only amphipods showed independence in presence-absence between the diet and fyke net (χ^2=2.259, p=0.132). Each of krill (χ^2=33.942, p<0.001), larval fish (χ^2=53.402, p<0.001), and copepods (χ^2=35.562, p<0.001) were observed in diets significantly less frequently than they were expected based on fyke net sampling. The strongest, though moderate, effect size was seen in larval fish (φ=0.50), but both copepods (φ=0.41) and krill (φ=0.40) showed moderate effect sizes as well.

Discussion

Sculpin fed successfully during the brief Arctic summer, with few individuals having empty stomachs and many individuals feeding intensely. Although the percentage of empty stomachs (9.8%) was lower than the average of fishes analyzed worldwide (16.2%), it was well within the range of other fish populations, especially those in North America (Arrington et al.

2002). Regular and intense feeding is typical of a population exploiting a resource pulse (Foote and Brown 1998; Furey et al. 2016). Pulses are characterized by high, often excessive, magnitude resource availabilities and, as such, provide essential resources for consumers (Holt 2008). However, pulses occur in short, infrequent periods (Yang et al. 2008) making maximal exploitation difficult. Consumers can maximize the derived benefit through adaptive behavior (Armstrong et al. 2013, 2016), physiology (Armstrong and Bond 2013), and community structure (Scheuerell et al. 2007). Common among other adaptations is an exhibition of binge-feeding, or consuming more than can be metabolized (Furey et al. 2016). Formal classifications of binge-feeding requires intensive knowledge on the bioenergetic circumstances of feeding (cf. Furey et al. 2016; Hermann et al. 2020). However, other studies that have been able to define binge-feeding rarely report relative consumption exceeding 10% (Essington et al. 2000; Green et al. 2011; Furey et al. 2016; Hermann et al. 2020) with the highest being 13% in juvenile Coho salmon (*Oncorhynchus kisutch*; Armstrong et al. 2013). While definitively stating sculpin as exhibiting binge-feeding is beyond the capacity of this paper, their high levels of consumption in frigid waters is certainly indicative of intense feeding aimed at consuming the most resources possible in the short time available. I also acknowledge that the sculpin sampled (78.91 ± 5.05 g) are smaller than many fishes previously investigated for binge-feeding and small fish are known to feed at higher rates due to relatively faster metabolisms.

Beyond the challenge of exploiting a short window for feeding, the Arctic also presents abrupt variations in environmental conditions. Seasonal transition periods are known to inflict high costs on organisms (Piersma and van Gils 2011; Landes et al. 2017). As such, it is important that organisms exhibit rapid, continual adaptation to keep up with conditions. Sculpin did not show differences in the intensity of feeding throughout the summer period or between sample years. Consistent foraging success in novel conditions suggests sculpin are capable of matching the highly variable environment. An ability to maintain high foraging success in variable conditions may be increasingly important as the Arctic continues to change rapidly and grows increasingly unstable (Angeler et al. 2013; Overland 2020).

Shifts within and between years of diet composition show the influence of environment on the prey sculpin consume. Although diet quantities remained constant over time, composition was influenced by year and date. Consistently, sculpin in Tremblay showed themselves to be a population with a broad, generalized diet showing regular feeding upon many prey items, similar to other Arctic sculpin species found to be generalists (Gray et al. 2017). Though my study's prey sampling was not robust enough to show true selectivity, the shifting association in prey items may suggest the sculpin diet progresses along with the most abundant prey items. Associations with different prey items at different times suggests shifting foraging with variable pulses of prey, pulses which may be sequential or progressive during a transition season as is the ice-melt (Søreide et al. 2010). In the Arctic, the resource pulse progresses from sympagic prey, such as amphipods (Gradinger and Bluhm 2010), to an increasing contribution of open-water prey, such as krill and copepods (Hop et al. 2011), following the onset of ice-off (Søreide et al. 2010). Whereas this seasonal progression occurs annually and directionally, the timing of events is relative and is expected to occur at variable rates (Ji et al. 2013; Overland 2020).

Although sculpin have a flexible diet as prey availability changes throughout the ice-free season, it is unknown how changing ice dynamics may influence sculpin foraging. One mechanism of change is through increased contributions by pelagic prey (Sommer and Lengfellner 2008) due to rapid ice-melt (Høye et al. 2007). Although they showed trophic adaptability (Gerking 1994) by incorporating krill and copepods into their diet, these prey items still represent less important diet items that contributed less in mass and number. Further research should aim to investigate more directly the driver of this apparent preference for amphipods, whether they are physically more available, energetically optimal, or simply more readily recognized in stomachs due to their high indigestible content (Amundsen and Sánchez-Hernández 2019). Resolving these questions is especially important given the lack of specificity achievable in identifying amphipods. Without more detailed identifications, it is difficult to say whether sculpin were consuming benthic, pelagic, or sympagic amphipods primarily and, thus, makes it difficult to determine suitable foraging habitats for sculpin. This is of particular importance as changing ice dynamics (Comiso et al. 2008; Park et al. 2016) contribute to a shift toward more pelagic productivity (Hop et al. 2011). Even further, ecosystem modeling in the Hudson Bay suggested reductions in ice algae can lead to zooplankton losses despite increases in pelagic phytoplankton productivity (Hoover 2010). As such, the magnitude of marine seasonal pulses is expected to decline with earlier summers (Wasmund et al. 2019). The impact a pulse both reduced in magnitude and shifted to pelagic habitats might have on sculpin is unknown.

The possible impacts of changing resource availability due to environmental change is further complicated by encroaching southern species. With warming waters, many fishes seek cooler temperatures in deeper (Dulvy et al. 2008) or more poleward waters (Campana et al. 2020) introducing them to naïve communities (Kortsch et al. 2015). As a generalist predator, sculpin may prove resilient by consuming changing prey communities (Gray et al. 2016) or partitioning resources to limit competitive interactions (ct. Ogloff et al. 2019). However, generalist fish predators such as Atlantic cod (*Gadus morhua*; Kortsch et al. 2015) and harp seals (*Pagophilus groenlandicus*) may provide additional predation pressure, the latter documented in Cumberland Sound also of Baffin Island (Ogloff et al. 2019). Predation opportunities may even be exacerbated by sea-ice losses that increase the opportunity for visual searching by temperate species (Langbehn and Varpe 2017). Regardless of the trophic impacts from southern species, sculpin may be impacted energetically by direct interaction with changed climate conditions.

Sculpin use of energy may also be influenced by climate change. Increased temperatures are expected to simultaneously enable and require additional consumption due to increased metabolism. As sit-and-wait foragers, sculpin typically apportion large amounts of their metabolic budget to consumption and digestion because of their reduced aerobic demand (Clark et al. 2013). But if sculpin are required to engage in more pelagic foraging or active predator avoidance activities, this strategy may prove less profitable. Future work should attempt to measure the metabolic cost of the high consumption levels observed in sculpin in comparison to active foraging costs more typical of pelagic foragers (Clark et al. 2013) as well as the costs of active swimming. Sculpin physiology may be limited by temperature changes as many temperate, coldwater fishes have been observed in laboratory settings to feed at optimal levels over a relatively narrow temperature window of <4°C (Deslauriers et al. 2017). These optimal feeding windows are quite narrow compared with 1°C/decade temperature changes that are being observed in the Arctic (Jansen et al. 2020). Given the rapid and accelerating changes occurring in the Arctic, it becomes increasingly important to have multiple metrics and avenues for exploring the ecology of species threatened there. Beyond the field observations conducted in this paper, these include laboratory experiments, such as respirometry and aerobic scope measurements, and modeling, such as bioenergetic budgeting in multiple climate scenarios. The three-pronged approach helps to bolster the conclusions of each individual component but induces greater costs and can be infeasible in some circumstances, e.g., controlled laboratory techniques with rare species in isolated, undeveloped locations (Petersen et al. 2008). Collecting diverse and thorough field observations of the natural ecology of a species is, however, the first stage of research and informs the needed laboratory standards and support many modeling efforts.

Additional considerations for evaluating my research include those methodological limitations of data collection. First, visual identification of stomach contents for diet studies is difficult (Amundsen and Sánchez-Hernández 2019). Beyond the difficulty of accurately and precisely identifying partially digested contents, not all prey are digested at the same rates which can result in negatively biasing the relative abundance or occurrence of soft-bodied prey items (Amundsen and Sánchez-Hernández 2019). Amphipods, the dominant prey item found in sculpin stomachs, are also among the most recognizable and durable, and thus measures of their consumption may have been overestimated. However, given that amphipods were found in the majority of stomachs, they are surely an important prey item regardless. Beyond identification, the mass of diets is affected by how much digestion occurs between consumption and capture, possibly resulting in underestimates in warming waters, when metabolisms accelerate digestion (Mychek-Londer and Bunnell 2013). Digestion may also have been significant due to the passive collection method used. Using a fyke net enabled high catches with minimal effort, but may have resulted in some individuals that were captured for 12 hours before being sampled during which time up to 40% of their diet may have been digested (Mychek-Londer and Bunnell 2013). Alternatively, as the fyke net also captured zooplankton, the time between entering the net and being sampled may have allowed a sculpin to feed more intensely than naturally. Especially because the fyke net is positioned at a fixed location, both the sculpin and the prey they feed on may not be reflective of the entirety of Tremblay Sound. In addition to being in a fixed location, the fyke net requires open-water and, thus, limited the sampling period. While the range of dates sampled was broad, it represented just half the duration of the full ice-free period and may have missed early and late season changes in feeding intensity or composition as a result. This does not invalidate any observations made, but future work to target sculpin during periods with at least partial sea-ice coverage may reveal additional complexity. Despite flaws resulting from the use of a fyke net, alternative capture methods such as trawling would be inappropriate due to the abundance of protected species such as narwhal, Arctic char, and Greenland sharks.

Conclusion

Sculpin in the Arctic exploit the strong seasonality of the ecosystem through intense consumption during the spring ice-melt resource pulse. Consumption rates throughout much of the ice-free period were consistently high within and among years, with some individuals consuming over 12% of their body mass at one time. Feeding intensity was consistent despite variable diet compositions both within and among years with changing associations with prey items. It is likely that sculpin are adapted to exhibit flexible, generalized diets to best match the temporally heterogeneous resources of their local environment. However, sculpin feeding flexibility may make them a suitable indicator of localized prey communities (cf. Gray et al. 2018; Barton et al. 2019) and, thus, may compliment ecosystem monitoring from the distinct pressures faced by the many migratory species of the Arctic. The Arctic has been and is expected to experience more rapid impacts due to global climate change than any other region (Hinzman et al. 2005; Jansen et al. 2020), making species there highly threatened (Gilg et al. 2012). Continued research of these sensitive species can effectively expand our understanding of the threats faced by Arctic ecosystems and hopefully to mitigate their impacts.

Tables

Table 1. Model estimating relative consumption of sculpin collected in 2017 using individual metrics of gut fullness index (GFI), total length (TL), Mass, Sex, and Species that were collected in 2018. All models include an additional intercept term to improve model fit. Selection was done stepwise using AIC scores to determine the order of parameter removal and final selection. The saturated model and final model selection are shown.

Model	**Parameters**	**AIC**	**Adj. R^2**	**p-value**
$GFI + GFI^2 + TL + Mass + Sex + Species + \beta$	7	52.31	0.8185	<0.001
$GFI^2 + TL + Sex + \beta$	4	49.62	0.8187	<0.001

Table 2. Diet composition metrics for all diet items. Metrics include the frequency of occurrence (FOO), percent numeric contribution (PN), and percent mass contribution (PM). Values reported as mean ± SE for all diet items present. Metrics were calculated only for diets in which all items were identified (FOO), counted (PN), or massed (PM). PN cannot be calculated for algae, digested material, or undigestible material. Note variable sample sizes across metrics due to procedural and identifiability differences across diets that excluded some diets from having a metric calculated.

Prey Item	**FOO (n=158)**	**PN (n=111)**	**PM (n=45)**
	$\frac{D_i}{N} * 100$	$\frac{100}{N}\sum_{j=1}^{N}\left(\frac{C_{ji}}{\sum_{i=1}^{I} C_{ji}}\right)$	$\frac{100}{N}\sum_{j=1}^{N}\left(\frac{M_{ji}}{\sum_{i=1}^{I} M_{ji}}\right)$
Amphipod	45.56	29.25 ± 5.25	3.91 ± 6.18
Krill	39.87	22.39 ± 4.83	8.97 ± 7.70
Onisimus sp.	25.94	14.91 ± 5.43	6.15 ± 3.46
Fish	18.98	7.42 ± 4.54	0.85 ± 0.73
Gammarus sp.	17.72	9.83 ± 5.26	0.89 ± 1.02
Gammaracanthus sp.	12.02	1.56 ± 1.13	0
Copepod	10.12	4.81 ± 5.94	0.09 ± 0.61
Mysid	9.49	5.58 ± 5.26	0.03 ± 0.23
Miscellaneous Invert	6.96	2.35 ± 4.18	0
Undigestible	5.06	---	0
Chironomid	4.43	0.94 ± 2.24	0
Sea Angel	3.79	0.64 ± 2.88	0
Jellyfish	2.53	0.26 ± 1.39	0
Algae	1.89	---	1.52 ± 10.22
Digested	36.70	---	77.55 ± 5.86

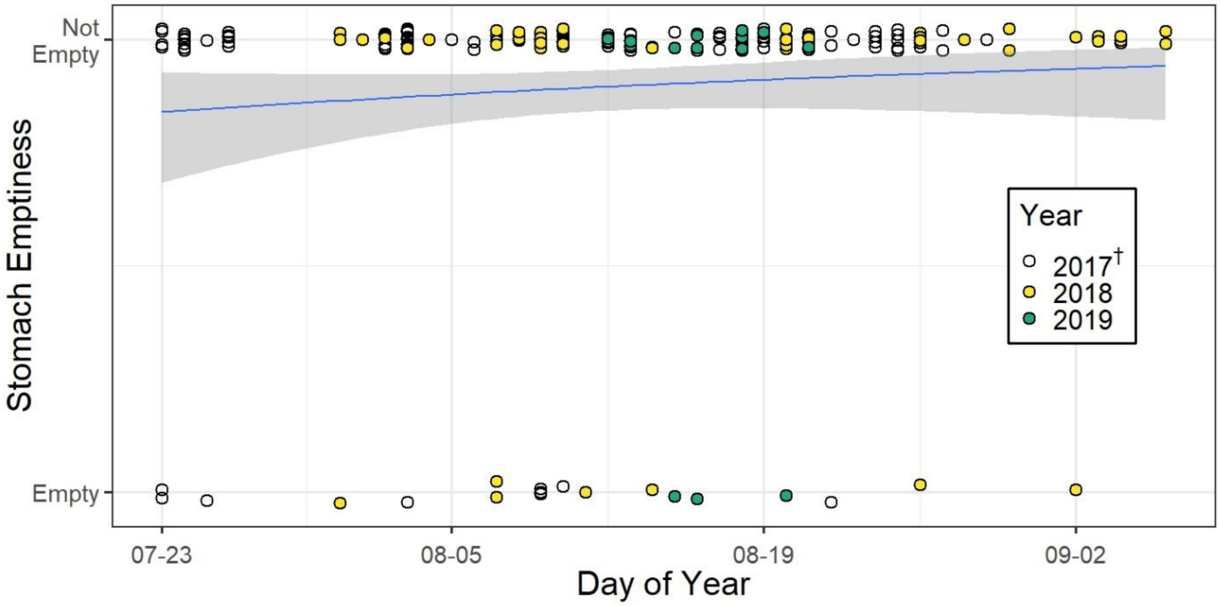
Table 3. Distances between and within time periods for multi-dimensional diet compositions using Bray-Curtis distance. Distances along the main diagonal (in **bold**) represent average distance of points to their group centroid whereas off-diagonal elements (in *italics*) represent the distance between pairwise group centroids. †Average distance to group centroid was significantly different among the groups ($p<0.001$) by a permutation test for homogeneity of multivariate dispersions.

	July 23-Aug 5	Aug 6-Aug 19	Aug 20-Sept 6
July 23-Aug 5	**0.5020**†	--	--
Aug 6-Aug 19	*0.3538*	**0.6216**†	--
Aug 20-Sept 6	*0.4919*	*0.2069*	**0.6131**†

Figures

Figure 1. Diet feeding intensity expressed as (a) a binomial variable of emptiness or not and (b) percent relative to whole fish mass (g/g). Both are expressed over date of collection and include a GLM line (blue) fit to just day of year to highlight consistency over time. Points are colored according to sample year (2017, 2018, or 2019). In (a), points on days with multiple samples are jittered vertically by 2.5% for clarity. †Diet mass was not measured in 2017, therefore relative consumption was estimated using gut fullness, TL, and sex of the fish according to Equation 2 (Table 1) and points are left white.

a



b

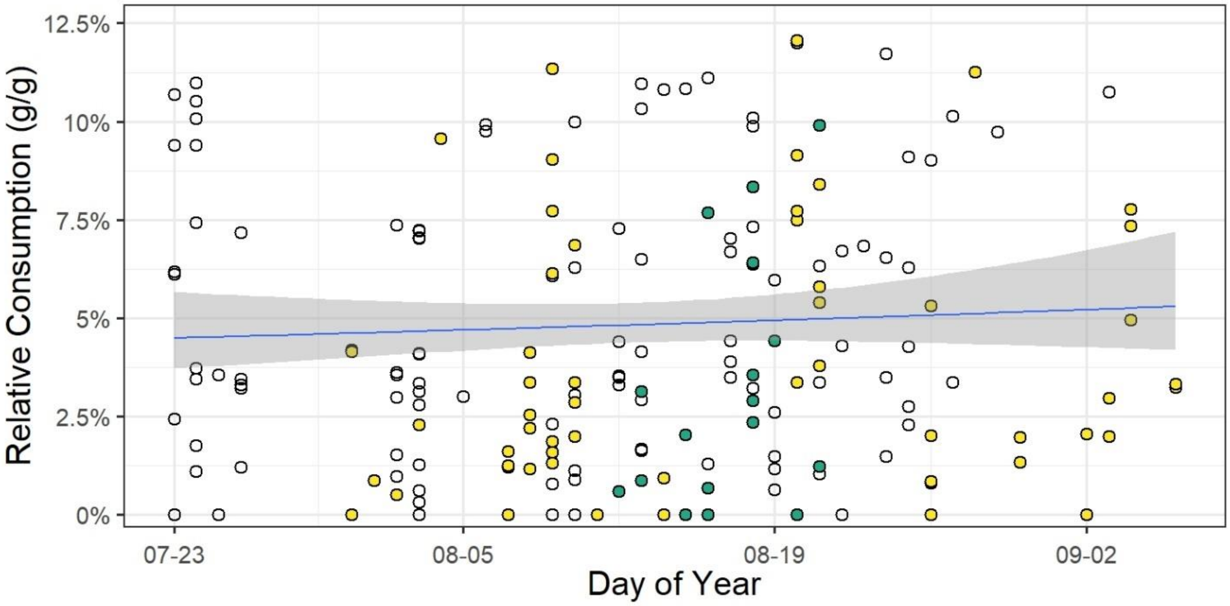


Figure 2. Prey-specific abundance vs frequency of occurrence indicating sculpin population feeding strategies. Abundance can be measured based on (a) prey count and (b) prey mass, but both indicate seasonal feeding changes within the population based on the two-week period in which the diet was sampled during the summer. Quadrants drawn to show approximate locations of prey that are consumed, clockwise from the top left, opportunistically, dominantly, generally, and rarely (Amundsen et al. 1996).

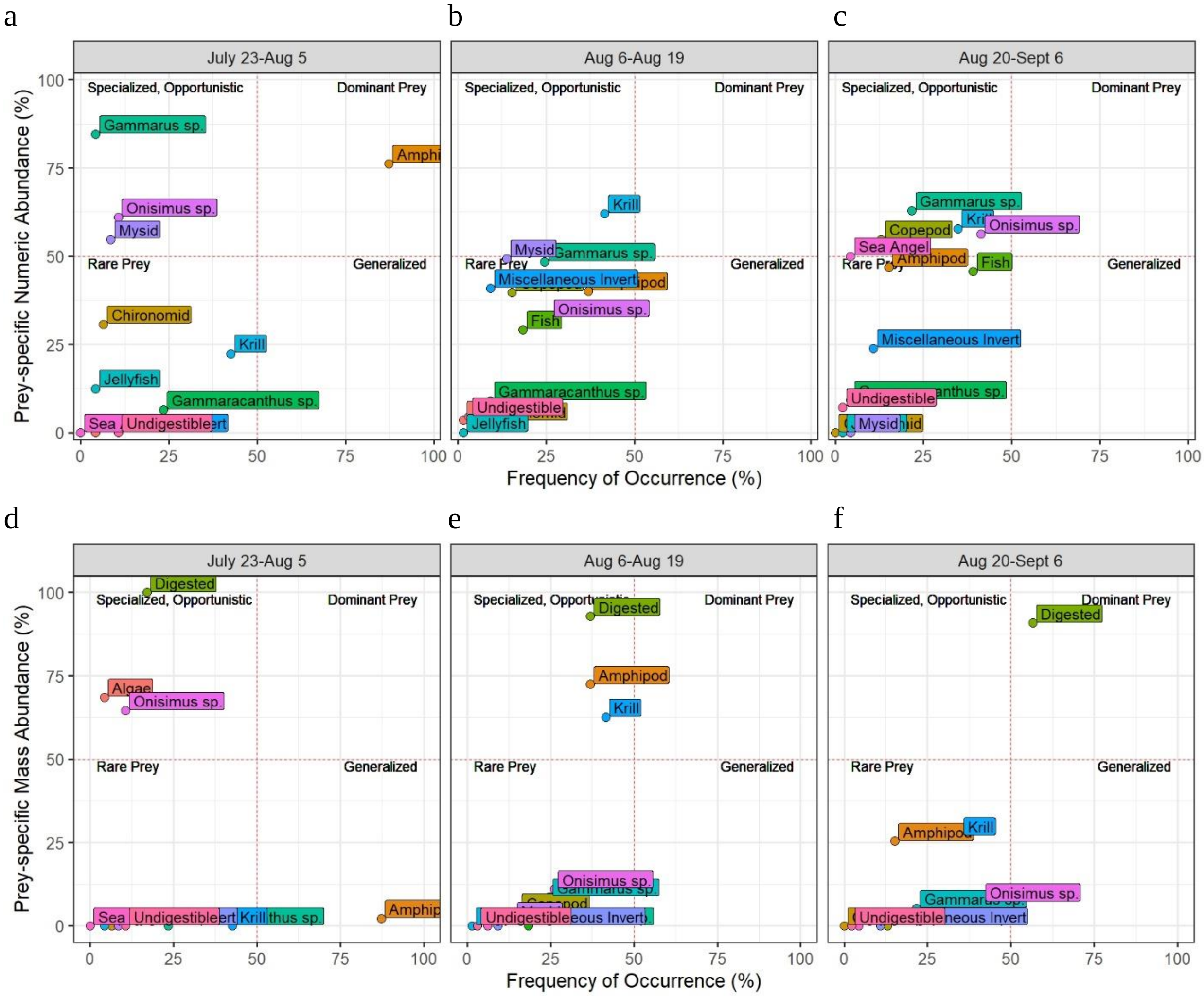


Figure 3. Levin's diet breadth over each summer sampling increased but did so more strongly in 2017 (blue) than in 2018 (yellow). Error bars represent bootstrapped 95% confidence intervals with letters indicating significant pairwise groups. Point size for each time period in each year is proportional to sample size (range n=4 to n=47) as a potential influence on estimates of diet breadth (cf. Randall and Myers 2001).

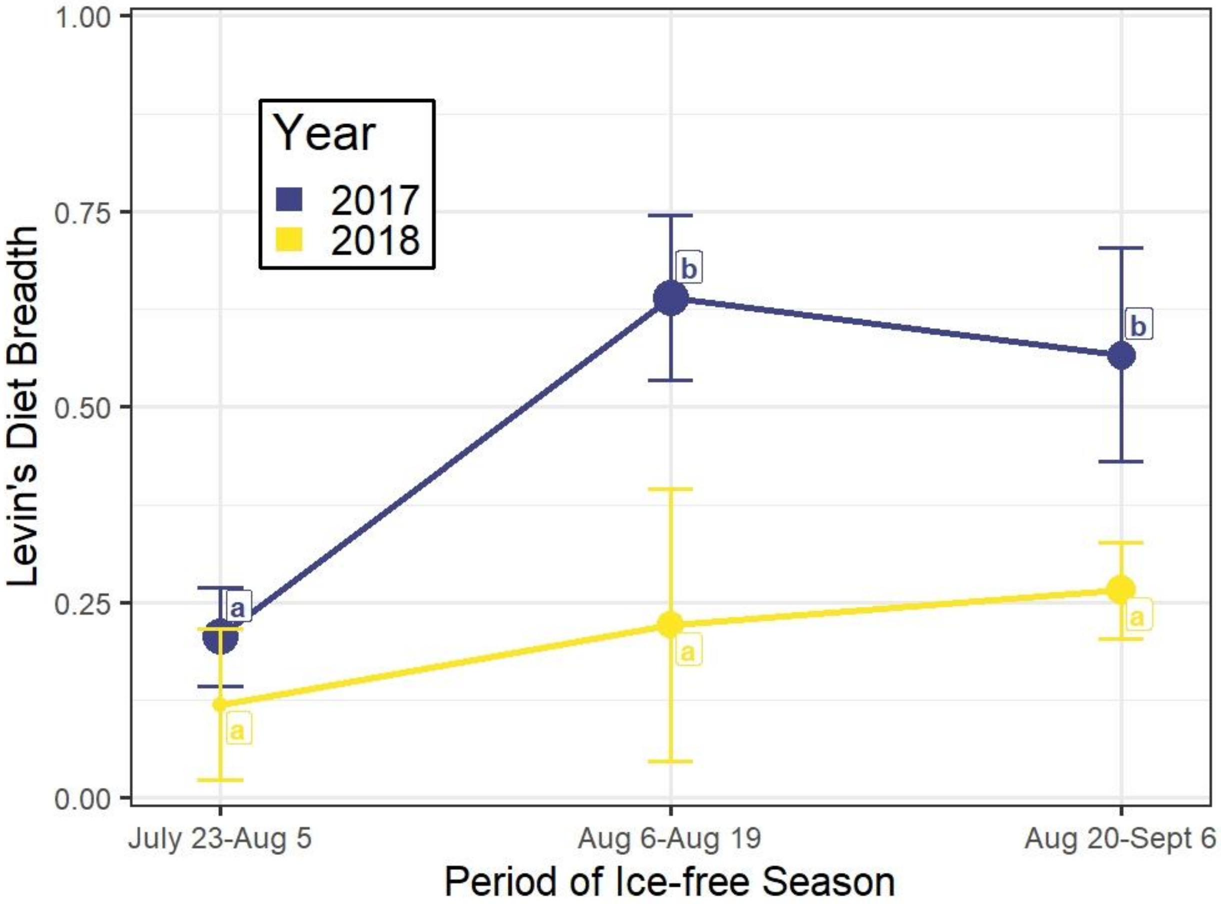
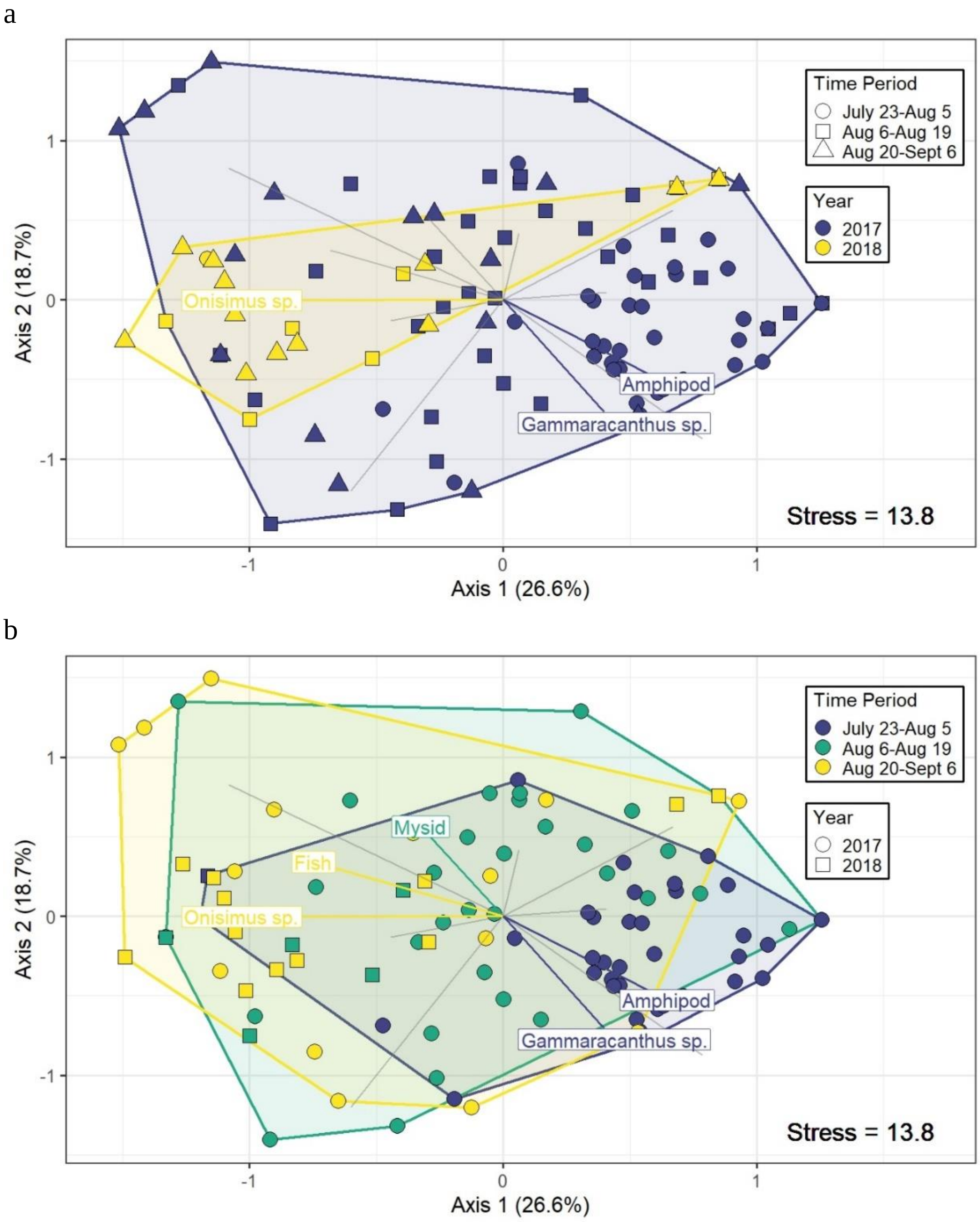


Figure 4. NMDS ordination of sculpin diet communities overlayed with effects of (a) year and (b) time period (Stress=13.8; Cumulative R^2=0.453). Significant indicator species are labeled and colored according to group association. 2017 was associated with unidentified Amphipods (A=0.766, p<0.001) and *Gammaracanthus* sp. (A=0.452, p=0.044) with and 2018 with *Onisimus* sp. (A=0.759, p<0.001). Early time period was associated with unidentified Amphipods (A=0.835, p<0.001) and *Gammaracanthus* sp. (A=0.433, p=0.014), the middle with Mysids (A=0.435, p=0.013), and the latest time period with *Onisimus* sp. (A=0.476, p=0.028) and larval fish (A=0.465, p=0.007). Time period and year were each significant PERMANOVA factors (p<0.001) by a combination of dispersion around and differing locations of group centroids.



Supplemental Figures

Figure S1. Prey accumulation curve for all uniquely identifiable diet items across individual sculpin stomachs. Mean (black) ± SD (grey shading) estimated from 1,000 random permutations of individual accumulation order. Accumulation curves were constructed separately from diets collected in 2017 (n=109) and 2018 (n=32).

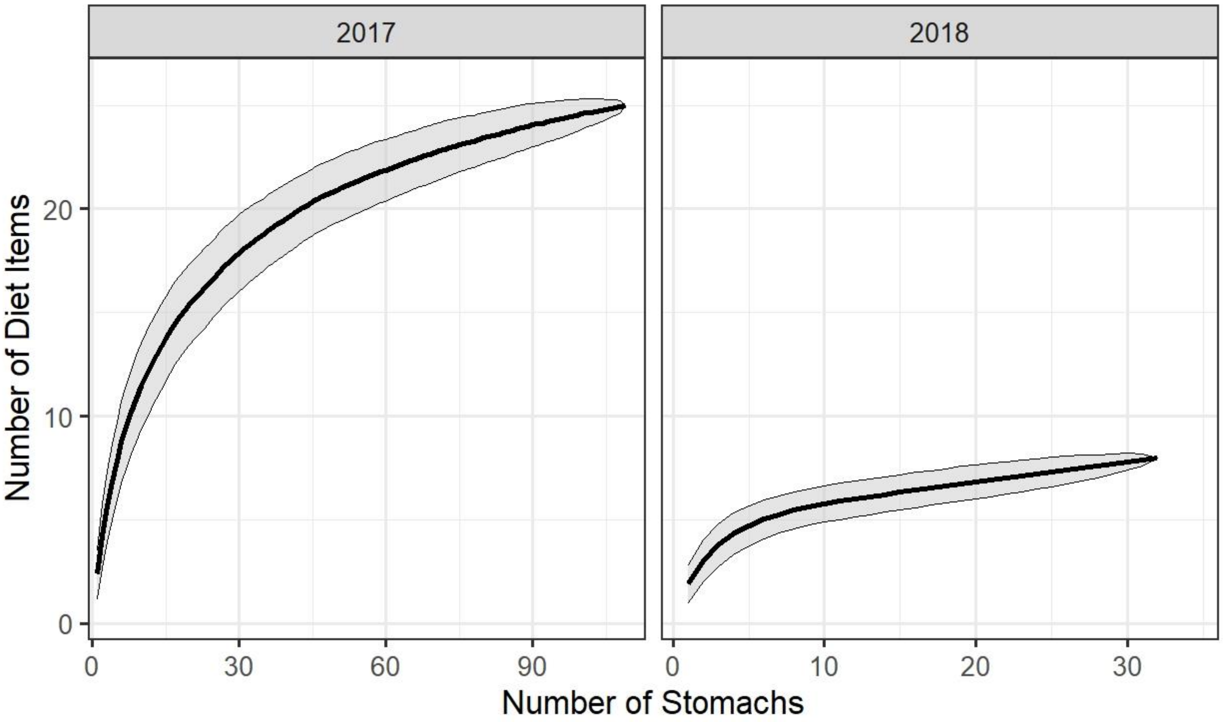
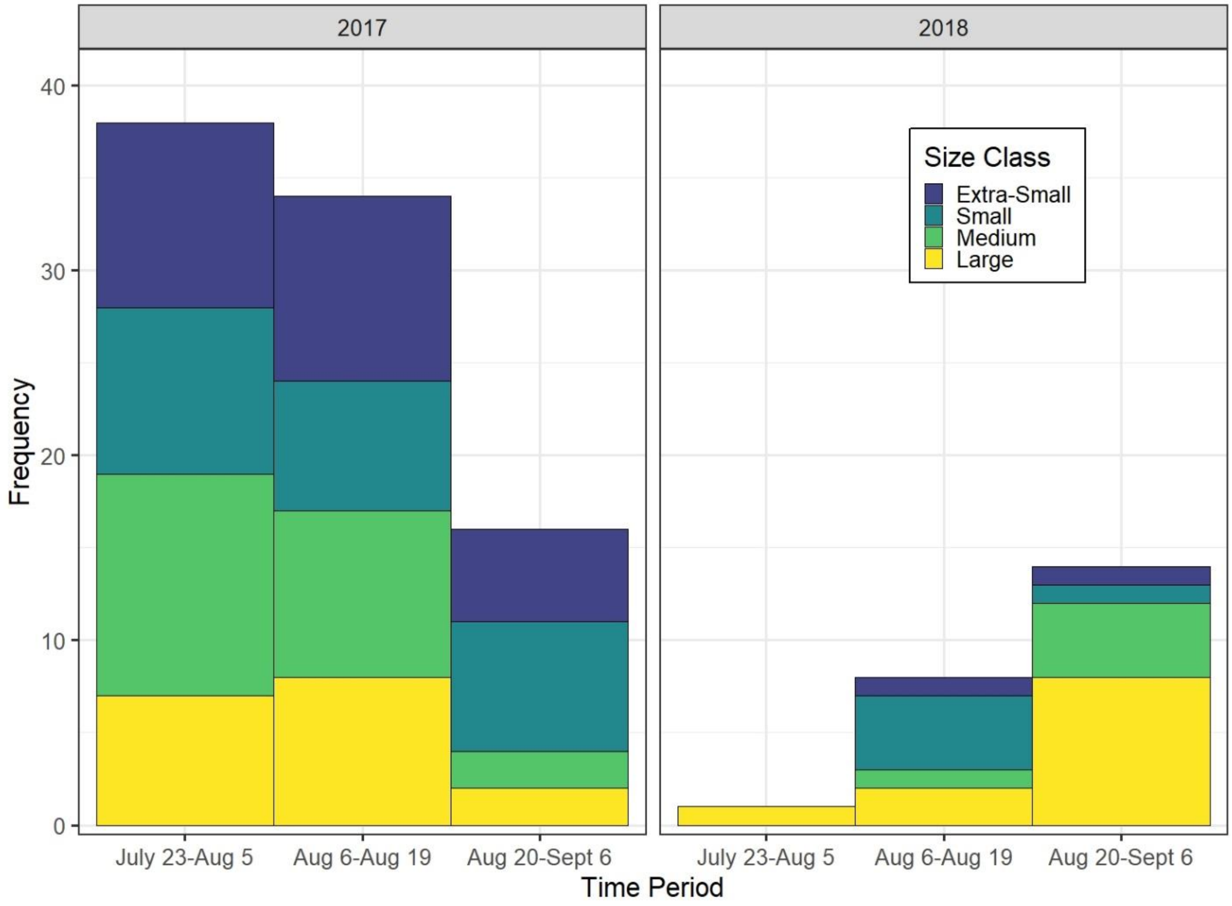


Figure S2. Sampling sizes of sculpin diets within time periods with size classes (Extra-small, Small, Medium, or Large) indicated by color. Bias toward later sampling and larger individuals occurring in 2018 is assumed to mediate the interaction of size with the time of diet collection.



CHAPTER 3: Year-round monitoring of Arctic sculpin with passive acoustic telemetry to identify seasonal behavior

Introduction

The Arctic is a dynamic environment with many coastal marine ecosystems that experience strongly contrasting seasons of ice-cover and open-water (AMAP 2017). The transition from a resting ecosystem state (Staggemeier et al. 2020) begins with algal growth beneath sea-ice (Søreide et al. 2010) which is grazed upon by amphipods and other ice-associated zooplankton (Michel et al. 1996; Gradinger and Bluhm 2010). As sea-ice begins to break-up, these sympagic (ice-associated) resources are released and pelagic productivity rapidly increases (Hop et al. 2011). Though occurring in two phases, the sudden rise in available resources occurs in a short period and infrequently, just once per year, thus covering the three components of a resource pulse (Yang et al. 2008). This short, but intense, pulse of productivity attracts a great number of migratory animals in all manner of directions including tundra-nesting and seabirds (Lameris et al. 2017; Descamps et al. 2019), anadromous fishes (Harwood and Babaluk 2014), and marine mammals (Thackeray et al. 2010). These animals are able to thrive in the Arctic by using spatially distinct resources that may be only temporarily available. These migratory species, such as Arctic char (*Salvelinus alpinus*) and narwhal (*Monodon monoceros*), arrive with the melting ice to feed upon the pulsed resources (Heide-Jørgensen et al. 2002; Swanson et al. 2011; Hammer et al. 2021). Though migrations are a known and well-studied mechanism to respond to seasonal change and migrants are successful in exploiting resource pulses, some organisms in seasonal environments are year-round residents.

Residency, especially in a dynamic environment like the Arctic where the difference between seasons is stark, requires unique adaptations to exploit the distinct conditions.

Adaptations might simply enable a resident to survive, such as anti-freeze proteins produced by some temperate-polar fishes, including sculpins (Yamazaki et al. 2019). Perhaps more importantly, residents must be able to exploit the changing available resources of their environment that may take the form of resource pulses (Yang et al. 2008). Indeed, it seems heterogeneous feeding may be the typical condition among fishes (Armstrong and Schindler 2011) and has been shown to exceed digestive capacity in select situations (Furey et al. 2016; Hermann et al. 2020). Often the types of adaptations considered here for resident species fall under examples of phenotypic plasticity where individuals, not populations, exhibit variable traits that allow them to withstand or exploit a dynamic environment (Piersma and van Gils 2011). Specialized movements, even for residents, may enhance an individual's ability to exploit heterogeneous resources (Armstrong et al. 2013). As such, monitoring the movements of residents across seasonal change (Marsden et al. 2021), can elucidate the behavioral adaptations they utilize to exploit a resource pulse which may otherwise be shrouded by their residency.

Monitoring animal movement on a broader scale is enabled by technological methods, acoustic telemetry being popular in aquatic settings (Hussey et al. 2015). Acoustic telemetry allows individually distinguishable transmitters implanted within an animal to be monitored through space and time, even multiple years. Because receivers are often, though not always (Hussey et al. 2015), positioned in fixed locations for future download, they facilitate over-winter monitoring of seasonal behaviors, even beneath complete ice cover (Marsden et al. 2021). Also due to fixed receiver positions, the scale and resolution are linked to the geometry of the array construction and habitat coverage (Heupel et al. 2006). Beyond positional data, additional data is also able to be transmitted to provide further context about, for example, the animal's depth and acceleration (Murchie et al. 2011; Landsman et al. 2015; Cruz-Font et al. 2016). In all, acoustic telemetry provides the means to parse out animal movement behaviors (Brownscombe et al. 2014; Landry et al. 2019) and assess the seasonality of those behaviors (Marsden et al. 2021). Therefore, acoustic telemetry can serve to monitor the seasonal behaviors of animals to identify their flexibility to changing conditions within their ultimately residential lifestyle.

Sculpin (family *Cottidae*) are a widespread and abundant family that includes many residents of the Arctic. Sculpin are small-bodied fish that are strongly associated with the benthos and are primarily ambush predators (Adams and Schmetterling 2007). They have a generalized diet (Moore and Moore 1974; Gray et al. 2017) and secure themselves to the benthos for lie-and-wait foraging (Kane and Higham 2012). Sculpin exist in a variety of habitats, both freshwater, estuarine, and marine, with some individuals showing a moderate ability to transition between them. Assessed in riverine systems, sculpin show high levels of site fidelity (Gray et al. 2004) rarely displaced >50 m (Breen et al. 2009). As a highly resident species, sculpin have been proposed to serve as sentinel species that indicate the condition of a relatively small local environment to which they are faithful (Gray et al. 2004, 2018). Though they have been shown to exhibit both foraging and transiting behaviors during Arctic summers (Landry et al. 2019), the extent that these behaviors may constitute seasonal changes has not been assessed. Comparisons of sculpin activity across Arctic ice-free and ice-covered seasons, which differ greatly in levels of resource availability (Søreide et al. 2010; Hop et al. 2011), may reveal possible exploitation of resource pulses within a resident species.

This study sought to evaluate the seasonality of sculpin behaviors in a coastal system of the high Canadian Arctic using year-round acoustic telemetry monitoring, including a small number of depth and acceleration transmitters. Specifically, I aim to evaluate the movements of sculpin individuals during the ice-free summer season of high marine productivity in comparison to the limited productivity and ice-covered Arctic winter. I first hypothesize that sculpin are indeed long-term residents; that year-round acoustic telemetry will reveal that sculpin do not leave the system. Second, I hypothesize that activity and space use will increase during the productive, ice-free season as sculpin seek to maximally exploit the abundant resources. And third, I hypothesize that, regardless of season, sculpin activity will be largely restricted to intermittent burst movements and at depths near or at the seafloor. In addressing these fundamental ecological components of their life history, I seek to improve the utility of sculpin as an example of resident behavior that can help expand the understanding of how animals in the Arctic may be expected to respond to climate change.

Methods

Study Design and Sampling

All field work was conducted at Tremblay Sound (72.35°N, 81.11°W) located at the northern end of Baffin Island, Nunavut, Canada. The sound largely lies within the Inuit owned land of the community at Pond Inlet and is traditionally known for supporting large migratory populations, most notably of narwhal (*Monodon monoceros*) and Arctic char (*Salvelinus alpinus*). The sound runs roughly north-to-south for 75 km and averages 2 km wide beyond the wide mouth of the sound (Figure 1). The average depth is 50 m (1-250 m) and grows shallower near the southern end, away from the mouth to the larger marine environment. Two rivers feed wholly into the sound, the first at the southern extent and the second near the midpoint.

The acoustic telemetry receiver array used was organized into a multiple gate design (Heupel et al. 2006; Figure 1). Each gate spanned the east-to-west width of the sound with receivers separated by an average of 451 m (SE=29.4 m) resulting in a variable number of stations within each gate (range 2-8). Each gate was separated by an average of 3933 m (296 m). Gates were labeled A-G, with A being nearest the mouth and progressing to the end of the sound roughly north-to-south, and receivers numbered 1-8, roughly west-to-east. A total of 36 receiver stations were placed throughout the sound, with one additional station located centrally at the mouth of the sound. Each receiver station consisted of an Innovasea (Boston, MA, USA) VR2W (in 2017-2018 only) or VR2AR for reception of 69 Hz codes and a VR2W for reception of 180 Hz codes. Receivers were linked in line between an anchor and submersible buoy such that they were held upright ~1 m from the seafloor. The complete array was deployed, and later re-deployed, in late July-early August (23 July-27 July, 2017; 23 July-29 July, 2018; 4 Aug-8 Aug, 2019) and left in position throughout the year monitoring occupants of Tremblay in both ice-free and ice-covered seasons until final removal on 24 Aug, 2020.

Sculpin were captured using a fyke net in a fixed location during three consecutive ice-free seasons (21 July-9 Sept, 2017; 31 July-6 Sept, 2018; 11 Aug-21 Aug, 2019). The net was positioned to open parallel to shore at a depth that at minimum would submerge the entire frame at high tide but would be in less than 1 m of water at low tide. At each low tide, all contents were removed from the back of the net into a water-filled container (150 L) for transport back to camp. Adult sculpin were separated from any other contents, identified as either Slimy Sculpin (*Cottus cognatus*) or Fourhorn Sculpin (*Myoxocephalus quadricornis*), and measured total length (TL; to nearest 0.1 cm) and mass (to nearest 1 g). Select individuals were equipped with an acoustic transmitter inserted into the ventral cavity through an incision of ~6 mm for V5 and ~10 mm for V9 and V9AP. Acoustic transmitters were one of either V5 (5 mm diameter, 12.7 mm length, 0.65 g in air, 140 days estimated battery life), V9 (9 mm diameter, 24 mm length, 3.6 g in air, 395 days estimated battery life), or V9AP (acceleration and pressure, 9 mm diameter, 48 mm length, 6.6 g in air, 246 days estimated battery life; Vemco, Bedford, NB, Canada; Table 1). Due to differences in transmitter programming and specifications, those individuals implanted with a transmitter were selected to maintain tag burdens, defined as the mass of the transmitter in air divided by the mass of the fish, less than 10% (Table 1). Prior to the incision, individuals were sedated in a solution of MS-222 (60 mg/L seawater) until unresponsive, no more than 5 minutes, and were flushed with seawater over the gills throughout the surgery. Two stitches in 2-0 coated suture (Ethicon, Somerville, NJ, USA) were used to close the wound. Total surgery time averaged 5.27 minutes (SE=0.48 minutes). All fish were monitored for at least 30 minutes after surgery to ensure normal behavior before being released by wading from shore. Quotas and methods were approved by the University of Windsor (AUPP:#17-12) and University of New Hampshire (IACUC:#180602).

Raw detections from acoustic telemetry receivers were filtered for quality assurance. Transmitters detected only once were removed. Single detections at a receiver that required an individual exceed 10 m/s traveling from a non-adjacent receiver were marked false and removed. Because sculpin are known to move very little and may reasonably stay within the radius of a single receiver (cf. Breen et al. 2009), no individuals were removed as mortalities. Filtered detections were then organized by individuals and times to assess the impact of seasonal change on behavior and evaluate characteristic differences in behavioral history through sequence analysis.

Seasonality

The seasons in the Arctic are primarily defined by the ice-melt and -freeze cycles and were used to define two major seasons within this system. The ice-free season was marked as beginning each year from the first day of visible open water on EOSDIS Worldview Satellite

Images (NASA 2021) and ending when open water was no longer visible. The ice-covered season was then defined as the stretch between ice-free seasons, but was assigned to the year in which it began, i.e., January 1, 2020 was part of the ice-covered season of 2019. As such, nearly 2/3 of each year was classified as part of the ice-covered season and all comparisons between the two seasons were normalized to the length of the season. Due to short battery life and poor detection, no V5 transmitters were detected in both the ice-free and ice-covered season and were dropped from all analyses of seasonality.

I broadly compared activity levels between the two seasons using three activity metrics. The first of these metrics was the calculated number of inter-gate movements, i.e., from A to B, B to C, etc. (Figure 1), observed within each season relative to the length of that season. Movements between adjacent gates represent movements of greater than 3 km. The second metric was the roaming index, or the ratio of detecting receivers to total receivers in the array (37) and was again normalized to season length. Although the receivers do not evenly cover the available space and thus the roaming index here does directly translate to an area an individual utilized, receiver spacing necessitates some level of movement to be detected at multiple receivers. The third metric was the length of time within each season a transmitter spent at a single gate. Gate residencies were defined as periods over which a transmitter was detected without gaps greater than 30 days by any receiver within a gate. Residencies were also cut at the transitions between seasons, even if the residency spanned the transition and continued into the next season. Residencies could range from 0-1 as the proportion of the season length. For all three metrics, individuals were paired across seasons (Ice-free or Ice-covered) and a separate paired t-test was performed for each of the three full years (2017, 2018, or 2019) with a

Bonferroni correction to account for multiple hypothesis testing resulting in an α=0.016. Each paired t-test was conducted in R (v4.0.2, R Core Team 2020).

I also estimated space use by sculpin using the lattice density estimation to account for the irregular shorelines of the sound (Barry and McIntyre 2011). A lattice network was constructed within the boundaries of Tremblay Sound with nodes spaced 300 m using up to 8-directional neighbors for each node; no neighborhood edits were made. The selection of the k smoothing parameter has significant impacts on home range estimation (Barry and McIntyre 2011), so a series from k=1 to k=60 was investigated to identify an adequate level of diffusion consistent with receiver detection ranges. However, because detections are limited only to the locations of intermittently placed receiver stations, sculpin positions between the array gates were interpolated using a refined shortest path (RSP) which accounts for land and other impassible obstacles. Paths were calculated using the function *runRSP* in the package *RSP* (Niella et al. 2020) with positions interpolated at 1-day intervals for any breaks in detection at a receiver of 1 day or more (Figure S1). Then, to remove bias toward the non-biologically relevant receiver locations, positions were reduced using a center of activity (COA; Simpfendorfer et al. 2002) at a 1-day interval as to not influence RSP positions but summarize multiple detections at single arrays and receivers. A 50% contour, the smallest area in which the probability an animal was present is greater than 50%, is considered an animal’s core area whereas the approximate full home range extent is defined at 95% according to convention across space use estimators (Fieberg and Börger 2012). Therefore, a series of home range areas at contours equally spaced by 7.5% from 50% to 95% were estimated to assess the impact of this convention and to evaluate far-reaching space use. While higher levels will, by definition, cover larger areas, the rate of increase from core to full range approximates those areas used with less regularity and, thus, represents a relative degree of exploratory behavior. A generalized linear model (GLM) with a Gamma distribution and log link function fit the response variable of lattice density areas for each individual to explanatory variables of season (Ice-free or Ice-covered), contour (50%, 57.5%, 65%, 72.5%, 80%, 87.5%, or 95%) and the season:contour interaction. All home range estimations were conducted in R using the *latticeDensity* package (Barry 2021).

Sequence Analysis

To observe broad patterns in movement across the tagged population, I assessed individual detection histories using sequence analyses (Lowe et al. 2020). Sequences were simplified by reducing positions to the gate of the receiver over evenly spaced time intervals. In instances when a transmitter was detected at multiple gates in a single time step, a majority rule was used to assign a position for the entire interval. For intervals with no detections, the position was imputed by carrying forward the last detecting gate unless the next detection was at a new gate. Positions were not imputed before a transmitter's first detection nor after its last detection. From this, equal length sequences were generated for each individual at a series of time steps: 1 hour (sequence length, 9500), 6 hours (1600), 1 day (401), 1 week (58), 2 weeks (28), and 1 month (14). The percentage of positions imputed was calculated for each matrix and was used to determine the best time step to proceed with for all sequence analyses methods. An interval of 1 day was selected as a balance of limited imputation, nearly all days had at least 1 detection at a gate, and ease of computation.

Sequences were analyzed using multivariate methods based on the comparison of sequences by optimal matching (OM). OM enables a dissimilarity to be calculated pairwise between each sequence, but several metrics exist (Studer and Ritschard 2016). In all metrics, the dissimilarity of sequences is measured by the number of operations required to convert from one sequence to another, using either insertions and deletions or substitutions. A matrix for the cost of substitutions was used to reflect the reality of movements within the telemetry array (Lowe et al. 2020). The matrix, which applied only to substitution operations, weighted any substitutions which resulted in single step movements, i.e., between adjacent receivers, as 1. All second-order or higher movements, i.e., movements between non-adjacent receivers, were weighted doubly to prevent the operation from including theoretically impossible movements—though some (total of 4) higher-order movements did occur due to missed detections. All insertion-deletion paired operations were weighted as 1.9 to favor them over higher-order movements but below single substitutions. This weighting scheme reflecting telemetry arrays has been shown to be effective at removing higher-order movements, to efficiently compare sequence costs, and to minimize time distortions (Lowe et al. 2020). The comparison cost, or dissimilarity, between all sequences was generated using the function *seqdist* in the R package *TraMineR* (v2.2-0.1; Gabadinho et al. 2011) and visualized using the package *plot.matrix* (v1.4; Klinke and Chevalier 2019). Each of the three tag types employed—V5, V9, and V9AP—have different battery life which sets the maximum dissimilarity and were, thus, analyzed separately.

Within the dissimilarity matrix generated for each tag type, clusters of related sequences were defined and sequences that represent each cluster were identified. Cluster identification was performed by the function *pvclust* in the R package of the same name (v2.2-0; Suzuki et al. 2019). Clustering was agglomerative using the Ward D^2 method, with significance identified by bootstrapping (n=1000) with $\alpha=0.05$. All sequences were assigned to the minimum number of significant groups using the function *pvpick* (Suzuki et al. 2019). Within each group, a minimum number of sequences was constructed that cover greater than 50% of the variation in all unique sequences of the group (Lowe et al. 2020). Representative sequences were created using the same custom distance criterion in the *seqrep* function and visualized with *seqplot* in *TraMineR* (v2.2-0.1; Gabadinho et al. 2011).

Acceleration and Depth

A small sample (n=7; Table 1) of V9AP transmitters provided additional *in situ* information on depth use and level of activity. Depths were converted from unitless transmitter values of pressure to meters below the sea surface using the equation:

(3) Depth (m) = 0.9097*TU – 3.6388

where TU represents the transmitter unit recorded by the receiver. Acceleration transmissions were similarly converted to tri-axial acceleration in units of m/s^2 using the constant 0.013588. However, due to merging all dimensions for transmission, measurements are simply reduced to a measure of overall dynamic body acceleration (ODBA; Brownscombe et al. 2014). Analyses of activity and depth use started with simple histograms of ODBA and depth to characterize behavior from overall patterns in the responses. Second, the link between depth and ODBA was evaluated to assess if activity was depth-dependent. As the window for acceleration measurement began at the transmission of depth data, only those instances when both acceleration and the immediately preceding depth transmission (delay≤180 s) were included for this analysis. A mixed effects model was constructed with ODBA as the response variable and included depth (m), seasonal environmental features—average hourly water temperature (°C; logged by the detecting receiver), sun elevation (°; above and below the horizon), and day length (hours)—and a progressive hourly time variable to capture temporal variation unaccounted for by measured conditions as explanatory variables. Each predictor was scaled and centered for comparison of importance and model contribution (Gelman 2008). Receiver and transmitter identity were included as random variables and an exponential autocorrelation structure accounted for temporal dependence in activity. All subsets regression was performed using the *dredge* function from the *MuMIn* package (Bartoń 2020) to rank top models by AICc. The top models with a cumulative Akaike weight of 0.95, or the relative likelihood of a model out of the total likelihood across all models, were selected for model averaging performed with the function *model.avg* (Bartoń 2020). Coefficient estimates and standard errors from averaging were used to calculate z-values of relative importance and variable significance.

Results

Over three summers of sampling, a total of 112 transmitters were implanted across the three types of tags used (Table 1). Of those released, 70.5% (n=79) were detected more than once by at least one receiver throughout Tremblay Sound. After filtering out 393 false detections (0.03% of total), a total of 1,123,168 detections were analyzed (mean=14,217; SE=3,156 detections/transmitter). All detections occurred between 24 July, 2017 and 23 August, 2020 with nearly every transmitter (91.1%) being detected on multiple days (mean=79.5; SE=10.13 days/transmitter). Most of the detected transmitters were detected at more than one receiver (n=68) and more than one gate (n=47) showing some level of movement throughout Tremblay Sound. Estimated conservatively, i.e., using only movements between gates, the total distance traveled by an individual averaged 8.7 km (SE=1.29 km) but with a maximum exceeding 66 km.

Seasonality

Seasonal measures of activity were, generally, higher in the ice-free summers than during the ice-covered season, although activity was highly variable among individuals. Some individuals exhibited up to 7 inter-gate movements in a single season with short residencies at each gate while others were detected at a single gate the entire battery life of the transmitter. On average, a fish was observed to make 2.14 (SE=0.32) inter-gate movements over the life of the transmitter, with more occurring during the ice-free season (mean=1.02; SE=0.14) than the ice-covered season (mean=0.55; SE=0.12). Inter-gate movements spanned multiple days (mean=10.3; SE=1.52 days; minimum 42 minutes), but were 2.78-times faster in the ice-free season (mean=7.5; SE=0.96 days) than the ice-covered season (mean=20.9; SE=2.57 days). From a paired t-test, the number of movements relative to season length increased significantly during the ice-free season of 2017 (t=3.33, p=0.003) and 2018 (t=3.16, p=0.008), though the higher number of movements in the ice-free season of 2019 was not significant (t=0.73, p=0.485; Figure 2a). Roaming index values ranged from 0.02-0.29, averaging 0.07 (SE=0.003) for both seasons before normalizing. After normalizing by the length of the season, the ice-free season showed a greater than 3-fold increase over the ice-covered season (mean=0.0011; SE=0.00008 vs. mean=0.0003; SE=0.00003). By the paired t-test, roaming was significantly higher in the ice-free periods of 2017 (t=4.63, p<0.001), 2018 (t=7.20, p<0.001) and 2019 (2.47, p=0.038) than in the respective ice-covered seasons of each year (Figure 2b). The average proportion of a season spent in residency at a single gate was 0.20 (SE=0.01) in the ice-free season and 0.24 (SE=0.02) during the ice-covered season. Individuals did not show a significant change in any paired t-tests for residency length relative to season (2017 t=0.33, p=0.737; 2018 t=1.25, p=0.232; and 2019 t=0.30, p=0.768; Figure 2c). However, when not scaled to season length, average residency duration was more than 4-times longer during the ice-covered season than the ice-free season (60.2 days vs. 15.1 days).

In accordance with relative metrics of activity, space use was individually variable but strongly seasonal. The most appropriate k smoothing parameter selected was 15 steps allowing sculpin to diffuse to neighboring nodes just beyond receiver detection ranges (Figure S1). The maximum home range for a single individual was 25.5 km^2, just 19% of the full extent of Tremblay Sound. Similarly, the home range of all sculpin combined across all 3 years was 22.7 km^2, just under 17% of Tremblay Sound. Home ranges, reflecting detection concentrations, were primarily concentrated along the western shore (Figure S2). Home ranges were larger at all levels during the ice-free period, indicated by a significant intercept term in the GLM (ice-covered -0.805 vs ice-free -0.489; p=0.043). The rate of increase for home range area from 50% to 95% contours was consistent in both the ice-free and ice-covered seasons (p=0.475).

Sequence Analysis

Qualitatively, the sequences reveal the more intensive movements of sculpin during the ice-free season with long residencies at a single gate during the ice-covered season (Figure 4). A very broad range of sequence histories were observed with dissimilarities ranging from 1-700.6 (Figure S3). This is greater than 90% of the maximum dissimilarity achievable of 761.9, implying strongly contrasting sequences were observed. A total of 10 cluster groups were identified: two within the V5 tags, six within the V9, and two within the V9AP. Representative sequences for each group (Figure S4) show differences are driven by what and how many gates are included within a sequence. Overall, representatives still follow similar patterns of long residencies during the winter with, among active groups, movements during summers beginning and ending the sequence. In V9AP and V5 tags, groups were primarily distinguished by the number of detections (Figure S4b,c).

Acceleration and Depth

Acceleration and pressure transmitters were able to reveal characteristic sculpin activity and depth use. ODBA ranged from 0-3.46 m/s^2 (mean=0.26; SE=0.003 m/s^2) and was highly right-skewed (Skewness=2.68). Skew was the result of the most common activity being resting, at levels below 0.06 m/s^2 (Murchie et al. 2011), and only 0.03% (n=5) of movements reaching full burst speed (Figure 5a). Depths at which sculpin occurred ranged from 0-53 m (mean=2.96; SE=0.02 m) but were highly right-skewed (Skewness=5.69) toward depths below 5 m (Figure 5b). Use of these shallow waters occurred even at receivers far from shore that were at depths well over 100 m (Figure S5). Via GLMM, ODBA increased over the monitoring period with notable increases in March-April. This increase was captured in the retention of the progressive hour variable and a significant coefficient estimate in model averaging (0.1509, p<0.001; Table 2). Similarly, depths decreased, i.e., grew shallower, during the latter portion of the monitoring period. Accordingly, depth was retained in the final model along with daylength and temperature. Depth and daylength had negative relationships to ODBA whereas temperature was positively related to ODBA, though all coefficient 95% confidence intervals included zero (Table 2).

Discussion

Sculpin demonstrated increased horizontal movements and space use during the ice-free season than during the ice-covered season. Both long scale movements and roaming increased while residency times shortened during to the productive ice-free season. Even further, home ranges at all levels were larger in the ice-free season despite having less than half the length of time compared to under ice. The sea-ice melt releases sympagic algae and amphipods (Michel et al. 1996), releases trapped nauplii within the ice (Hop et al. 2011), and shifts primary productivity to open-water phytoplankton (Park et al. 2015). This overall rise in ecosystem productivity results in a pulse of resources that sculpin activity and space use may suggest they are exploiting, even at great cost. Another possibility is individual displacement by the growing presence of larger-bodied migrants, including common predators (Chivers et al. 2001). While they may be displaced by other predators, such as Glaucous gulls (*Larus hyperboreus*) or Bearded seals (*Erignathus barbatus*), sculpin have not been found in the stomachs of any Arctic char that are very abundant in Tremblay (L. Hammer, *pers. obs.*). As such, it may be unlikely that predator avoidance contributes to significant changes in activity. Activity may also change in response to warmer temperatures and opening habitats from ice-melt (Lindstrom and Hubert 2004), though temperature was only a weak factor in the mixed model on ODBA. Additionally, rising summer temperatures would force increased foraging regardless of availability making the seasonal behavior still reflective of increased foraging. As movement sequences show a tight association between the day of first open-water and increased activity that carries through the ice-free season, but appreciable temperature increases primarily follow the completion of ice-melt (Søreide et al. 2010; N. Hermann *unpublished data*), the rapid rise in productivity is the most likely initial impetus for increased activity. Therefore, despite being unable to collect sculpin beneath the sea-ice and during the first ice-melt, I believe intense feeding rates may begin at this time and continue through the ice-free season when diet samples were collected.

Sculpin habitat usage also may be indicative of seasonal exploitation of changing resources. The mixed effects model showed a weak relationship between ODBA and depth in which sculpin were more active at shallower waters during March-April. Unfortunately, restrictive battery life prevented a longer monitoring period to observe trends through to ice-off in June-July, but a rise in algal productivity is expected to occur beneath the ice before the transmitter batteries died (cf. Søreide et al. 2010). Production may begin as early as 1 month after the first appearance of the sun (January 28th at Tremblay; http://www.esrl.noaa.gov/gmd/grad/solcalc) with algae and grazer abundance continuing to rise through March and April (Gradinger and Bluhm 2010; Søreide et al. 2010). Given the approach of sculpin to the water's surface in February and significant increase in small-scale activity, it is possible that their movements may indicate an exploitation of this sympagic productivity. If this is the case, this exploitation even months before the beginning of the ice-free season may only be available to residents as migratory species are unable to return to the system at this time (Heide-Jørgensen et al. 2002; Harwood and Babaluk 2014; Hammer et al. 2021). Many fish are assumed to enter a state of dormancy in winter (Marsden et al. 2021), but my results suggest this is not the case with sculpin in this Arctic system. Certainly, activity did reduce during the ice-covered season with many individuals showing long, even full season length, residencies within the detection radius of a single receiver. Perhaps, due to the length of the Arctic winter (Berge et al. 2015), sculpin energy reserves cannot last until the onset of the ice-free season without some feeding under ice-cover (ct. Biro et al. 2004). In foraging under sea-ice, sculpin would largely lack competition making this a resource opportunity unique to residents. Incomplete dormancy may also reflect sculpin reproductive patterns that are poorly understood but known to primarily occur during the winter (Goldberg et al. 1987) and involves males nest-guarding (Leonardsson et al. 1988). The timing and duration of reproduction warrants further investigation for its possible influence on movement, especially during the winter. More generally, it is also important to understand the timing of reproduction due to the importance of matching larval development with spring productivity (Fortier et al. 2006). Even with limited knowledge of the reproductive behavior of sculpin, the reproductive status of those sculpin given acoustic transmitters is unknown nor were individuals reliably sexed. As such, no speculations are made here to the influence reproductive behavior may have had on the movements observed, though its nature should be more closely assessed for its impact on seasonal activity.

Despite the strong seasonality in sculpin movements in response to ice-off and presumed feeding opportunities, sculpin were shown to remain in Tremblay Sound year-round as residents of the marine system. Sculpin have previously been highlighted as having high site fidelity (Gray et al. 2004) as I confirmed in Tremblay Sound. Given the residency and limited mobility of sculpin has primarily been evaluated in riverine systems previously (Gray et al. 2004; Breen et al. 2009), this further shows that their constricted ranges are not due solely to constricted habitats. As the only known resident fishes of Tremblay Sound, sculpin may benefit from a lack of both predators and competition for resources that are limited during the less productive majority of the year. Though it has been suggested elsewhere that Fourhorn sculpin may be estuarine fish that quickly return at ice-melt (Barton et al. 2020), my telemetry results suggest they primarily remain present in marine waters underneath the ice. The receivers positioned just off the bottom of the sound allowed them to continue recording transmissions from fish present underneath solid sea-ice to investigate their winter movements (Marsden et al. 2021). Doing so allowed me to identify the contrast in seasonal behavior that is suggestive of their exploitation of the resource pulse in the ice-free season and more conservative behavior during the stress of winter (Biro et al. 2004).

Sculpin movements were largely intermittent, but not strictly associated with the benthos. The distribution of sculpin activity, from those few individuals that were so monitored, was indicative of a lie-and-wait predator with the most abundant behavior being resting. A highly right-skewed distribution similarly resembles that of other ambush predators, including the muskellunge (*Esox masquinongy*), though sculpin show a greatly truncated upper limit (Landsman et al. 2015). The range closely resembles that of bonefish (*Albula vulpes*), though their dominate foraging behavior was characterized by searching (Brownscombe et al. 2014) leading to a distribution shifted toward low-activity over resting (Murchie et al. 2011). While resting was the predominant activity by sculpin, results from the mixed effects model exploring drivers of ODBA suggest individuals may express more active behaviors at particular times. Sculpin have long been understood to be benthic fishes (Gray et al. 2018), with all species in the family having flattened features and cryptic coloration (Whiteley et al. 2011; Kane and Higham 2012), and even pectoral fins for holding position in fast-moving water (Kane and Higham 2012). However, sculpin here were shown to be quite regularly using shallow waters surrounding receivers even in very deep waters far from shore. More directly, sculpin were never found at depths greater than 53 m despite maximum depths in Tremblay exceeding 250 m and depths at frequently visited receiver stations (e.g., D1 and D2) of more than 100 m (Figure S5).

Given their resident life history, sculpin must be able to withstand seasonal environmental conditions and variable feeding opportunities. Heterogeneous conditions are very common across fishes and a common strategy to cope is binge-feeding (Armstrong and Schindler 2011), effectually using stomach volume as the limiting factor rather than digestion rate (Furey et al. 2016). Binge-feeding is particularly useful in cold-water, as is typical in the Arctic, due to slowed metabolic rates (Furey et al. 2016) and can be paired with behavioral responses such as specialized food handling (Hermann et al. 2020) or seeking warmer refugia (Armstrong et al. 2013). The resolution of temperature coverage in Tremblay Sound was too coarse to address microhabitat targeting, but future studies may address if refugia exist or the impact of rising to shallower depths. The warm summer of 2019 corresponded to fewer sculpin being caught in shallow waters nearshore, i.e., relative to previous summers 2017 and 2018 (Hermann, N.H. *unpublished data*), suggesting sculpin may, even temporarily, seek deeper, cooler waters (Dulvy et al. 2008). As depth sensors were only deployed in 2019, depths cannot be compared across years directly but the average depth of receivers at which sculpin were detected in 2019 does not appear to be different than 2017 or 2018. Next steps might serve to characterize the available and utilized environmental features of Tremblay Sound to identify sculpin preferences for temperature, substrate, and ice accessibility. Use of other acoustic transmitters can make *in situ* measurements of temperature experienced by the fish compared to a network of loggers recording available temperatures over space and time. Corresponding measurements of prey availability can then correlate movements and temperature seeking with prey availability to address prey selection (Isaac et al. 2012) and habitat motivation (Armstrong et al. 2013). Without this deliberate work it can be difficult to speculate to the direct impact warming waters might have upon sculpin in the Arctic. Indirectly, however, sculpin may be sensitive to changes in abundance, accessibility, and duration of prey availability.

Climate change, advancing quickly in the Arctic (Overland et al. 2019), can have a multitude of impacts on the ecology of native fishes, including sculpin. Though direct impacts remain unmeasured, a variety of other changes documented in the Arctic may indirectly alter the flow of resources to sculpin. First, it has already been observed in sub-arctic waters that productive seasons are lengthening with dampened peaks during seasonal transitions (Wasmund et al. 2019). Though changes in timing may not result in a phenological mismatch for sculpin as it would for migratory species, due to consistent spatial overlap, a change in the abundance and location of resources may hinder sculpin. With rapid ice loss and thinning (Høye et al. 2007), the primary and secondary productivity of sympagic organisms is largely being replaced by open-water phytoplankton and zooplankton (Søreide et al. 2010; Park et al. 2015). In contrast to benthic or sympagic foraging, pelagic foraging may exert a greater energetic cost on sculpin (cf. Clark et al. 2013). Additionally, diet observations during the ice-free season (Chapter 2), revealed open-water zooplankton such as copepods are minor prey items compared to benthic and sympagic amphipods. Though my results suggest that sculpin may be flexible in their movements and habitat utilization, I cannot estimate the exertion of open-water swimming without both a detailed image of temperature and measurements of sculpin respiration rates (Murchie et al. 2011; Cruz-Font et al. 2016). Future work to estimate fish respiration relative to body size and temperature can allow researchers to evaluate the effects year-round of an altered climate regime. Losses in prey accessibility may be exacerbated by encroaching lower-latitude species (Campana et al. 2020) that may disrupt the Arctic food web (Kortsch et al. 2015; Ogloff et al. 2019; Griffith et al. 2019) as it continues to grow less seasonal with climate change.

There are important considerations and limitations in interpreting fish movements from acoustic telemetry. As acoustic telemetry relies on inserting a transmitter into the body cavity of the fish being monitored, it is assumed that this surgery does not influence behavior. Often cited is the potential impact of the transmitter mass relative to the animal's mass, known as tag burden, on swimming ability or long-term growth (Carrera-García et al. 2017; McCabe et al. 2019). Indeed, the sculpin I tagged had relatively high tag burdens, in some cases nearly 10% of their body weight (Table 1). While these burdens are relatively high, the need to maintain these low burden has been debated (Jepsen et al. 2005) and is species-specific. Higher tag burden was not associated with less movement, suggesting sculpin, as a benthic and largely inactive fish, may be capable of withstanding these high tag burdens. As the rate of tag recovery was lowest among the smallest transmitters, it is likely that recovery was limited by detection efficiency rather than fish mortalities from handling or tag burden. Detection efficiency was low due to receivers being deployed in east-west gates that were widely-spaced north-south (Figure 1) that was designed primarily for tracking migrations (Heupel et al. 2006) such as those by Arctic char tagged in the same system (Hammer et al. 2021). As this array structure is best suited for larger, more mobile animals, refined details about sculpin behavior were surely missed both within and between gates. Despite simplified behaviors, broad observations were sufficient for characterizing the seasonality of sculpin activity. Similarly, reflecting the occasional detection patterns common across many transmitters, the small subset of V9AP transmitters primarily monitored sculpin beneath sea-ice. Although this bias prevents me from making similar seasonal comparisons with depth and activity as with the V9 transmitters' broad movements, the progressive increase in activity over time is still noteworthy. Also limiting is the use of a single capture and release point, possibly resulting in monitoring sculpin that may not be entirely representative of the total population in Tremblay Sound. Individuals did show movements throughout much of the sound, but it is unknown, especially along the eastern shore where sculpin were least observed, if the observed movement patterns are universal. Ultimately, the technological limitations of acoustic telemetry with the biological limitations of low mobility fishes like sculpin may make discerning behavior more difficult, but they do not invalidate that which can be identified such as the dramatic seasonal change observed here.

Conclusion

From my monitoring of sculpin in the marine Arctic year-round, I was able to identify their responses to seasonal dynamics. Firstly, I did identify sculpin as being entirely residential with individuals being regularly detected within Tremblay Sound at all times of the year. Even further, this residential behavior was commonly concentrated within only a portion of the sound confirming sculpin are tightly linked to local conditions. Though present in consistently small home ranges, there was a notable uptick in activity during the warmer, more productive, ice-free months, with individuals moving more and, on average, staying put for shorter times. This increased activity is most likely linked to an exploitation of only briefly available resources resulting from the annual ice melt. However, from finer-scale monitoring of depth and activity, I found that sculpin do not seem to go entirely dormant beneath the ice and may begin utilizing under-ice resources well before melt. Through this research I hope to broaden the mechanisms by which Arctic organisms may be threatened by climate change by their unique seasonal life histories.

Tables

Table 1. Innovasea transmitter specifications and tag burdens imposed on sculpin in this study. All specifications are nominal with slight deviations possible. Burden is estimated as the mass in air of the tag divided by the mass of the fish.

Specification	**V5**	**V9**	**V9AP**
Mass in water (g)	0.38	2.0	3.6
Mass in air (g)	0.65	3.6	6.6
Length (mm)	12.7	24	48
Diameter (mm)	5	9	9
Frequency (kHz)	180	69	69
Transmission Delay (sec)	30-90	100-180	100-180
Nominal Battery Life (days)	140	395	246
Number Implanted	45	60	7
Tag Burden (± SD)	0.82% (± 0.51)	3.80% (± 2.89)	6.89% (± 2.67)

Table 2. Mixed effects model of overall dynamic body activity (ODBA) selection and coefficient estimations. All models were constructed with transmitter ID and receiver location as random variables and with an exponential autocorrelation structure across hours. Top four models ranked by AICc score, those contributing a cumulative 0.95 Akaike weight, from all subsets regression with full model average coefficients and relative z-scores in parentheses. All main effects were scaled and centered.

Model	**Intercept**	**Date and Hour**	**Day Length (hrs)**	**Depth (m)**	**Temperature (°C)**	**Sun Elevation (°)**	**df**	**log-Likelihood**	**AICc**	**ΔAICc**	**w**
Model 1	-1.971	0.1486	---	---	---	---	10	-2906.2	5832.7	0.00	0.75
Model 2	-1.976	0.1488	---	-0.0266	---	---	11	-2906.8	5835.8	3.10	0.16
Model 3	-1.956	0.1899	-0.0484	---	---	---	11	-2907.9	5837.9	5.27	0.05
Model 4	-1.960	0.1506	---	---	0.0237	---	11	-2908.3	5838.8	6.13	0.04
Model Average	-1.970*** (17.089)	0.1509*** (3.741)	-0.002 (0.947)	-0.004 (0.112)	0.0008 (0.518)	---					

*** 99.999% CI Does not include 0

Figures

Figure 1. A bathymetric map of Tremblay Sound with the receiver array (white points), campsite (red star), and fyke net (green square) locations noted. Bathymetry data from GEBCO Compilation Group (2020) GEBCO 2020 Grid (doi:10.5285/a29c5465-b138-234d-e053-6c86abc040b9). Map imagery from Google using *ggmap* (Kahle and Wickham 2013) in R (v4.0.2 R Core Team 2020).

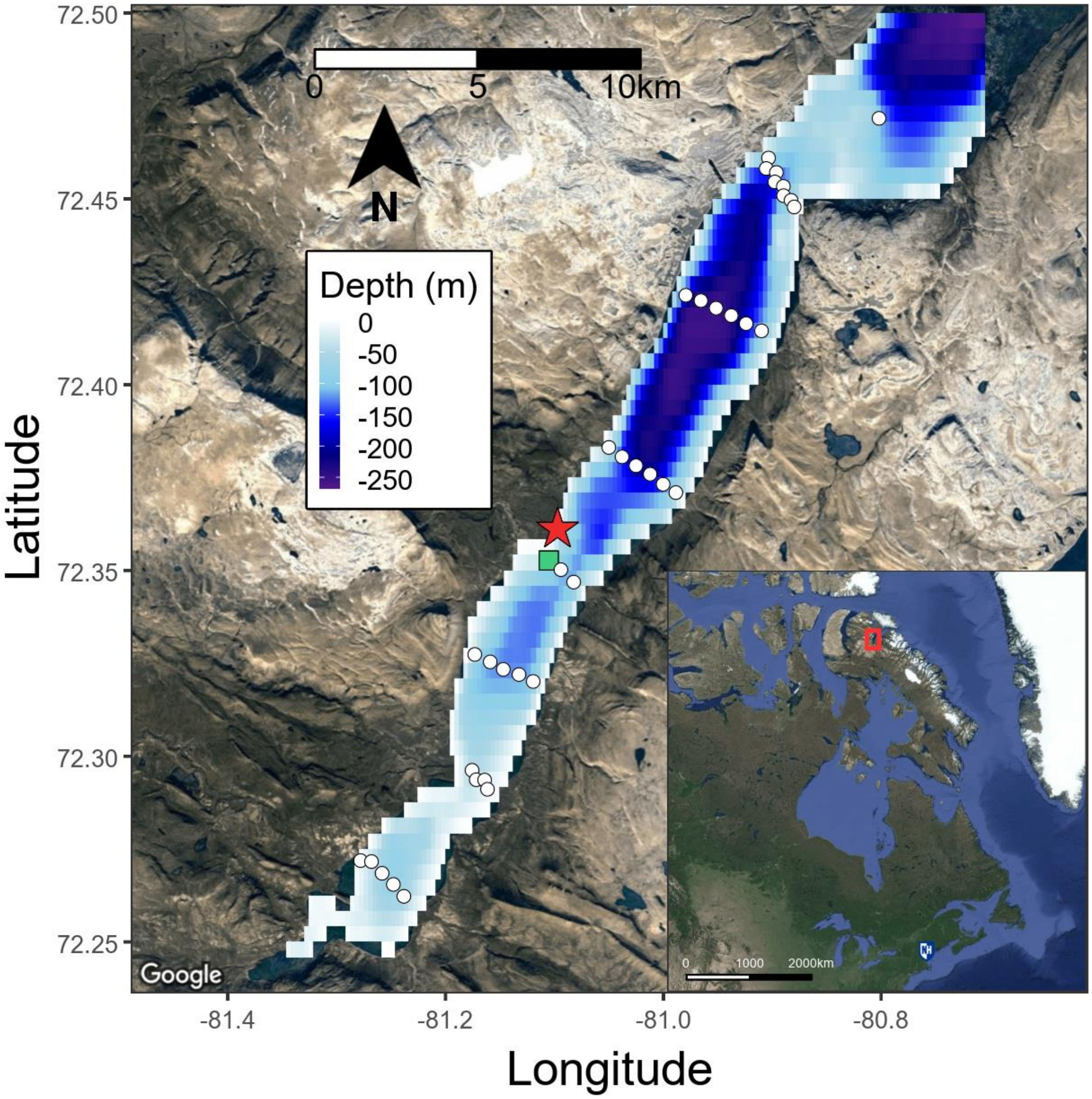


Figure 2. Comparison of the seasonal sculpin activity for each of the three observation years. (a) The number of inter-gate movements, (b) roaming index, the proportion of detecting receivers to the total in the array, and (c) residency duration were all normalized by the length of time the transmitter was operating in each season. Sample sizes show the number of transmitters detected in each season and do not reflect the sample size in the paired t-test that requires detection in both seasons. Grey lines show pairing of same transmitters between seasons relevant to the paired t-test results shown in each panel. The ice-free period was marked as beginning at the first visible open water and ending when no open water was visible in the sound from EOSDIS satellite imagery (NASA 2021). *p<0.05 ***p<0.001

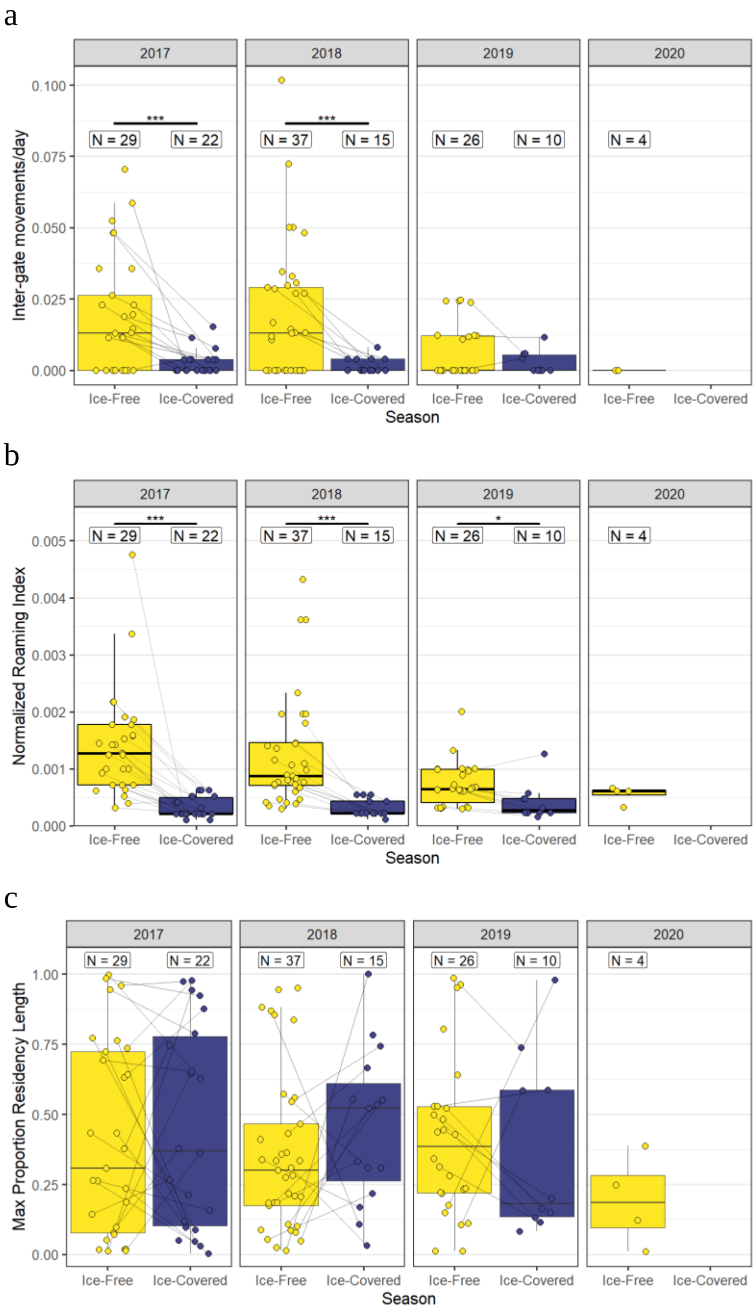


Figure 3. Generalized linear model (GLM) of lattice density home range areas for each season (ice-free or ice-covered) and home range contour (50%, 57.5%, 65%, 72.5%, 80%, 87.5%, or 95%). The ice-free season (yellow) home ranges were significantly larger than the ice-covered (blue) at all percentages (p=0.04). The ice-free period was marked as beginning at the first visible open water and ending when no open water was visible from EOSDIS satellite imagery (NASA 2021). The total area of Tremblay Sound is 134.4 km^2.

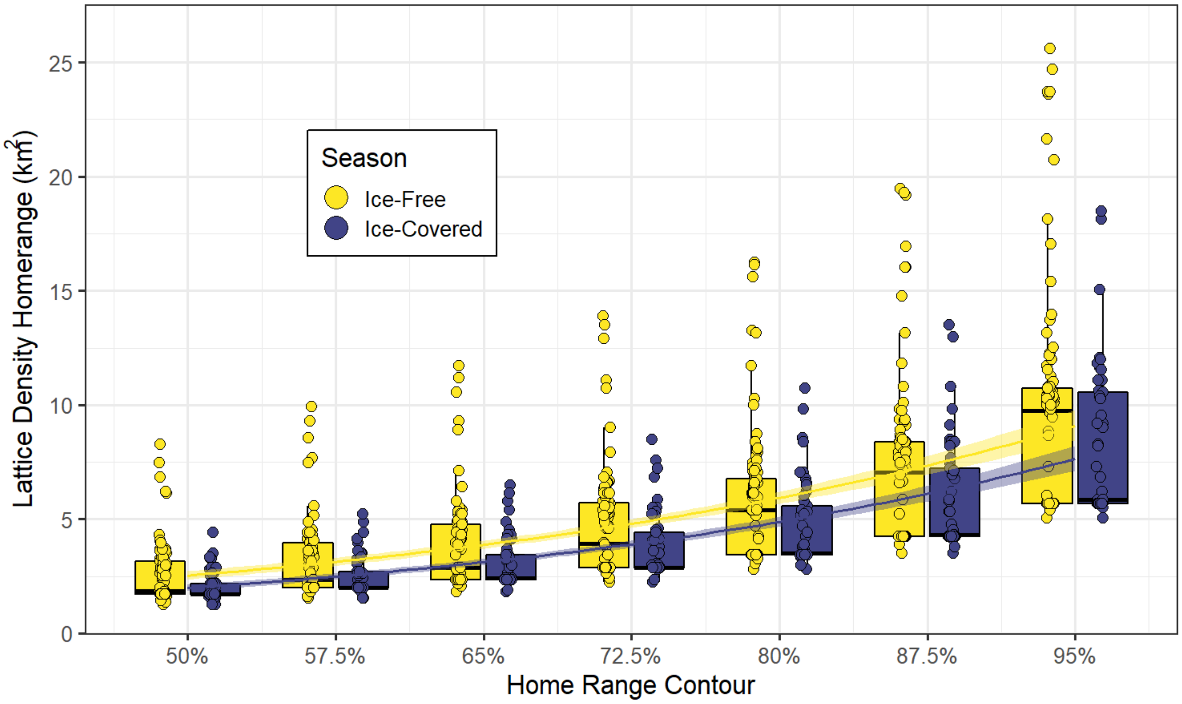


Figure 4. Sequence history for each unique transmitter grouped by the year in which the transmitter was released. Grey shading indicates ice-free periods whereas unshaded areas are ice-covered. Vertical black lines indicate the extent of battery life in V5 and V9AP transmitters; V9 transmitters nominal battery life spans the entire period shown. Changes in color within a sequence indicate inter-gate movements.

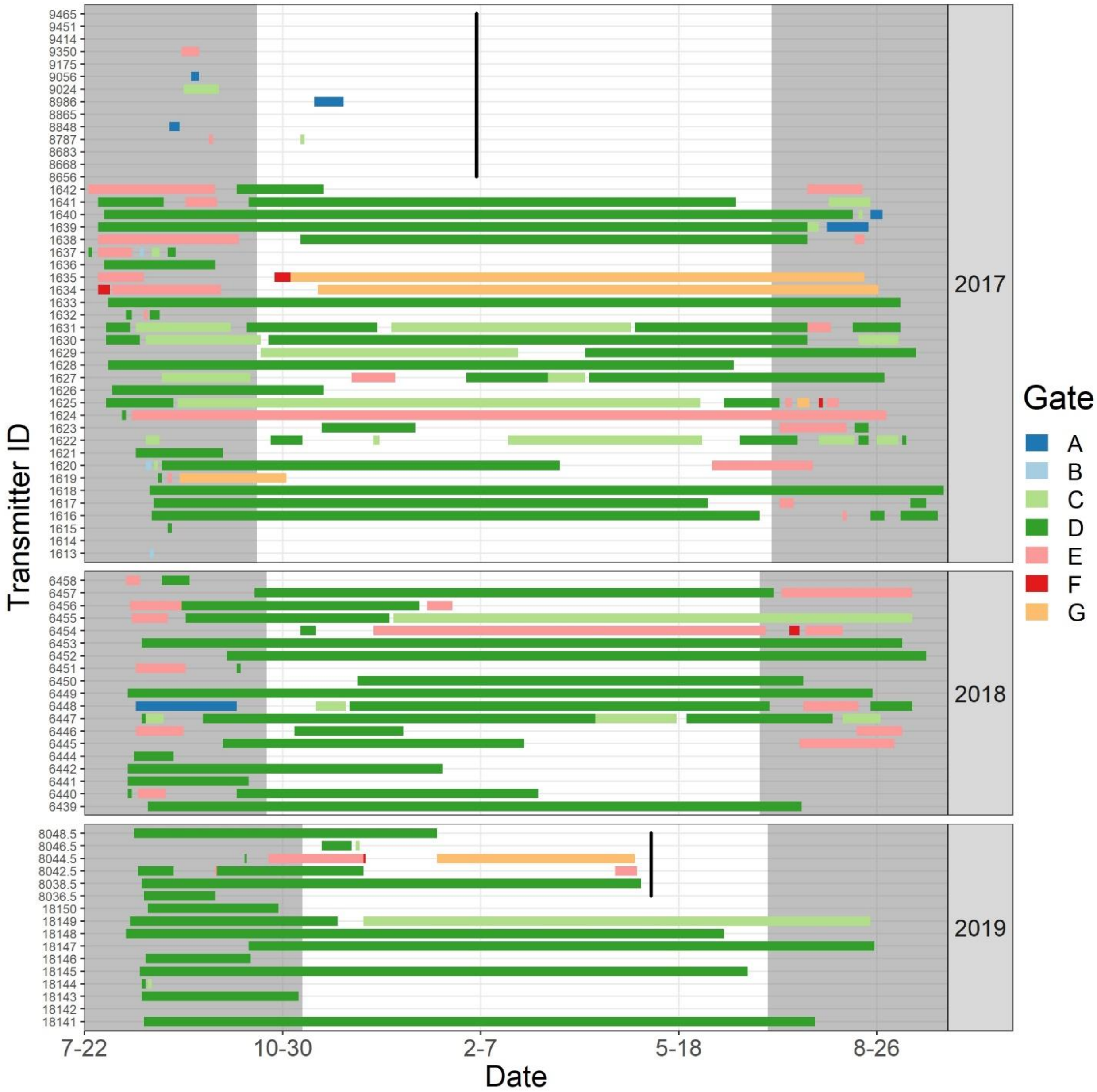
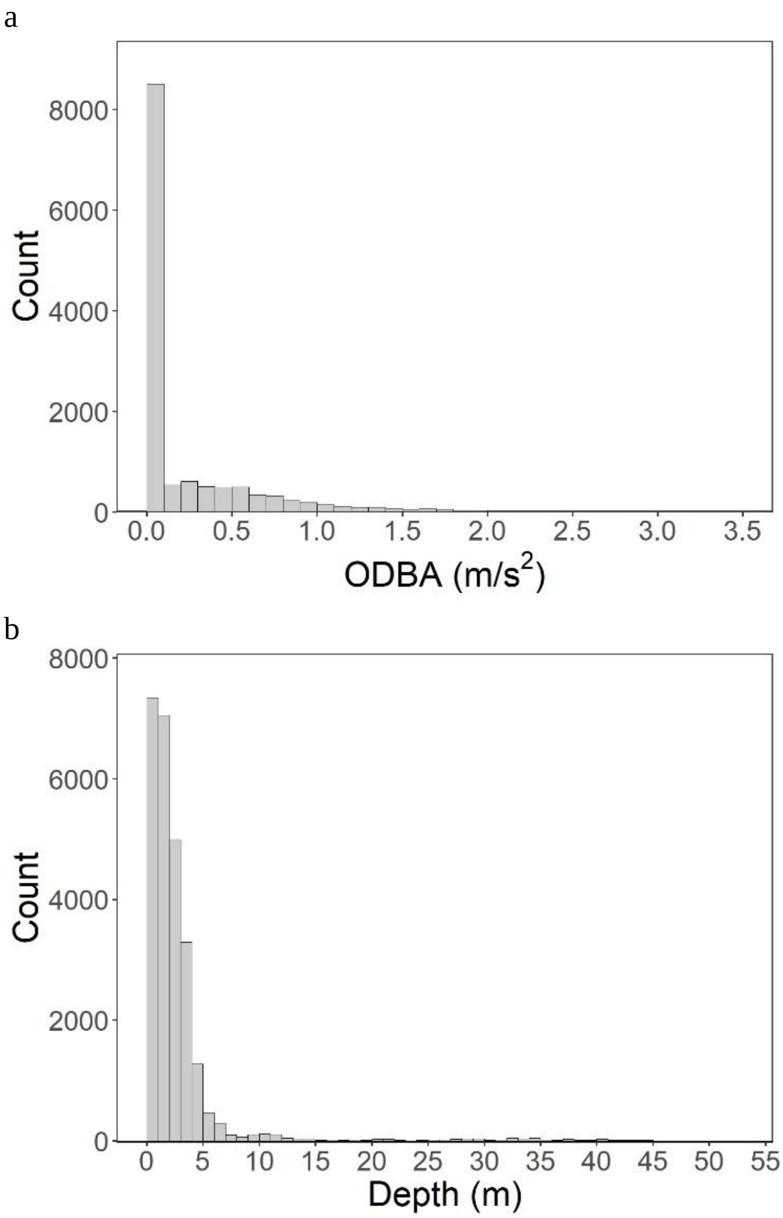


Figure 5. Histograms of (a) overall dynamic body acceleration (ODBA) in m/s^2 and (b) depth in m from V9AP transmitters over 2019-2020.



Supplemental Figures

Figure S1. Home range area estimation patterns at a series of Refined Shortest Path (RSP) interpolation intervals and k smoothing parameters. RSP intervals increase left to right from 2 minutes, equivalent to the nominal tag delay, to 1 year, equivalent to no interpolation. k smoothing increases from top to bottom from 1 to 60 reflecting the number of timesteps across which diffusion away from path locations was estimated. At each combination, a GLM was fit across home range percent and between ice-free and ice-covered seasons to compare the absolute and relative extent of the area. The combination showing the greatest compromise between effort, plausibility, and complexity was selected for analyses, k=15 and t=1 day, though patterns were retained across all combinations.

Figure S2. Cumulative (a) detection and (b) home range of monitored sculpin population throughout the entire 3-year observation period. Detection map restricted to assumed 500 m detection radius around receiver positions and colored relative to the number of total detections at that receiver location (note log scaling in legend). Detections overlaid on Tremblay bathymetry shading with contours at 50, 100, and 250 m depths. In home range, grey points represent lattice density nodes; those superimposed in red exist within the 95% home range contour. The total estimated home range was 22.7 km^2 or ~20% of available space in Tremblay.

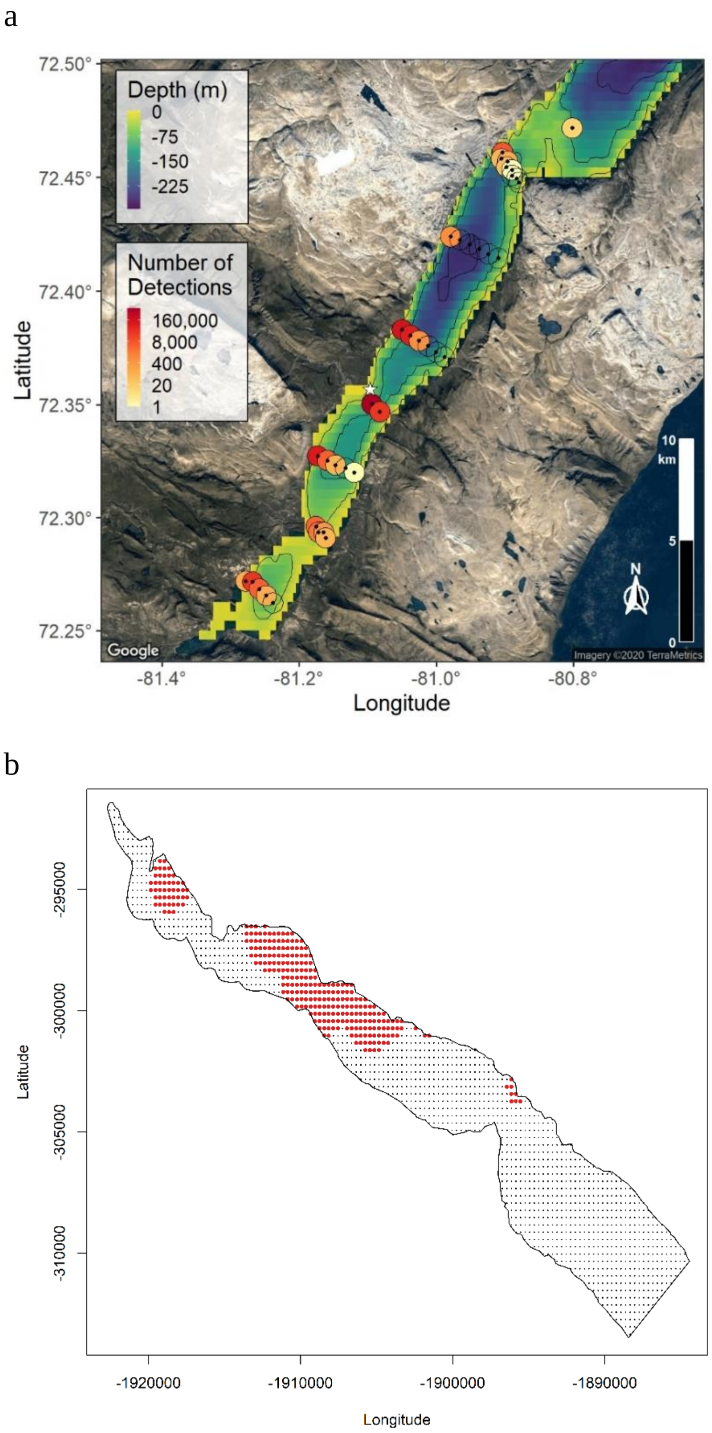


Figure S3. Distance matrices for sequences within (a) V9, (b) V5, and (c) V9AP transmitter groups. Cooler colors indicate greater dissimilarity between two sequences. The maximum dissimilarity observed was 700.6 for V9, 147.4 for V5, and 363.3 for V9AP.

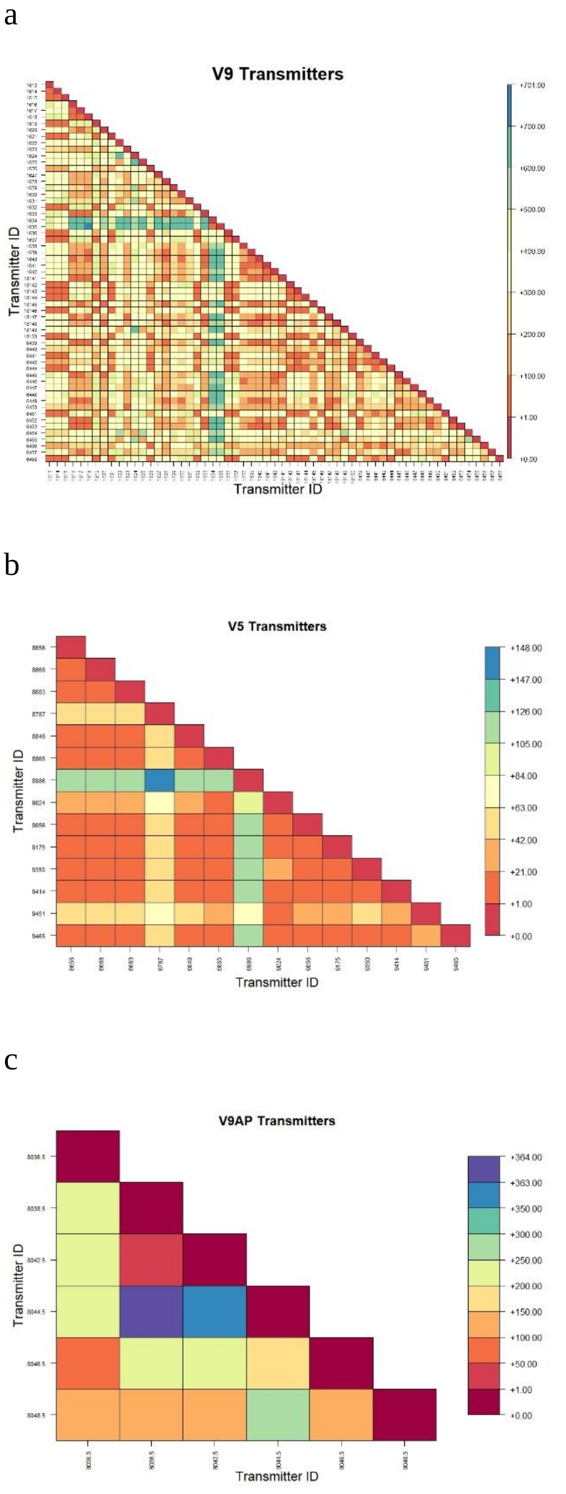


Figure S4. Representative sequences for each group identified by cluster analysis on transmitter sequences. Clustering and grouping was done only within shared transmitters due to distinct battery life determining maximum sequence length. Sequence height is proportional to the number of sequences represented (within 50% overlap with representative centroid) and the order of sequences from bottom to top represents the representative's distance from the overall group centroid sequence. Block (a) are V9 groups, block (b) are V5, and block (c) are V9AP.

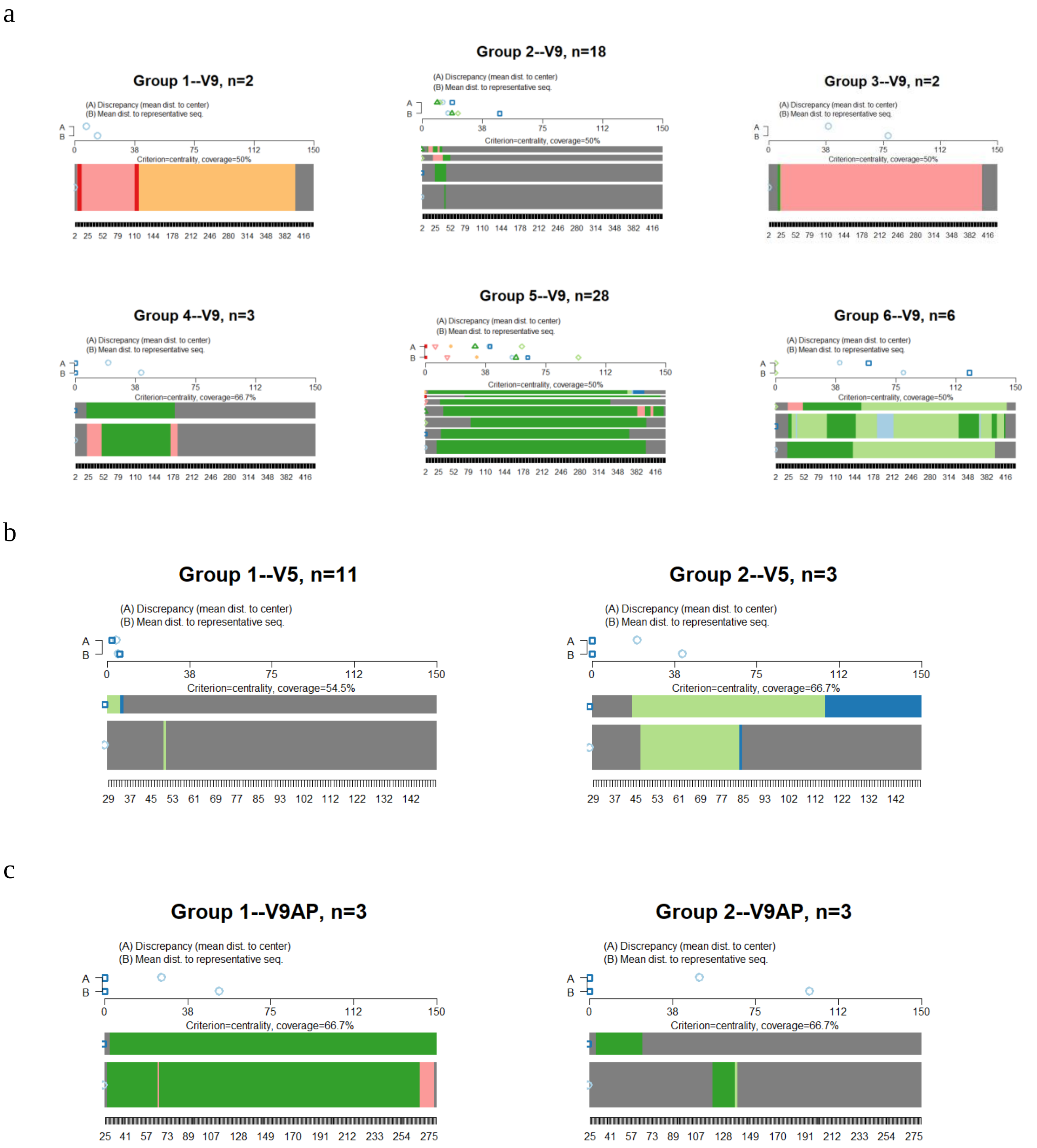
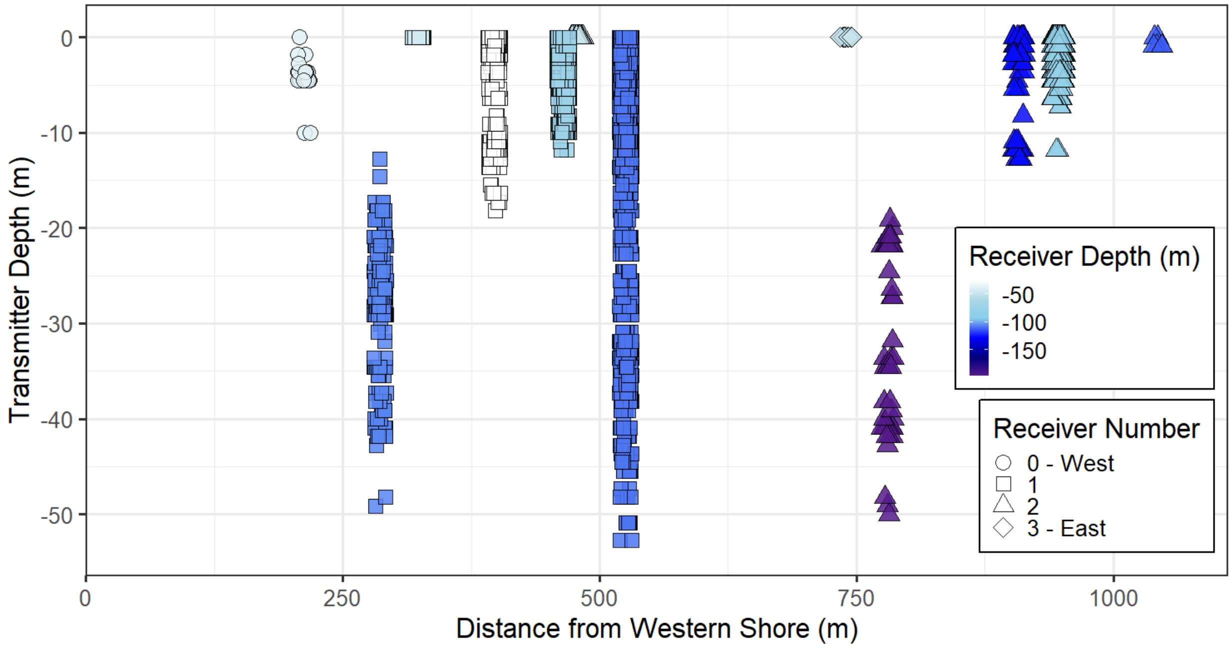


Figure S5. Depth below the surface of sculpin from V9AP transmitters deployed in 2019-2020 compared to the detecting receiver. The x-axis shows the distance of the receiver from the western shore of Tremblay Sound and the shape of the point is the receiver number where higher numbers (2-triangle, 3-diamond) being further east than low numbers (0-circle, 1-square). The depth logged by the receiver is shown by the coloring of point with darker blues being the deepest locations.



CHAPTER 4: Conclusion

Sculpin are residents in the marine Arctic that exhibit seasonal behaviors consistent with exploiting ephemeral resource pulses. From year-round acoustic telemetry (Chapter 3), sculpin were confirmed to not enter freshwater or stray from the Tremblay system where they were captured. Despite being residents, sculpin still exhibited a clear increase in activity, mobility, and size of area used during the ice-free season. While they still exhibit limited mobility overall, the distinct change at the onset of ice-melt shows that mobility may be part of their exploitation of the seasonal resource pulse. Throughout the ice-free season, intense foraging was observed through diet content analyses (Chapter 2) on a variety of prey items—predominantly structure-associated amphipods. Whereas diet composition broadened and varied within the ice-free season and between years, relative consumption was consistently high. Beyond exploring the basic seasonal ecology of sculpin, this thesis can help to further the importance of the seasonal ecology of polar systems including for resident species and, possibly, position sculpin as a useful biological indicator species.

Polar Ecology and Seasonality of Resource Pulses

Sculpin are known to be largely inactive fishes, and yet an appreciable degree of activity is paired with their exploitation of resource pulses. Productivity in the Canadian Arctic may begin as early as March following the end of the polar night (Søreide et al. 2010). Correspondingly, depth data from transmitters revealed a gradual rise in the water column paired with accelerometry that suggested increased activity over time. These observed behaviors beneath still solid sea-ice may indicate exploitative behavior of early sympagic productivity (Gradinger and Bluhm 2010; Søreide et al. 2010). Increased acceleration occurs prior to the observed increase in horizontal movements that was tightly linked with ice-melt when resources are presumed to become more available (Bradstreet and Cross 1982; Hop et al. 2011). The pulse occurs due to algal sloughing, zooplankton release, and open-water phytoplankton productivity (Hop et al. 2011; Ji et al. 2013). It is just at this time that early migrants, such as Arctic char (*Salvelinus alpinus*), can arrive (Hammer et al. 2021) and effectively forage in the pulse (Swanson et al. 2011). Additional migrants may follow the ice-melt including Arctic cod (*Boreogadus saida*; Forster et al. 2020) and narwhal (*Monodon monoceros*; Heide-Jørgensen et al. 2002). Thus, many animals show changes in activity or behavior (Yang et al. 2010) in response to predictable resource pulses (Meyers and Bull 2002; McNamara et al. 2011). Within the resource exploitation of the Arctic, a key feature of the marine environment contributing to the pulsed productivity is sea-ice.

Sea-ice and its dynamics are central to the seasonal resources of the Arctic because it provides essential structure for primary production and secondary consumers. Algae use sea-ice for substrate (Michel et al. 1996) and phytoplankton bloom within the high-nutrient meltwater (Hop et al. 2011). The concentration of productivity around sea-ice is transferred to zooplankton through grazing (Werner 1997) and incubating (Søreide et al. 2010; Hop et al. 2011). Members higher up the food web also use the ice; Arctic cod not only feed from the underside of ice, but also use wedges in melting ice for protection (Gradinger and Bluhm 2004), Arctic char coordinate their marine migration to follow ice-melt (Hammer et al. 2021), and narwhal associate with dense pack ice year-round (Heide-Jørgensen et al. 2002). Sculpin similarly change their behavior by becoming 2-3-times as active while ice melts around them, though the deliberate association with ice warrants further study to refine the positions of activity and depth. Around this change in activity, sculpin also rise in the water column; the top 5 m, where sea-ice meltwater can drive rapid production (Hop et al. 2011), constituted over 92.5% of depths visited by sculpin. In shallow waters, sculpin were then captured with large, diverse diets including sympagic prey such as amphipods (Gradinger and Bluhm 2010). As they are active around ice-melt, rise toward the sea-ice productivity, and found foraging upon zooplankton in these surface waters, sculpin too may be considered strongly associated with, and reliant upon, ice dynamics. Thus, it is important to consider the consequences of potential alterations to the predictable and productive seasonality of Arctic sea-ice due to climate change.

The Arctic is changing due to global anthropogenic activity more rapidly than any area due to amplification (Serreze and Barry 2011; Cohen et al. 2014) and feedback mechanisms (Curry et al. 1995; MacDougall et al. 2012). As a result, changing ice phenology (Ji et al. 2013; Park et al. 2016) has resulted in a lengthening of the duration of the growing season in open water (Park et al. 2015; Wasmund et al. 2019). Beyond phytoplankton itself contributing to further ocean warming (Park et al. 2015), the shift in productivity may have two largely consequential impacts to sculpin and the ecosystem broadly. First, more rapid ice melt can dampen the productivity of spring blooms (Sommer and Lengfellner 2008), especially by sympagic algae. Although reduced productivity by some algae, primarily diatoms, can be partially compensated for by diverse algal communities (Wasmund et al. 2019), the primary compensatory production occurs in pelagic environments (Sommer and Lengfellner 2008). This shift of primary production toward open-water is the second potential consequence of shifting ice dynamics as it can reduce trophic transfer efficiency (Sommer and Lengfellner 2008; Gradinger and Bluhm 2010) and especially limit provisions to benthic environments (Hjerne et al. 2019). With so many Arctic marine organisms adapted to utilize sea-ice, this relocation of production could potentially be limiting.

Consumers throughout the Arctic region are threatened by losses of ice due to climate change. The most widely publicized instance of sea-ice dependence resulting in limited foraging with earlier melt occurs in polar bears (Ware et al. 2017) that have seen reduced reproductive success (Rode et al. 2018), shifted diet and trophic interactions (Johnson et al. 2019), and novel foraging behaviors (Dyck and Romberg 2007) in recent years. These types of consequences are likely to similarly impact many other Arctic consumers (see Bradstreet and Cross 1982), potentially including sculpin. Though perhaps buffered by their flexibility in prey selection and regular coordination of activity with productivity (Gray et al. 2016), the energetic cost of more extensive open-water foraging by sculpin is not known. More precise observations of sculpin accelerometry at depth can help identify levels of activity when away from the benthos. Further research to then quantify the metabolic costs of that activity for sculpin should be undertaken, but are severely limited by the remoteness of their environment in collecting tightly controlled measurements (but see Gilbert et al. 2020). Alternative strategies may include using measures from closely related species (after Petersen and Paukert 2005; Macnaughton et al. 2019), though assumptions about the generalizability of bioenergetics models have not been well vetted. An additional complication from shifting toward active foraging comes in the reduced proportion of aerobic capacity that can be taken up by digestion (Clark et al. 2013). Sculpin are designed as ambush predators and may be physiologically limited to a degree of continuous locomotion insufficient to gather pelagic resources, especially as a species shown to feed at consistently high rates over a short period of time. Changes to ice dynamics are one central threat to ecosystem function in the Arctic felt across marine habitats and niches (Bradstreet and Cross 1982; Fortier et al. 2006; Amélineau et al. 2016; Hjerne et al. 2019), including a possibly distinctive impact upon residents.

Insights on Resident Species

Within the Tremblay Sound system, both the resident sculpin (this thesis) and migratory Arctic char (Hammer 2021; Hammer et al. 2021) have been studied, providing comparisons in the ecology of these two strategies with potential implications with climate change. The two species differ considerably in overall body morphology and size (average adult char 2.99 kg, average sculpin 79 g). These physical differences translate predictably to the scale of movements in response to the annual ice-melt. As a migratory species, char return to the marine environment of Tremblay just before summer ice-off (Hammer et al. 2021), sometimes traveling as far as 100 km through marine waters (Hammer 2021). Though sculpin activity and range also increased around ice-off (Chapter 3), the extent is much less and they are not traveling between distinct locations. Char come to the more productive marine environment to feed (Swanson et al. 2011). In doing so, char swim actively throughout Tremblay Sound even with daily home ranges (~4.24 km^2; Hammer et al. 2021) being nearly 60% larger than those of sculpin throughout the entire ice-free season (2.66 km^2; Chapter 3). By their movements, char and sculpin appear to both rely on the pulse, but, although char utilize much more of Tremblay Sound, sculpin feed at higher relative rates (maximum relative consumption for char 4.63% (Hammer 2021); maximum relative consumption for sculpin 12.1% (Chapter 2)). Though lower relative consumption is certainly a reflection of char's much larger body mass, the difference may also reflect foraging ecology. As an active forager, char must maintain a level of aerobic capacity for swimming that ambush predators do not, enabling sculpin to commit greater metabolic effort to digestion (cf. Clark et al. 2013). Sculpin and char consumed many of the same prey items with amphipods being a major resource for char as well, though char consumed a higher percentage of and more types of fish (Hammer 2021). Char occasionally consumed fish larger than those observed in sculpin diets, or even the sculpin themselves, but the majority of prey sizes overlap (L. Hammer, *unpublished data*). In foraging upon these similar items, Arctic char are capable of seeking new foraging opportunities even straying between multiple marine and freshwater systems (Moore et al. 2017). Meanwhile, individual sculpin are constrained to the productivity of a single area and, as a species, are limited to slow, population-based range shifts caused by broad changes in survivorship at the edges of the range (Pinsky et al. 2020). As such, losses of productivity confined to the Tremblay Sound system might be expected to negatively affect sculpin more than char that may compensate by utilizing neighboring inlets. Similarly, shifts in locations of productivity from sympagic-benthic to pelagic (cf. Sommer and Lengfellner 2008; Ji et al. 2013) may be more readily exploited by mobile char than sculpin (Chapter 3). Finally, both species are presumed to face the poleward or deepening pressure of many temperate and polar fishes (Dulvy et al. 2008), but, as coastal fishes in the high Arctic, are largely restricted in their ability to shift ranges in either direction and may experience pressure from encroaching southern species (Kortsch et al. 2015; Campana et al. 2020). Though both abundant fishes of Tremblay Sound, Arctic char and sculpin uniquely exploit the seasonality of the system reflecting their life histories as migrants and residents, respectively. As such, sculpin can serve as a representative of resident species in discussing the general threats and values of the niche in the Arctic.

Sculpin are of high ecological value to their ecosystems. Despite being small, their abundance contributes substantial biomass to their ecosystems. Because they are resident, their biomass contribution is stable throughout the year, unlike more ephemeral organisms such as zooplankton. This stable biomass can be useful by providing temporal stability in the food web despite unstable environmental conditions (McMeans et al. 2015) that are characteristic of the marine Arctic (AMAP 2017). Resident species also maintain food web stability spatially by capturing and retaining energy and nutrients they consume within an area, rather than transporting resources in a migration (Bauer and Hoye 2014). Sculpin also exhibited flexibility in their diet composition with no change in feeding intensity, potentially due to their seasonal movements. This flexibility can allow sculpin to operate as valuable links within Arctic food webs (Tamelander et al. 2006) and this value may increase with the introduction of southern species (Kortsch et al. 2015). Therefore, despite there being little human interest for sculpin commercially or recreationally, they are still ecologically important residents.

Climate change threatens all inhabitants of an environment, but residents face unique threats due to their characteristic life history. Residents withstand seasonal changes, commonly through phenotypic plasticity (Piersma and van Gils 2011) or robustness (Congdon et al. 1994; Figure 1.1), that non-residents avoid. However, such plasticity is limited in scope (Meyers and Bull 2002) and may prove insufficient for an evolving climate regime. Being unable to change phenotypically in tune with climate change can result in mismatch with environmental resources that can have consequences for survival (Zimova et al. 2016). Additional climate-induced mismatch can result from spatially disconnected environments changing at different rates (Lameris et al. 2017), which does not threaten residents species like short or long-distance migrants (Both et al. 2010). Though residents may, then, be at a lesser risk of mismatch than the more common migrants of the marine Arctic (Tallman et al. 2019), appropriately timing life history events with resource pulses is still critical, especially reproduction (Visser et al. 1998). As winter spawners, sculpin primarily time larval hatching with the warm, productive ice-free season (Leonardsson et al. 1988) to ensure consistent larval survival (Fortier et al. 2006). Advancing ice-melt could result in larvae and post-reproductive adults missing this critical pulse for growth and energy recovery. Evidence for summer spawning (Goldberg et al. 1987) may be an indication of regional differences in spawning or the use of two spawning cohorts to bet-hedge the timing of growing conditions come spring, both effective strategies for increasing offspring survival (Fortier et al. 2006). However, temporal flexibility is the only known and feasible strategy in response to mismatch for resident species with limited mobility, making them sensitive to phenological change. As a sensitive niche, residents can prove to be valuable indicators of ecosystem health and, due to several other important features, sculpin are especially appropriate.

Sculpin as Indicator Species

Through characterizing the ecology of resident sculpin in the marine Arctic, I suggest that these fish can serve broadly as indicator species. Indicator species are those which can signal the status of their ecosystem before broader changes occur to the rest of the community, also known as sentinel species (Gibbons and Munkittriek 1994). Previously defined requirements for a species to serve as an indicator are to have high (1) site fidelity, (2) abundance, and (3) representativeness of the ecosystem (Gray et al. 2018). As has been advocated before (Gray et al. 2018; Barton et al. 2019b) and advanced by this research, sculpin demonstrate these characteristics and others of an ideal model organism to indicate ecosystem condition.

Sculpin are effective early indicators of ecosystem health because of their residential behavior and high site fidelity (Gray et al. 2004; Barton et al. 2019a). Any signs of ecosystem change that might be detectable in sculpin—prey abundance or composition changes, pollutants, temperature fluctuations—will have occurred within a confined region, no greater than 30 km^2. For managers, this is a useful assurance compared to migratory species that complicate management plans as they suffer from combined breeding, transitory, and non-breeding habitat and climate changes (Fromentin and Powers 2005; Rushing et al. 2016) or transport pollutants and parasites across boundaries (Blais et al. 2007). More practically, due to their narrow home ranges, sculpin are unlikely to span regulatory zones allowing for less bureaucratic decision-making (Fromentin and Powers 2005). Within those constricted ranges, sculpin also serve as a quality representative of habitat.

Sculpin are a generalist predator embedded within the Arctic food web. I have shown that not only do sculpin consume a variety of prey items, but the composition of their diet is likely responsive to changes in their environment. Such generalist predators sample the prey base in their environment well, which is essential for their usage as an efficient indicator species (Depot et al. 2020; Dunphy et al. 2020). However, as non-specific feeding may enable sculpin to buffer against losses in one or more prey items (Gray et al. 2016), it is important to assess composition and not simply foraging success that can remain consistent. Monitoring the composition of sculpin diets can be a more efficient approach for identifying major zooplankton community contributors that are more ephemeral and are first affected by mismatches with primary productivity (Edwards and Richardson 2004; Winder and Schindler 2004). Coupled to their ecology as generalist predators is the mesotrophic position of sculpin such that they are simultaneously indicative of prey and contribute to the success of their predators, including bearded seals and many Arctic seabirds. As generalist, mesotrophic predators, sculpin have been identified as holding positions within the Arctic food web that link modules together (Kortsch et al. 2015) and couple habitats (Tamelander et al. 2006). This not only makes them valuable fish for food web stability, but they increase visibility of changes in multiple habitats and portions of the food web. Though their feeding position makes sculpin a more visible indicator of changes throughout the ecosystem, they are also highly visible to human managers for practical reasons.

Although above reasons make sculpin an efficient indicator, their ease of access make them a practical one as well. Firstly, sculpin are abundant both in biomass and numerically, facilitating easy collection in monitoring efforts. Capture effort is also reduced by their being a predominantly nearshore species that only rarely moves out to deeper waters. In the nearshore, a number of accessible capture methods are available that collect sculpin efficiently including fyke net (Hermann, N.H., *this study*) and beach seine (Barton et al. 2020). Large populations make them accessible to humans, yet they are of little commercial or recreational value to humans currently. This not only helps maintain high populations, reducing chances of damage due to monitoring, but also limits the impacts felt by the population and thus simplifying the assessment. Without direct human intervention, any changes observed to occur within the population can be readily attributed to environmental or ecological change. In the contrasting example of Atlantic cod (*Gadus morhua*), the intense fishing pressure contributing heavily to their eventual population crash may have shrouded additional underlying environmental impacts. These rises in temperature have since hindered a recovery by cod stocks, but their strong influence became visible only after fishing pressures were removed (Engelhard et al. 2014). As the Arctic continues to warm, larger and broader fisheries are developing (Christiansen et al. 2014) making a fisheries-independent system for monitoring ecosystems even more important. Sculpin are already spatially linked to valuable Arctic char despite their contrasting life histories using coastal waters such as Tremblay Sound, but may also indicate overlapping conditions with Arctic cod, Greenland halibut (*Reinhardtius hippoglossoides*), and several encroaching southern species. As such, with these human interests developing in the Arctic it becomes increasingly important to work to ensure that the often pristine ecosystems are so maintained.

I have identified sculpin as a valuable study organism to indicate ecosystem productivity and health. As they exhibit seasonal behaviors, they expand the general thinking of strongly seasonal resources being primarily exploited by migratory species to include resident species just as strongly. Through the intense feeding I observed among sculpin, I can speculate that they are reliant upon peaked resources in the short period of productivity in the Arctic. As such, following this research, sculpin should continue to be monitored for a more diverse understanding of the impacts felt by species with climate change and as early indicators of biotic impacts to ecosystems.

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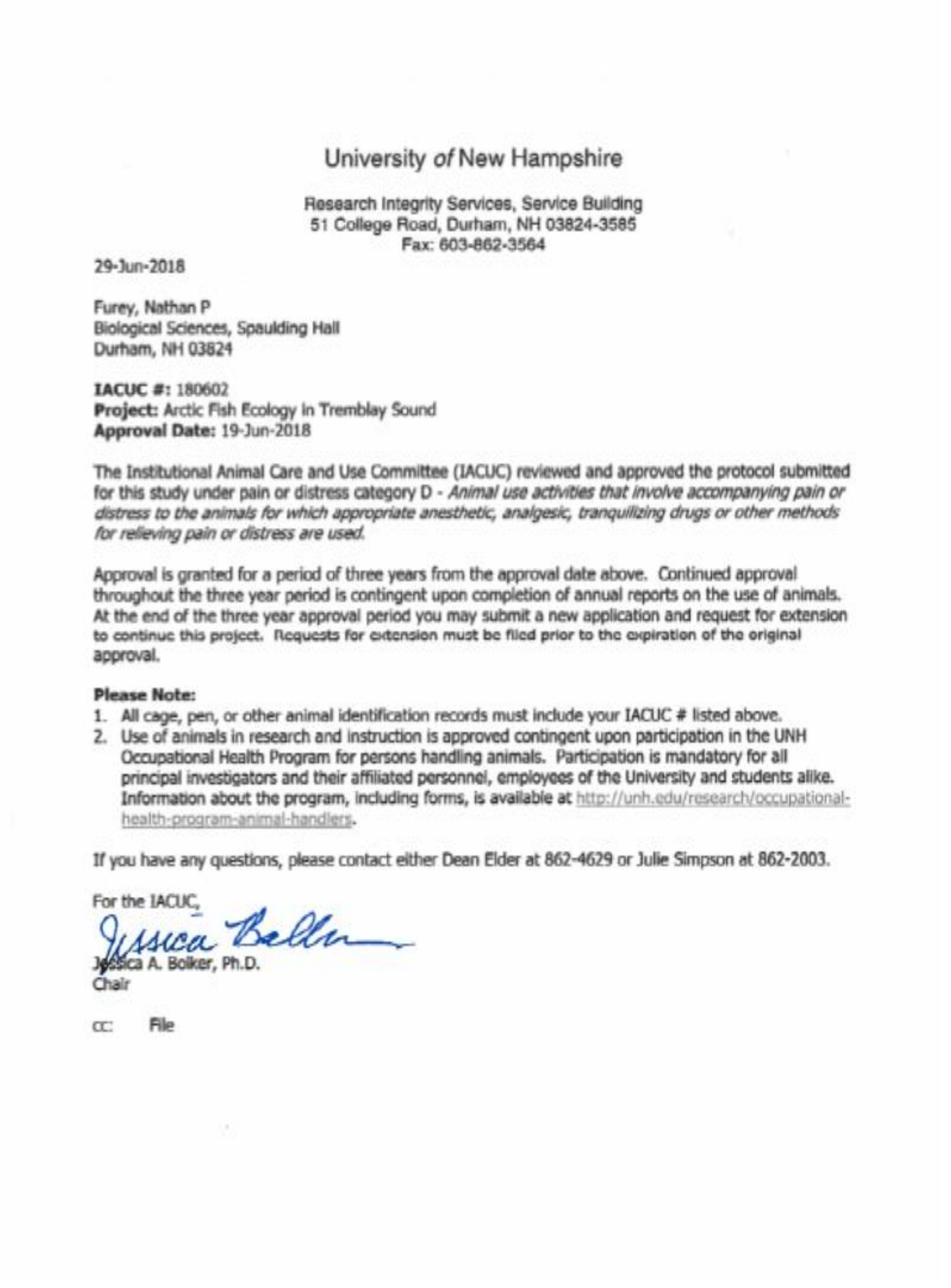
APPENDIX

IACUC Approval Letter



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29-Jun-2018

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IACUC #: 180602
Project: Arctic Fish Ecology in Tremblay Sound
Approval Date: 19-Jun-2018

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under pain or distress category D - *Animal use activities that involve accompanying pain or distress to the animals for which appropriate anesthetic, analgesic, tranquilizing drugs or other methods for relieving pain or distress are used.*

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:

1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. Information about the program, including forms, is available at http://unh.edu/research/occupational-health-program-animal-handlers.

If you have any questions, please contact either Dean Elder at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,

Jessica A. Bolker, Ph.D.
Chair

cc: File