# Diets of resident and migrant fishes during a seasonal resource pulse in the Canadian high Arctic reflect their contrasting life history strategies

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# Abstract

Dramatic seasonal changes occur annually in the Arctic, requiring organisms to withstand harsh conditions and exploit favorable conditions as they occur. Foremost among these changes is the sudden abundance of resources and habitats following receding sea-ice in the summer. Many marine organisms respond behaviorally to maximally exploit this resource pulse; however, the strategy by which this is done varies among organisms. To assess the means and degree of resource exploitation by the fishes of a coastal Arctic community, we collected stomach contents from migrant anadromous Arctic char (*Salvelinus alpinus*; n = 91) and resident sculpins (*Myoxocephalus* spp.; n = 190) in Tremblay Sound, Nunavut, Canada during the ice-free seasons of 2017-2019. Feeding intensity (as both percent of empty stomachs and relative consumption) and diet composition were compared between the two fishes to identify differences in their feeding within a shared environment. Despite eating larger prey items, Arctic char consumed less relative to body weight (mean ±SD; 1.92% ±1.38%) than sculpin (2.88% ±2.93%). Arctic char also had fewer empty stomachs than sculpins (1.96% vs 14.7%). For diet consumption, 52.6% of identified prey categories were shared by both predators. Non-metric multidimensional scaling (NMDS) ordination and discrimination tests showed dietary distinctions were primarily driven by Arctic char’s higher consumption of fishes and copepods whereas sculpin diets were dominated by several types of amphipods. Our findings are consistent with understandings of life histories for relatively sedentary, benthic-oriented, resident sculpins intermittently consuming small, benthic prey items at very high levels whereas mobile, semi-pelagic, migratory Arctic char consume pelagic prey items at more consistent levels that do not impede aerobic activity. Ultimately, we have shown that, unsurprisingly, diets are reflective of predator physiology but also of life history traits, such as migratory behavior, that differentiate Arctic char and sculpins as common predators within an Arctic food web.

**Keywords:** Arctic char, sculpins, Arctic, feeding ecology, diet analyses

# Introduction

The Arctic is a highly dynamic environment, experiencing dramatic seasonal change in environmental conditions (AMAP 2017). Winter in Arctic ecosystems is generally characterized as a resting state, exhibiting low productivity, almost complete darkness, and ice-covered landscapes for much of the year (Berge et al. 2015). At the end of this winter however, comes a rapid transition between ice-cover and open-water (AMAP 2017). This spring transition, coupled with increased daylight, causes a primary productivity bloom that provides key nutrients for Arctic consumers (Hop et al. 2011; McMeans et al. 2015). Increasing temperatures associated with climate change have altered these phenological patterns by gradually reducing the duration and extent of sea-ice cover across much of the Arctic (Johannessen et al. 2004; Stroeve et al. 2007; Dai et al. 2019). Consumers that rely on the regularity of transitions in sea-ice cover may be negatively affected by changes in ice phenology, and understanding those relationships is critical to predicting their future climate resilience.

Large resource pulses attract a wide variety of migratory animals that presumably exploit these seasonally abundant resources (Melnikov 1997), including birds (Lameris et al. 2017; Descamps et al. 2019), marine mammals (Heide-Jørgensen et al. 2002; Harwood et al. 2012), and anadromous fishes (Harwood and Babaluk 2014; Hammer et al. 2022). These species generally arrive at the start of ice melt to exploit pulses in productivity and depart before the transition back to ice cover when conditions are harshest (Edwards et al. 2022). In contrast to migratory animals, Arctic resident species remain in these habitats year-round. To live in these harsh environments continuously requires residents exhibit specific adaptations to changing conditions through the tradeoff for reduced mobility costs being a usage of physiological adaptations (Harwood and Babaluk 2014; Baumgartner and Tarrant 2017) or lipid storage (Biro et al. 2004). In Arctic systems both resident and migratory species take advantage of resource pulses to varying degrees, likely based on their life history requirements and capacity for feeding.

Migratory and resident organisms possess different anatomical features, physiological capabilities, and behavioral characteristics. Among the most visible differences between migratory species and their resident counterparts is in the standard of mobility, namely that migratory species possess a capacity for persistent, directed movements which define migration (Bauer and Hoye 2014). While residents can still exhibit high mobility within a single area (Becker et al. 2020) and some migrants are famously slow-moving (Blake et al. 2013), the anatomical features which influence an organism’s migratory behavior will similarly influence their foraging. In poikilothermic fishes, the scope of activity is influenced by water temperature, but a portion of that metabolism is dedicated to activity such as digestion (Clark et al. 2013). Therefore, the metabolic costs of digestion necessarily impede aerobic scope for other necessary functions such as mobility. Alternatively, fishes may raise their total aerobic scope during times of high consumption by seeking warmer temperatures (Armstrong et al. 2013), though conditions for this strategy are rare. From this, we can see that the feeding behaviors of fishes are linked to the broader life history elements based on adaptations of anatomy and physiology; but to understand this more fully we must understand their feeding.

Diet analysis is a common method for understanding the feeding behaviors of fishes. Assessments of stomach contents can effectively reveal the recent feeding of an individual (Amundsen and Sánchez-Hernández 2019) with the major characterizations of feeding being composition and magnitude. Composition can not only describe all the prey items which a predator consumes, but also details about the generality/selectivity of their foraging (Gerking 1994). Additionally, when the ecology of prey items is known, then deductions about a predator’s foraging habitats can be made as well, i.e., those consuming only benthic prey items likely feed at and occupy the benthos. Diet magnitude, often presented relative to the weight of the fish, can provide a proxy for energetic intake and overall productivity. Further, higher magnitudes of feeding increase aerobic investments and, in turn, decrease mobility allowing for deductions about movement behaviors to be made (Clark et al. 2013). Finally, the variance in magnitude can indicate feeding patterns reflecting fish behaviors and environmental conditions where low variance may indicate active feeding and/or high productivity whereas high variances, especially if samples include extreme values or frequently empty stomachs, may opportunistic feeding and/or patchy environments (see Arrington et al. 2002; Armstrong and Schindler 2011). As such, diet analyses are a useful tool for exploring the ecology of species and to contextualize them with other inhabitants of the same ecosystem.

Arctic char (*Salvelinus alpinus*) are a relatively large and mobile pelagic migratory fish that provides an important source of protein to indigenous communities throughout the Arctic (Booth and Watts 2007). In addition to their migratory capabilities, Arctic char are known to exhibit highly diverse movements and life history patterns (Beddow et al. 1998; Jensen and Rikardsen 2008; Moore et al. 2017). In contrast, sculpins (family Cottidae) are small to moderately sized benthic fishes with those of the genus *Myoxocephalus* being cold-water, Northern temperate-polar fishes of primarily marine environments (Balakirev et al. 2020). Sculpin are sit-and-wait ambush foragers (Landry et al. 2019) and maintain small home ranges in coastal Arctic waters year-round (Barton et al. 2020; Hermann et al. 2023). The summer resource pulse occurring with ice-melt in Arctic systems provides abundant resources that both species can presumably exploit.

With both Arctic char and sculpins present within the shared ecosystem of Tremblay Sound, we sought to use diet analyses to understand their exploitation of this resource pulse. Tremblay Sound was identified as a model system to achieve this objective as it experiences an annual ice-on/ice-off cycle which produces a pulse of productivity. Included as occupants of Tremblay Sound are Arctic char which are anadromous migrants in coordination with the sea-ice (Hammer et al. 2022) and sculpins that are year-round residents exhibiting flexible behaviors across seasons (Hermann et al. 2023). Specifically, the objective of this study was to compare the feeding rates and diet composition of a resident and migrant fish through the seasonal prey pulse. We hypothesize that several metrics of diet will differ between Arctic char and sculpins reflecting their contrasting behaviors surrounding the pulse. We predict that while Arctic char will feed on energetically dense prey items at consistent rates, sculpins will intermittently gorge on a broad, benthic diet.

# Methods

Fish were captured in Tremblay Sound, Nunavut, Canada (72.357° N, 81.108° W) in the summers of 2017, 2018, and 2019. Arctic char were primarily captured using gillnets with a ~15 cm stretched mesh between 19-Jul-2017 and 4-Sep-2017, 20-Jul-2018 and 28-Aug-2018, and 8-Aug-2019 and 14-Aug-2019. Nets were carefully watched during deployment and any fish that hit were immediately removed from the net. Sculpin species (*Myoxocephalus* spp.) were captured using a fyke net deployed between 23-July-2017 and 26-Aug-2017, 31-Jul-2018 and 11-Sep-2018, and 12-Aug-2019 and 21-Aug-2019. The fyke net was checked and fish and other organisms were collected at every low tide resulting in 85, 79, and 18 collections in 2017, 2018, and 2019, respectively.

Captured fish were euthanized and were measured for total length (TL) and weight. Additionally, a Fulton’s condition factor (𝐾 = 100\*(); where W = weight; Ricker 1975) was calculated for each fish. Measured fish were then dissected and their stomachs were removed. In 2017, stomach contents were picked at the field site without a microscope and were not weighed. In 2018, stomachs were weighed in the field, frozen, and shipped whole to the University of Windsor for storage. One 2018 char sample was not relocated after shipping. In 2019, stomach contents were removed from the stomach, weighed, frozen, and shipped to the University of New Hampshire. Empty stomachs were weighed and discarded in 2019. Fresh diet items from 2017 and thawed diet items from 2018 and 2019 were sorted to the lowest taxonomic level and each taxa present was enumerated and massed. All capture and dissection methods were approved by the University of Windsor (AUPP: #17-12) and the University of New Hampshire (IACUC:#180602). Sampling protocols also followed a quota set by the local Pond Inlet Hunters and Trappers Organization, which defined the maximum number of individuals that could be sacrificed for dissection.

Feeding intensity was expressed for both species as relative consumption, calculated as the wet mass of the diet contents divided by the wet mass of the fish (g/g). The wet mass of diet contents was calculated as the weight of the full stomach divided by the weight of the empty stomach. Diet content mass was not measured for 2017 fish, so a relative consumption could not be calculated, and they were removed from further analyses of feeding intensity.

A generalized linear model (GLM) framework was used to analyze factors contributing to relative consumption. Explanatory variables in the models included species (char, sculpin), year (2018, 2019), and month (July, August, September). The initial GLM was constructed with a binomial distribution to determine the factors contributing to empty (0) or not-empty (1) stomachs. A second GLM containing the same explanatory variables was run with a gamma distribution for only those fish that fed (i.e., relative consumption > 0). This hurdle GLM allowed the determination of variable importance to whether individuals fed (binomial model) and when they had, the magnitude of their consumption (Gamma model; Bolker et al. 2009). All subsets regression was performed using the *dredge* function from the *MuMIn* package (Bartoń 2020) in R (v4.0.2; R Core Team 2020). The model with the lowest Akaike Information Criterion with a correction for small sample size, AICc, was selected as the most parsimonious model. Akaike weights (Wi) were used to determine the models with highest likelyhood, where higher weights indicate higher relative likelyhood.

Diet composition was assessed using frequency of occurrence (FOO; Garvey and Chipps 2013). FOO for each prey type (lowest taxonomic level) was calculated for each species (Arctic char and sculpins) and year as the percentage of diets that contained a specified prey item. Other common diet analysis metrics (percent numeric abundance and percent mass; Garvey and Chipps 2013) were not included in this study due to procedural variations (i.e., diet contents were not consistently counted or massed in 2017) and inconsistencies in identifiability across diets (i.e., percent numeric abundance and percent mass could not be calculated for diets with unidentifiable prey). Presence-absence data was ordinated by NMDS to assess diet composition differences between species and years. Distance matrix created using Bray-Curtis distance, 250 random starts for axes 1-6 with *metaMDS* function from the *vegan* package in R (v4.0.2; R Core Team 2020) then selecting the best based on being < 20 stress and not reducing by > 5 with an additional axis. Selected ordination is then visualized with functions from the *ggplot2* package (Wickham 2016) in R (v4.0.2; R Core Team 2020) and each point is labeled according to species (Arctic char and sculpin) and year (2017, 2018, and 2019) with convex hulls built around those points. The consistency of composition for each group (combination of taxa and year) was tested using Permutational Multivariate Analysis of Variance (PerMANOVA) with the *adonis* function from the *vegan* package in R (v4.0.2; R Core Team 2020) with any significant factors being tested pairwise with the function *pairwise.perm.manova* from the *RVAideMemoire* package in R (v4.0.2; R Core Team 2020). As PerMANOVA significance can be driven by differences in both position (centroid values in multivariate space) and dispersion (variance in individual positions within a group) a *post-hoc* estimation of both values was made for each group to compare their influence on inter-group differences as well as identify those groups which are most different. Inter-group centroid distances are calculated using the function *dist\_multi\_centroids* from the package *usedist* in R (v4.0.2; R Core Team 2020) resulting in a 6x6 symmetrical matrix. Dispersion is calculated by calculating the distance between each individual and its group centroid and estimating the average, in this case a median was used to mitigate the effects of outliers. As dispersion is calculated in multivariate space, units are meaningless but are restricted to values ≥ 0.

To assess how well our sampling of Arctic char and sculpins stomachs captured variability in prey items, we used prey accumulation curves. Prey accumulation curves were constructed for both species in each year, and combined across study years (2017, 2018, and 2019). The analysis was designed to calculate the expected (mean) species richness within diets using the *accumcomp* function from the *BiodiversityR* package (Kindt 2023) in R (v4.0.2; R Core Team 2020).

# Results

A total of 91 Arctic char and 190 sculpin were captured for diet analysis from 2017–2019 (Table 1). Char samples were distributed relatively evenly across the three years (n2017-2019:37, 23, 31), while sculpin samples were mostly collected in 2017 and 2018 (n2017-2019:114, 59, 17; Table 1). Sampled Arctic char had an average TL of 62.1 cm and an average mass of 2,609.2 g (Table 1). Sculpin were smaller than char at an average of 18.5 cm and 78.9 g (Table 1). Char had an average Fulton’s K of 914.1 (±176.5), with sculpin being slightly better conditioned (mean = 1,062.1; SD = 572.3; Table 1).

A total of 51 char and 75 sculpin from 2018–2019 were available for analysis of feeding intensity. The initial GLM examining factors related to whether a fish consumed prey or had an empty stomach only retained the species variable (Table 3). Eleven sculpin (14.67%) had empty stomachs, while only a single char (1.96%) was found with an empty stomach. The second model investigating factors relating to feeding intensity retained the species and year variables (Table 3). In general, sculpin (mean = 2.88%; max = 10.5%) fed more intensely than char (mean = 1.92%; max = 4.63%). Both predators fed more intensely in 2019 (meansculpin = 3.19%; meanchar = 2.42%) than in 2018 (meansculpin = 2.79%; meanchar = 1.16%).

Between the two predators there were 15 identifiable prey types among all stomachs and 19 total categories. Both char and sculpin each consumed 12 distinct prey types with 10 common between the two predators (52.6%; Figure 1). Of the prey items consumed, frequencies ranged from <1% to 93.3% for a taxon in a given year. The most commonly consumed prey items were Amphipods (n = 199, 75.6%) with the most common among those identified more specifically being *Onisimus* sp. that were found in 81 stomachs (30.7%). The prevalence of amphipods as a top prey item was consistent across years for sculpins (2017: FOO = 81.0%; 2018: FOO = 53.0%; 2019: FOO = 75.0%) and for Arctic char (2017: FOO = 71.4%; 2018: FOO = 77.2%; 2019: FOO = 96.6%; Figure 1). The largest difference of the total FOO for a prey item between the two predator taxa was for total fish that were consumed more often by Arctic char (57.4% FOO vs sculpins 21.0% FOO). Other taxa consumed more often by Arctic char include *Themisto* sp. (32.1% FOO vs 0% FOO) and copepods (35.6% FOO vs 10.7% FOO) whereas sculpins consumed unidentified amphipods more often (47.7% FOO vs 28.7% FOO).

Diets were successfully ordinated on three axes through NMDS with a stress of 9.04 (Figure 2). The majority of the ordination space for a predator taxon in a sampling year was overlapping across taxa and years with differences being driven by the inclusion of variably abundant prey items, e.g., *Themisto* sp. by Arctic char in 2019 (Figure 2). ISA revealed stronger associations between Arctic char and their prey than those by sculpins. Arctic char possessed 6 significant prey types (Arctic cod, Sand lance, Fish, *Onisimus* sp., *Themisto* sp., and Copepods) whereas sculpins had just two (Amphipods and Mysids) as well as an association with Digested materials (Table 2). All groups (combination of predator taxa and year) were significantly different via PerMANOVA (p = 0.0015 – 0.0310) with centroid distances ranging between 0.220 and 0.664. Typically, centroid distances between the predator taxa within the same year were smaller (mean = 0.364, range = 0.220 – 0.571) than for the same predator taxa across years (mean = 0.456, range = 0.228 – 0.638; Figure 5a). Dispersion values for individuals ranged from 0 – 0.879 (a Sculpin from 2018) with groups showing variation in their averages (Figure 5b) but no consistent effect of predator taxa nor of year was observed.

# Discussion

Both sculpin and char exploited the brief prey pulse, with few individuals exhibiting empty stomachs, and many feeding intensely. The percentage of empty stomachs (char = 1.96%; sculpin = 14.67%) was lower than the average for fishes analyzed worldwide (16.2%), but was within the range of other fish populations, particularly in North America (Arrington et al. 2002). Levels of consumption were high on average for both Arctic char (1.92% ± 0.19%) and sculpins (2.88% ± 0.33%) with individuals reaching 4.63% for Arctic char and 10.50% for sculpins. Previously, definitions of binge-feeding have been made for fishes based on their capacity for digestion and assimilation based on detailed bioenergetics models (Hanson et al. 1997; Furey et al. 2016). Unfortunately, as neither Arctic char nor any *Myoxocephalus* sculpins have had such models parameterized we rely on observations from similar species, especially Bull trout (*Salvelinus confluentus*; Mesa et al. 2013) and Prickly sculpin (*Cottus asper*; Moss 2001), that suggest binge-feeding may occur with consumption rates between 1.5-3.5%. Compared to these estimates, excessive consumption occurred often in both predator groups (15.4% of Arctic char; 52.0% of sculpins). Both the regular and intense feeding observed here has been found as characteristic fish responses to other large resource pulses (Furey et al. 2016; Hermann et al. 2020). Despite using a definition of binge-feeding not specific to Arctic char or *Myoxocephalus* spp. sculpins, the relatively intense feeding by both predators during the short ice-off season is likely to be important to their year-round energy budgets and success.

Though both Arctic char and sculpins fed intensively, their diets differ in ways which may reflect differences in their mobility and migratory behavior. Mobility may explain the higher presence of more mobile or pelagic prey items in the diets of Arctic char such as fish and copepods. Conversely, sculpins are primarily benthic predators with prey items being dominated by small benthic invertebrates (Moore and Moore 1974), consistent with our observations across years. Similarly, the higher percentage of empty stomachs by sculpins may suggest they are less capable of seeking consistent feeding opportunities and, as such, when they do feed do so at rates that are generally higher. This would be accurately reflective of their lie-in-wait foraging style and general sedentary lifestyle (Moore and Moore 1974; Breen et al. 2009). These two observations help contrast the foraging strategies of Arctic char and sculpins, the former moving quickly (Hammer et al. 2022) between patches of productivity within Tremblay Sound to feed consistently whereas sculpins occupy one area and consume the resources opportunistically available and only being able to slowly move between patches (Hermann et al. 2023). Perhaps, these differences position the two predators within the two categories of predatory responses to resource pulses defined by Yang et al. (2008): mobile specialists (Arctic char) and opportunistic residents (sculpins). However, it is possible that Arctic predators require additional plasticity (e.g., digestive capacity flexibility in Dolly Varden (*Salvelinus malma*); Armstrong and Bond 2013) and, as such, may not fit neatly into categories defined primarily from temperate environments (Yang et al. 2008). Future studies should investigate whether there is a limit to diet plasticity to further inform how Arctic predators will respond to continued and more severe impacts of climate change, including shifts in the timing of summer ice-off, changes in overall ice distribution, and resultant impacts on the prey community. Additional adaptations include the migration behavior which is in addition to the marine mobility of Arctic char.

The migratory behavior of Arctic char and high activity levels within Tremblay Sound (Hammer et al. 2022) presents a significant undertaking which their summer feeding must be capable of supporting. Brief summer feeding opportunities are so important that char have been shown to arrive in marine waters prior to the initiation of ice-off (Hammer et al. 2022b). The energetic expense of migration is well understood for many taxa (birds, McWilliams and Karasov 2014; mammals, Harwood et al. 2012; and fishes, Wilson et al. 2013) including for Arctic char specifically (Spares et al. 2012, 2015; Harwood and Babaluk 2014; Moore et al. 2017). For some migrants, the expense of the extended movement is exacerbated by the minimal or absent feeding throughout migration (Harwood and Babaluk 2014). Anadromous Arctic char typically fast during the winter and largely rely on energy stores built up during the summer, meaning this approximately two month foraging period must be maximized (Dutil 1986; Klemetsen et al. 2003; Spares et al. 2012, 2015; Hammer et al. 2022). However, the ability to consume high levels of prey by maintaining digestive machinery can be expensive in its own right (Cant et al. 1996). Alternatively, other adaptations relying on flexibility (Armstrong and Bond 2013) or binging (Furey et al. 2016) can impose high costs by absorbing the aerobic capacity that could otherwise be used for mobility (Clark et al. 2013). While this can clearly contribute to the observation of limited feeding during migrations (Clark et al. 2013), it can additionally influence how fishes exploit resources during a period when foraging is the primary focus such as the Arctic summer (Harwood and Babaluk 2014; Landry et al. 2018). While having an anatomical ability for mobility can enable foraging behaviors by Arctic char such as the mobile specialist categorization discussed earlier, maintaining that level of mobility can put an upper limit on the magnitude of feeding they can undertake. In this sense, for fishes the choice to be mobile and to feed comes as a trade-off wherein the two capacities must be balanced for each species based on the internal characteristics of that species and the external features of their environment, both biotic and abiotic (see Armstrong et al. 2013). Our observations comparing the diets of sculpins and Arctic char support such a trade-off among fishes experiencing the same resource pulse but experiencing distinct anatomical and life history characteristics.

Another important contributing factor behind dietary differences is the average and maximum body size between Arctic char that >3x larger than sculpins from our sample. The prey consumed by Arctic char included more fish than did the diets of sculpin likely due to gape limitation common among fishes (Urban 2007). In fact, the incorporation of larger prey items while still consuming small items follows the same pattern of many fishes (Scharf et al. 2000) resulting in many larger fishes having more prey options than smaller fishes which can result in rapid growth (Urban 2007). Though larger fish can consume larger prey, the trade-off with large diets is large aerobic investments that can limit mobility (Norin and Clark 2017). Both predators must balance these impacts of consumption and metabolism, but the high rates of relative consumption observed in sculpins may suggest that they are less constrained by needing to maintain excess aerobic scope in favor of increasing growth rates (Norin and Clark 2017). Also contributing to impacts of body size on feeding is the scaling of space use wherein larger organisms rely on larger areas to acquire sufficient resources (Tamburello et al. 2015). As such, the obvious differences in body size between the predators sampled within this shared environment may contribute further to subtle differences in feeding magnitude and composition.

Though the difference between sculpins and Arctic char can be observed and attributed to life history differences between the taxa, there were also observed differences between sampling years. Indicator species analysis was able to identify prey items that were significantly associated with certain sampling years, most notably different taxa of amphipods for each year: *Gammaracanthus* sp. in 2017, *Onisimus* sp. in 2018, and *Themisto* sp. in 2019. Summer environmental conditions varied in Tremblay Sound between years (N. Hussey, *pers obs*), with regular fast ice in 2018 and only a single iceberg in 2019. Perhaps *Onisimus sp.* are sympagic amphipods, and their presence in 2018 diets and absence in 2019 diets was reflective of the current environmental conditions. Environmental conditions have been linked to changes in the composition of macrofauna, particularly in amphipods (Hop et al. 2011; David et al. 2015). Variability in the faunal community between years could be confirmed by future research which collects both the diets of major predators and the sympatric prey base. Both predators are limited to the prey that are available; however, based on centroid distance between years Arctic char (mean distance = 0.55) may be more sensitive to the changing prey base than sculpins (mean distance = 0.36). Sculpins, that are known to be opportunistic predators, may not reflect dominant taxa inter-annually as their mobility may impede their ability to select prey items. Ultimately, more intensive sampling of prey availability, especially in the dominant habitats which these predators utilize, is required to identify selectivity of feeding as it may contribute to inter-annual variability in diet composition.

Though these results are valuable, it is important to acknowledge the limits of diet analyses in representing broader feeding behavior and the generalizability of observations from one system during a rapidly varying seasonal pulse. Though our study was successful at generating samples in different years, the time of year contained some variation with 2017 and 2018 being collected over a longer time than 2019. Additionally, all years began well after complete ice-melt when the resource pulse begins (Ji et al. 2013) with successive changes as the season progresses (Hop et al. 2011). Much of this feeding period was missed by our samples (Søreide et al. 2010) and may present a different story on the foraging of these predators. Beyond the timing of sampling, the methods for collecting fish may have resulted in a narrow understanding of the feeding behaviors of Arctic char and sculpins. Individual specialization was observed within our sample (Bolnick et al. 2002), but we believe that a sufficient number of diets was collected to fully encapsulate the prey consumed (via prey accumulation curves) even if some responses may be less well represented. Specifically, collection occurred at just one site which, for sculpins especially, may result in a biased sample of the population due to limited mixing. Telemetry studies have identified that both predators can access the entirety of Tremblay Sound (Hammer et al. 2022; Hermann et al. 2023), but differences may exist between subpopulations or reflecting variable resources within different regions of the system (see Armstrong et al. 2013). Finally, we acknowledge the limitations of visual gut content analysis to misidentification, underrepresenting soft-tissued prey items, and providing information on only the recent feeding history (Amundsen and Sánchez-Hernández 2019). The improvement of gut content analyses with metabarcoding or integration of stable isotope or fatty acid analyses could provide a deeper understanding on the history of feeding by individuals and populations (Giraldo et al. 2016), albeit at increased cost to researchers.

Despite the caveats above, our analyses have documented differences between two important predators feeding on a resource pulse in the same system. Predator responses to the resource pulse and differences in feeding are directly reflective of their life history traits (e.g., migratory vs resident) and broader ecology (e.g., mobile vs sedentary, small vs large). Regardless of differences in life history and ecology, both predators were able to exploit the dynamic summer prey pulse in Tremblay Sound. However, primary productivity in high Arctic systems is at risk from shifts in sea-ice phenology due to climate change. A completely ice-free summer is a likely possibility in the near future (Overland and Wang 2013, Wang and Overland 2012), with implications for prey pulses and the consumers that exploit them. Both predators in this study demonstrated diet plasticity and the ability to feed at high rates, which could indicate resilience to climate related shifts in prey availability and abundance. Despite consistencies in the two predator types here in being capable of exploiting the Arctic resource pulse, the patterns observed differed in a manner reflecting the life history patterns of the predators themselves.

# Tables

Table 1. Summary of Arctic char and sculpins from which stomachs were collected with subsets across sampling years. Metrics of condition are hepatosomatic index (HSI), gonadosomatic index (GSI), and Fulton’s K. Values shown are mean (±SD).

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Species --Year** | **n** | **Mass**  **(g)** | **TL**  **(cm)** | **Fulton’s K** | **% Empty** | **Relative Consumption** |
| Arctic char | 91 | 2609.2 (±1494.4) | 62.1  (±15.7) | 914.1 (±176.5) | 3.33 | 1.92  (±1.38) |
| --2017 | 37 | 1956.4 (±1397.8) | 55.4  (±17.2) | 855.7 (±175.8) | 5.40 | --- |
| --2018 | 23 | 3194.3 (±1781.1) | 70.0  (±16.7) | 793.6 (±123.8) | 0 | 1.16  (±1.07) |
| --2019 | 31 | 2970.9 (±1093.5) | 64.2  (±9.3) | 1061.5 (±86.1) | 3.22 | 2.42  (±1.35) |
| Sculpins | 190 | 78.9  (±69.3) | 18.5  (±5.4) | 1062.1 (±572.3) | 7.36 | 2.88  (±2.93) |
| --2017 | 114 | 76.5 (±69.7) | 17.8  (±5.2) | 1176.5 (±686.9) | 2.63 | --- |
| --2018 | 59 | 100.1 (±69.0) | 21.1  (±5.3) | 923.4 (±266.4) | 13.55 | 2.79  (±2.88) |
| --2019 | 17 | 22.4 (±4.7) | 14.2  (±1.2) | 774.9 (±150.2) | 17.64 | 3.19  (±3.15) |

Table 2. Results from indicator species analysis indicating associations between diet items and the species (Arctic char or Sculpin) or year (2017, 2018, or 2019) of consumption. Significant associations for the prey species (row) with the predator species or year (column) are denoted in bold. Missing values indicate that diet item was not consumed by that species or during that year.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Species** | **Arctic char** | **Sculpins** | **2017** | **2018** | **2019** |
| Arctic cod | **0.442\*\*\*** |  | 0.1291 | 0.0295 | **0.3188\*\*\*** |
| Sand lance | **0.2397\*\*** |  | 0.0579 | 0.1786 |  |
| Unid. Fish | **0.5335\*\*\*** | 0.2637 | 0.1914 | 0.1764 | **0.6702\*\*\*** |
| *Gammarus* sp. | 0.1538 | 0.3693 | 0.235 | 0.2732 | 0.1622 |
| *Gammaracanthus* sp. | 0.0914 | 0.286 | **0.3371\*\*** | 0.0693 |  |
| *Onisimus* sp. | **0.5057\*\*** | 0.3125 | 0.1265 | **0.4943\*\*** | 0.4618 |
| *Themisto* sp. | **0.5673\*\*\*** |  |  |  | **0.7802\*\*\*** |
| Unid. Amphipod | 0.3286 | **0.5458\*** | **0.6531\*\*\*** | 0.1314 | 0.1803 |
| Krill | 0.339 | 0.4748 | 0.3991 | 0.2688 | 0.3276 |
| Mysid |  | **0.2919\*\*** | **0.2892\*** | 0.0425 |  |
| Copepod | **0.5229\*\*\*** | 0.1584 | 0.2648 | 0.0908 | **0.4203\*\*** |
| Chironomid |  | 0.1994 | 0.219 |  |  |
| Jellyfish | 0.0621 | 0.1229 | 0.1345 | 0.0692 |  |
| Sea Angel | 0.0879 | 0.1737 | 0.1224 | 0.0839 | 0.1295 |
| Miscellaneous Invertebrates |  | 0.0754 | 0.0828 |  |  |
| Miscellaneous | 0.1072 |  |  |  | 0.1474 |
| Algae |  | 0.1306 | 0.0822 | 0.0845 |  |
| Undigestible Material |  | 0.2132 | 0.2341 |  |  |
| Digested Material | 0.2739 | **0.4814\*** | 0.1756 | **0.6668\*\*\*** | 0.1715 |

\*\*\*p<0.001 \*\*0.001<p<0.01 \*0.01<p<0.05

**Table 3.** Generalized linear model (GLM) with model weight > 0.10 determined via all subsets regression. AICc: Akaike’s information criterion adjusted for small sample size; Wi: Akaike weight. The response variables and best-fit models are presented in **bold**. Additional models for a given response variable fall below the best-fit model, and the response variable is not shown.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Response | Model | loglik | AICc | Wi |
| Food in Stomach (0 or 1) | Species | -36.188 | 76.5 | 0.473 |
| Species + Year | -35.982 | 78.2 | 0.203 |
| Species + Month | -35.132 | 78.6 | 0.164 |
| Relative Consumption | Species + Year | -222.535 | 453.4 | 0.582 |
| Species | -224.346 | 454.9 | 0.279 |

# Figure Legends

Figure 1. Frequency of Occurrence for diet categories for both Arctic char (blue) and sculpins (yellow). Silhouettes indicate the general appearance of the diet item, note that all amphipod categories are covered under the same silhouette despite differences in genera. Dotted vertical lines separate rough groupings of diet items (from left to right): Fish, Amphipods, Zooplankton/Invertebrates, Miscellaneous. Total Fish and Total Amphipods represent diets possessing any of the more specific or unidentified categories, respectively.

Figure 2. Non-metric multidimensional scaling ordination of predator diet compositions simplifying a 3-dimensional ordination to 2-dimensions. Points, which represent an individual, and convex hulls are group by species (Arctic char in blue; Sculpin in yellow) and year (2017 circle points and solid line; 2018 square points and dashed line; 2019 diamond points and dotted line). The group (species and year) centroids are indicated with a red point color and shape coded in the same manner. Black lines and prey items indicate the impact of that item on diet ordination position.

Figure 3. Boxplots of relative consumption (percent body weight consumed) between years for Arctic char and sculpin. Each dot represents an individual stomach, with open circles marking empty stomachs. Midlines indicate median values, hinges indicate the first and third (25th and 75th) percentiles, and whiskers extend to 1.5-times the interquartile range from each hinge.

Figure 4. Yearly prey accumulation curves for Arctic char and sculpin. The dashed line indicates a cumulative curve without discriminating between years. Circles mark random samples along the curve.

Figure 5. Distance (a) between centroids of different groups and (b) between individuals to the centroid within a group. Groups are a combination of predator taxa (Arctic char and Sculpins) and year (2017, 2018, and 2019). In (a), cells include both the distance value and are color coded according to that value. Fully black cells are those between the same groups and represent a distance of 0. Black outlines highlight cells which are between the same predator taxa across years, red outlines highlight cells comparing predator taxa within the same year.

# Figures

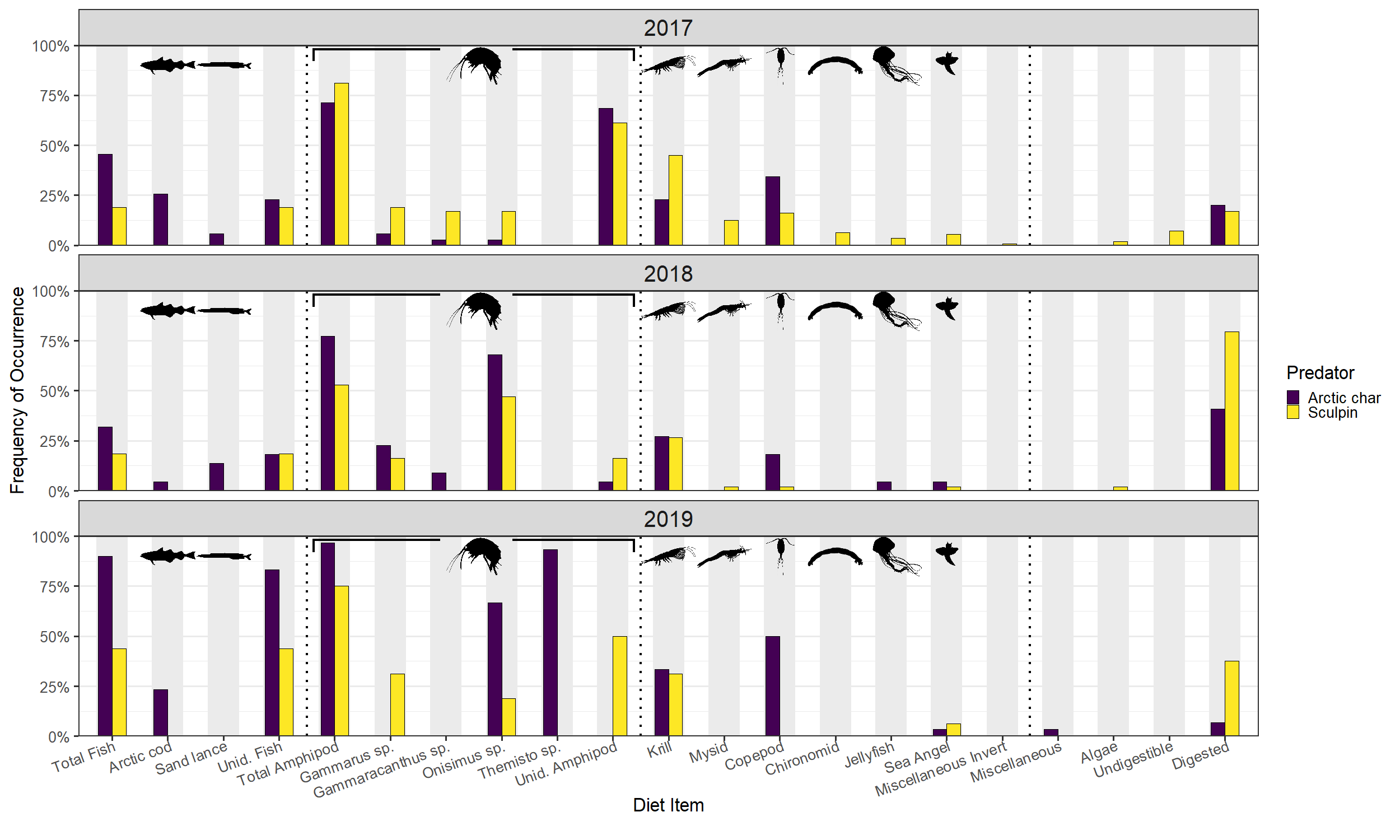
Figure 1

Figure 2

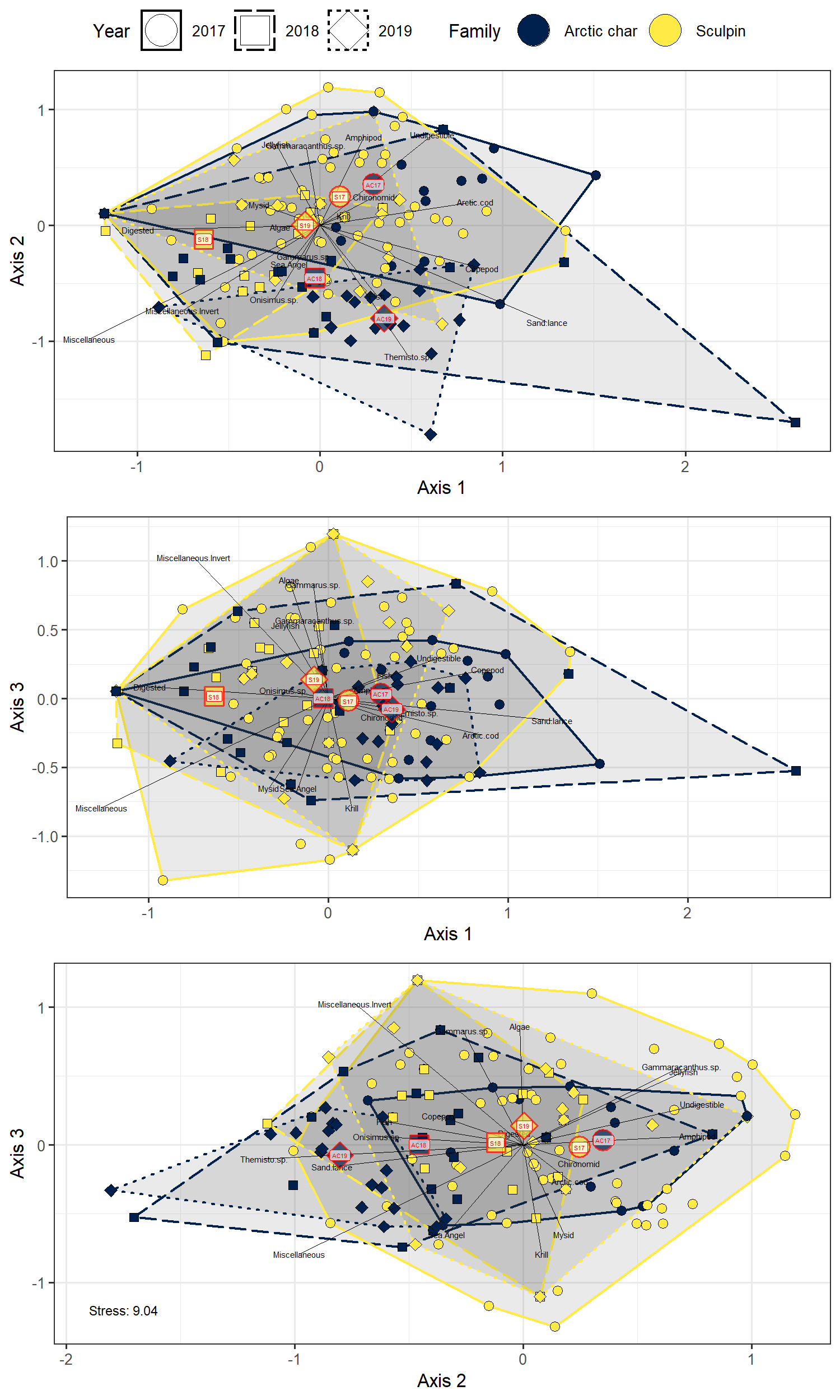


Figure 3

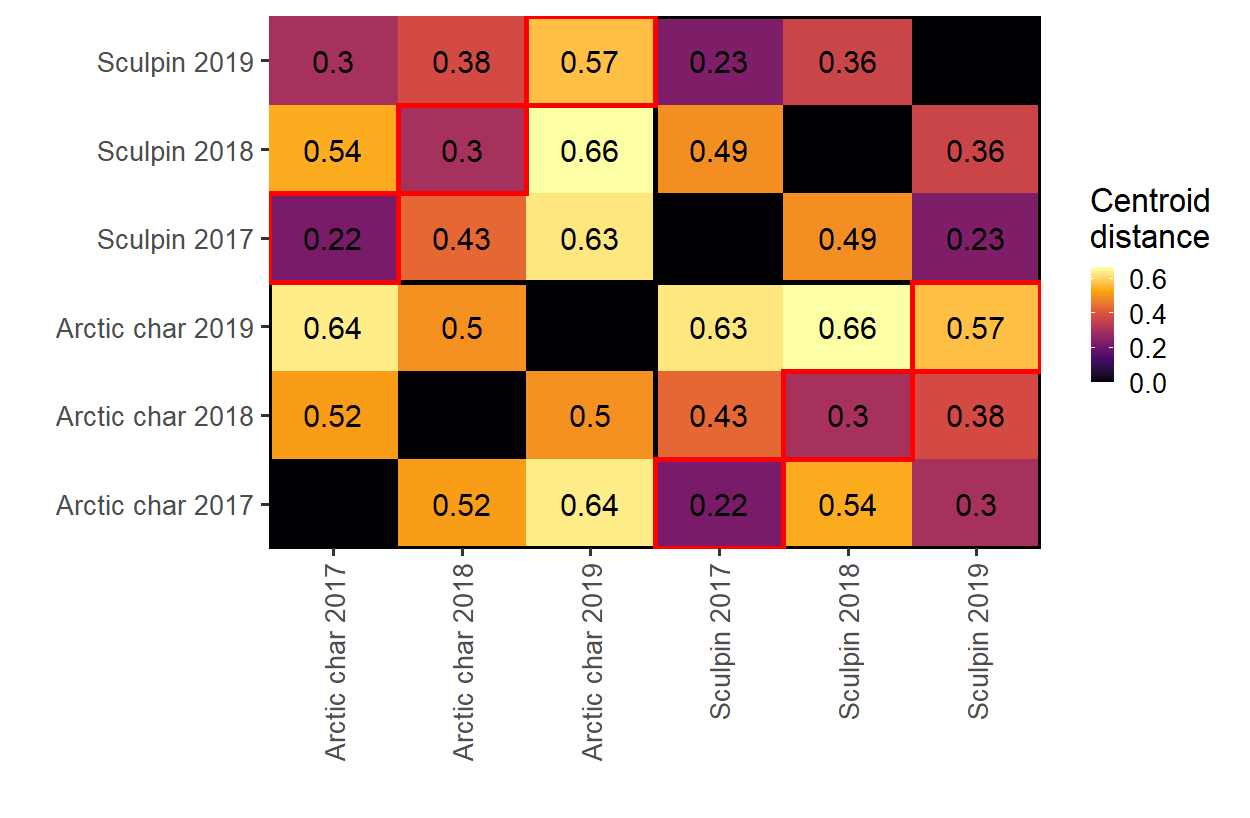


Figure 4

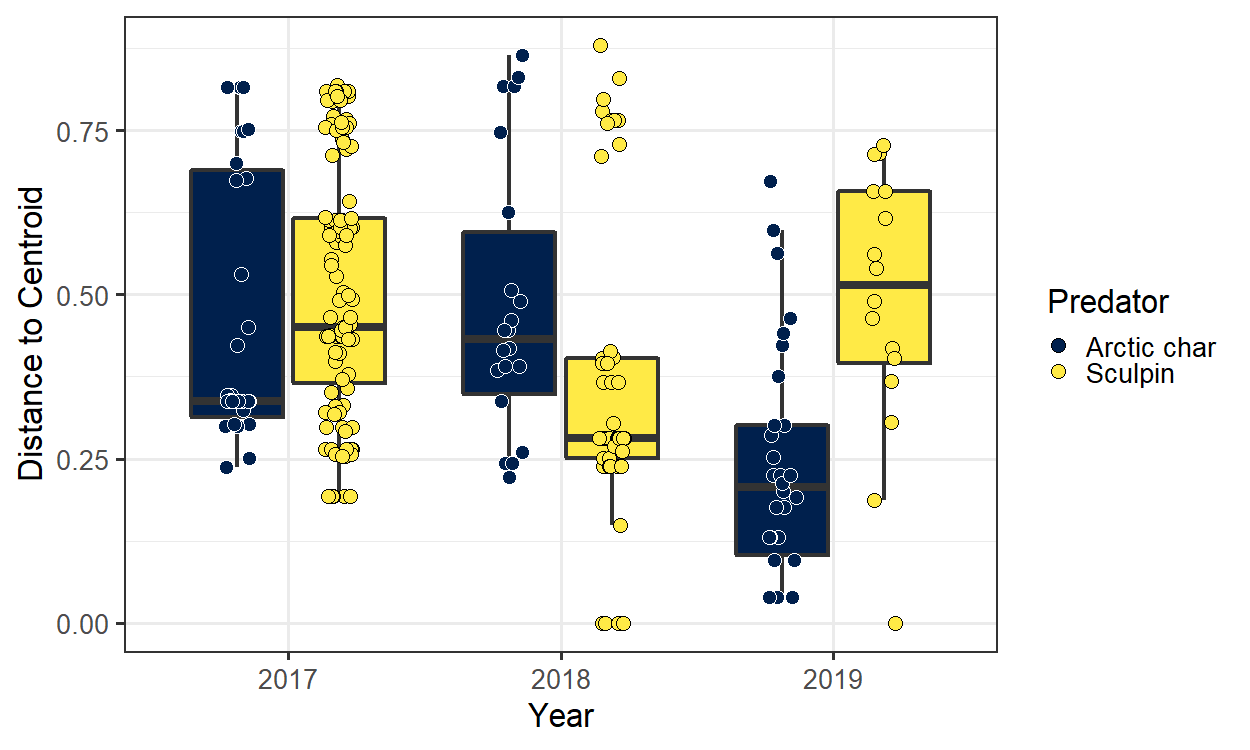


Figure 5

a



b



# Declarations

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**Conflict of Interest:** The authors declare that they have no conflict of interest.

**Ethical Approval:** All applicable institutional and national guidelines for the care and use of animals were followed as approved by the University of Windsor (AUPP:#17-12), University of New Hampshire (IACUC:#180602), and the local Mittimatalik Hunters and Trappers Organization.

**Availability of data and material:** The datasets used and analyzed during the current study are availability from the corresponding author on reasonable request.

**Code availability:** All code used for data analysis was completed in R and is available at: <https://github.com/nhermann1/Hammer_Hermann>

**Author Contributions:** NEH, MM, and KJH contributed project design for the initial field program. Field work was completed by NEH, LJH, and NTH. Analyses were completed by LJH and NTH with advisement by NBF and NEH. LJH and NTH equally contributed to the writing of the manuscript with all other authors providing editorial advice.

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